Epiphytic bryophytes in Canarian subtropical montane cloud forests: the importance of the time since disturbance and host identity

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Abstract: The aim of this study was to determine the short- and medium-term effects of forestry practices on epiphytic bryophyte communities growing on whole trees of three host species (*Erica arborea* L., *Laurus novocanariensis* Rivas-Mart., Lousa, Fern. Prieto, E. Días, J.C. Costa & C. Aguilar, *Myrica faya* Aiton) in subtropical montane cloud forests on La Palma (Canary Islands, Spain). Specifically, we investigated differences in temporal and spatial shifts of species composition and richness of phylogenetic groupings among host species. The most common harvest method in the study area is clear-cutting. Four different postharvest successional stages (8, 15, 25, and 60 years after harvest) were studied. Temporal bryophyte species turnover varied according to host species. Most of the later-successional bryophytes with narrower ecological requirements had low abundances on *L. novocanariensis*; this host experienced a gradual increase of epiphytic richness along the chronosequence. Temporal changes for *E. arborea* and *M. faya* were different; they showed increasing richness during the second period (15–25 years) followed by a drop in richness during the last period (25–60 years), and early-successional species dominated throughout the chronosequence. We conclude that the protection of "old-growth stands" containing trees of selected species can contribute to the survival of epiphytic bryophytes in managed cloud-forest landscapes.

Résumé : Cette étude avait pour but de déterminer les effets à court et moyen termes des pratiques forestières sur les communautés de bryophytes épiphytes qui croissent sur les tiges saines de trois espèces d'hôtes (*Erica arborea* L., *Laurus novocanariensis* Rivas-Mart., Lousa, Fern. Prieto, E. Días, J.C. Costa & C. Aguilar, *Myrica faya* Aiton) dans les forêts subtropicales montagneuses humides de La Palma, une île des Canaries en Espagne. Nous avons étudié en particulier les différences dans les changements, dans le temps et dans l'espace, de composition et de richesse en espèces des groupements phylogénétiques selon l'espèce hôte. La méthode de récolte la plus utilisée dans la zone d'étude est la coupe à blanc. Quatre stades de succession post-récolte différents (8, 15, 25 et 60 ans) ont été étudiés. Le renouvellement temporel des espèces de bryophytes variait selon l'espèce hôte. La plupart des bryophytes de fin de succession avec des exigences écologiques plus strictes étaient peu abondants sur *L. novocanariensis*; sur cette espèce hôte, la richesse en épiphytes augmentait graduellement en cours de succession. Dans le cas de *E. arborea* et *M. faya*, les changements temporels étaient différents; la richesse en épiphytes augmentait durant le deuxième stade (15–25 ans); cette augmentation était suivie d'une baisse durant le dernier stade (25–60 ans) et les espèces de début de succession dominaient tout au long de la chronoséquence. Nous concluons que la protection des vieux peuplements contenant des tiges des espèces choisies peut contribuer à la survie des bryophytes épiphytes dans les paysages de forêt humide aménagée.

[Traduit par la Rédaction]

Introduction

Silvicultural practices are one of the greatest threats to the future of many forest ecosystems. Among harvesting techniques, clear-cutting potentially has the greatest impact. Dramatic alterations in surface area and habitat quality may occur when forests are subjected to silviculture (Hazell and Gustafsson 1999; Vanderpoorten et al. 2004; Åström et al. 2005). Consequently, biodiversity loss and changes in species composition may be exacerbated in taxonomic groups that have narrow ecological niches (Moen and Jonsson 2003). Hence, patterns of spatial and temporal recovery in richness and composition after harvest are a central research topic in conservation biology (Fenton and Frego 2005; Pharo and Zartman 2007). However, the majority of studies have traditionally focused on more conspicuous organisms such as vascular plants, amphibians, birds, and mammals (Colón and Lugo 2006; Bermúdez et al. 2007; Ortega-Huerta 2007).

Although epiphyte bryophytes play crucial ecological roles (e.g., retaining rainfall and fog, providing microhabitats) in a wide variety of forest types (Wolf 1995; Nadkarni et al. 2001; Chang et al. 2002; Pypker et al. 2006) and recent studies have stressed their potential as indicators of "old-growth-forest" conditions (Drehwald 2001; McGee and Kimmerer 2002; Acebey et al. 2003), they have been largely ignored by management programs.

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Bryophytes are particularly sensitive to environmental disturbances caused by harvesting (Vanderpoorten et al. 2004; Fenton and Frego 2005; Zartman and Nascimento 2006), in part, because of their simple morphology and subsequently poikilohydric nature (Barkman 1958). Limited diaspore dispersal is another factor that makes many bryophytes particularly susceptible to habitat alterations (Miles and Longton 1992; Hedenâs et al. 2003; Pohjamo et al. 2006). Furthermore, phylogenetic groupings of bryophytes show a sensitivity gradient, with a smaller proportion of liverworts than mosses being tolerant to disturbance, especially to anthropogenic canopy removal (Moen and Jonsson 2003; Pharo et al. 2004; Hylander et al. 2005; Nelson and Halpern 2005).

Previous studies on the effects of clear-cutting have concluded that when old-growth forests are transformed by tree harvesting, dramatic modifications in species richness, abundance, and composition occur in the epiphytic bryophyte flora (Lesica et al. 1991; Boudreault et al. 2000; Acebey et al. 2003; Hylander et al. 2005; Dynesius and Hylander 2007). Indeed, many epiphytic bryophyte species (and some of their growth forms) exhibit a high fidelity to particular environmental conditions (Mägdefraü 1982; Sillett et al. 1995; Holz et al. 2002; Pharo et al. 2004; Andersson and Gradstein 2005; Bardat and Aubert 2007). Thus, within harvested lands, specialist bryophytes with narrower niches (e.g., later-successional species) usually disappear and are replaced by generalists species with wider niches (e.g., early-successional species) that are relatively unaffected by environmental changes caused by forestry practices (McGee and Kimmerer 2002; Acebey et al. 2003; Kantvilas and Jarman 2004).

Despite these studies, knowledge of species turnover through time and space in epiphytic bryophyte communities is still fragmentary. Comparative studies of epiphyte vegetation dynamics across multiple host tree species following clear-cutting are scarce (e.g., McGee and Kimmerer 2002); further, floristic and ecological changes over time have rarely been analysed for whole trees (e.g., Holz and Gradstein 2005). Thus, the ecology of the canopy-dwelling bryoflora remains largely unknown in many forest ecosystems (Nadkarni et al. 2001; Acebey et al. 2003), including Macaronesian subtropical montane cloud forests.

Subtropical montane cloud forests in the Canary Islands (hereafter laurel forests) constitute a relic fragment of the humid evergreen forests that originally covered most of central and southern Europe during the Tertiary (Sunding 1979). Laurel forests are defined as one of the most important natural resources in the European political context (Martín et al. 2005), showing important biological and ecological similarities with some tropical cloud forests (Ohsawa et al. 1999). Moreover, laurel forests are characterized by luxuriant bryophyte assemblages, in terms of biodiversity, endemicity, and biomass (Zippel 1998; González-Mancebo et al. 2003). However, despite these high conservation values, laurel forests have been subject to long-term forestry operations and currently cover less than 20% of their potential area, largely consisting of young forests (Fernández-López 2001). The harvest method most commonly employed in the Canarian laurel forests is clear-cutting, which is still carried out on islands such as Tenerife and more intensely on La Palma (Bermúdez et al. 2007).

We studied bryophyte community turnover (species composition and richness in liverworts and mosses) through time and space on three host tree species in laurel forests that had been clear-cut at different times. Specifically, the working hypothesis was that the effects of short- and midterm clear-cutting on bryophyte communities vary and depend on the host-tree identity. In other words, we expected to find different richness patterns and replacement rates of "early-successional" by "later-successional bryophyte species in relation to their host trees. We also expected that liverwort and moss richness would increase on each host species during a period of 60 years following harvest. Management strategies that could favour the sustainability and survival of bryophyte assemblages across these emblematic subtropical montane cloud forests are discussed. To our knowledge, this is the first direct study on bryophyte succession dynamics on whole trees of different host species in Macaronesian laurel forests.

Methods

Study area

Fieldwork was carried out in laurel forests on La Palma, Canary Islands (28°25′–28°51′N, 17°43′–18°00′W). The study area is affected for most of the year by prevailing northeastern trade winds. Such winds favour the formation of a bank of strata–cumulus clouds over the island, where fog drip can increase water availability, even quintupling it in summer when the highest cloud level usually lies between 800–900 m a.s.l. (Marzol and Valladares 1998). The study area is located above 1200 m; hence it is affected by those cloud banks, albeit only weakly during summer. The mean annual temperature and precipitation are 13.6 °C and 960.2 mm, respectively (Del Arco et al. 1999).

The study area is located in a managed landscape (designated to meet the timber and woody biomass needs of the local population) except a small part that is within the "Parque Natural de Cumbre Vieja" protected area. Different sectors within this managed area are periodically selected for harvesting. As a consequence, most of the forests analysed here will be clear-cut in the near future. Managed stands on La Palma are small because of the high demand for forest products, and therefore rotation periods are short (Bermúdez et al. 2007). Consequently, most clearcuts on this landscape are estimated to be less than 5 ha.

A particular limitation of our study is that the current forest stands are small (<5 ha). Some studies have noted that separating edge effects from size effects is difficult because both effects are often strongly correlated (see Moen and Jonsson 2003). Our data may therefore be limited by edge effects due to the small size of the stands, and care must be taken while interpreting results. However, edge effects are stronger in dry environments (Moen and Jonsson 2003; Hylander et al. 2005) or if forest patches are isolated (Zartman and Nascimento 2006). Because the studied stands are influenced by moist conditions and are surrounded by a mosaic of disturbed forest patches, edge effects may be partially attenuated.

Although laurel forests can harbour a diversity of tree species (Arévalo et al. 1999), *Erica arborea* L., *Laurus novocanariensis* Rivas-Mart., Lousa, Fern. Prieto, E. Días, J.C.

Costa & C. Aguilar, and *Myrica faya* Aiton were the only abundant tree species in the study area (Bermúdez et al. 2007). These three host species, which differ in their structural features, are likely the most abundant species of the Canarian laurel forests (Ohsawa et al. 1999; Bermúdez et al. 2007). The smaller leaves, more open canopy, and weaker bark of *E. arborea* and *M. faya* provide a more limited environment for bryophyte growth (see González-Mancebo et al. 2003) because these features create a drier microclimate (e.g., low funnelling ratios; Aboal et al. 1999) than that of the bark of *L. novocanariensis*.

Nomenclature for the vascular plants follows Acebes et al. (2004); for the mosses and liverworts, nomenclature follows Hill et al. (2006) and Losada-Lima et al. (2004), respectively. For the classification of bryophyte growth forms, we follow Mägdefraü (1982) with modifications. We considered five growth forms in our study: turfs, cushions, mats, wefts, and hanging forms (i.e., tails, fans, and pendants).

Stand description

Four medium-sized stands, all between 0.5 and 5 ha, were selected in the study area. These sites had very similar environmental conditions, e.g., altitude (1260 ± 84.85 m), topography (midslope), angle (0°–5°), orientation (NE–E) (Bermúdez et al. 2007). Age since the last harvest varied among stands (8, 15, 25, 60 years after harvest (YAH)). Although stands resulting from more recent harvests (0.5, 1, 3 YAH) were originally included in the chronosequence, they were ultimately discarded because of the absence of epiphytic bryophytes. All stands were spatially independent of each other, i.e., not part of the same patch or in direct contact.

To survey successional processes after harvest, a study should include a control (i.e., an old-growth forest) and an adequate selection of stands representing various ages. We do not have data from a control and are aware of this limitation. However, we believe it is important to include data for short-term succession for two reasons: (1) we believe this is the first study of epiphytic bryophyte communities on whole trees in the Macaronesian laurel forests, and (2) short-term studies have been solicited by other authors to improve our ecological understanding of secondary forests, especially when silvicultural cycles prevent examination of late-successional stages altogether (Nelson and Halpern 2005; Bardat and Aubert 2007). In most Canarian islands, secondary forests make up larger areas than primary forests (Fernández-López 2001), and the current silvicultural cycle is based on a ca. 10 year rotation. This indicates the importance of studies on earlier and intermediate successional phases within laurel forest landscapes.

The limited number of stands (i.e., the number of stands per forest age-class with suitable tree species composition on sufficiently similar sites) and the absence of true replication are likely the greatest limitations of this study. Despite these shortcomings, small-scale experiments (i.e., microcosms) have often helped to analyse large-scale terrestrial ecosystems when replicating an experiment is problematic or when the organisms exhibit relatively fast population dynamics (Oksanen 2001), such as do many bryophytes (e.g., Pharo and Zartman 2007). Moreover, because La Palma Island displays strong mesoclimatic gradients (that may affect species composition of epiphytic bryophyte communities; see González-Mancebo and Hernández-García 1996) across its altitude and topography (Del Arco et al. 1999), smaller-scale experiments are likely more suitable, as they better limit variability in environmental conditions.

Despite the aforementioned shortcomings, two features of the present study provide a unique opportunity to investigate the effects of silviculture on epiphytic bryophytes: (1) the extensive historical documentation of silvicultural practices, and (2) the natural process of forest regeneration after harvesting. This is a very rare combination across Canarian harvested laurel forests (unique on La Palma Island) where, in general, there is no historical documentation of harvesting activities.

Plot selection and description

In each stand of the chronosequence, three 25 m^2 (5 m × 5 m) plots were systematically placed at regular intervals of 20 to 100 m along a transect. Because of the lack of true replication, observed differences in bryophyte assemblages among forest age-classes were assumed to be due to subplot characteristics. In stands with 8 and 15 YAH, an additional plot was installed and measured because of the low number of bryophyte samples. Each plot was designed to include the three most abundant tree species and to be as similar to one another as possible in structural features. To avoid edge effects, all plots were placed at least 35 m from roads. However, as previously stated, we cannot presume that this sampling strategy is free of any environmental edge effect. The forest stands studied here have been described in detail elsewhere (Bermúdez et al. 2007).

At each plot, trees were identified to species, and their densities and diameters (>2.5 cm diameter at breast height) were measured. The variation in main structural parameters for each plot has been shown to be continuous and monotonic over time (Bermúdez et al. 2007). Thus, in the initial years after harvest, the plots (i.e., clearcuts) were obviously open and bare. Tree density peaked 8 YAH. Then, basal area, biomass, and light incidence increased, while trunk density decreased, the sole exception being basal area of *M. faya*, which decreased dramatically in the 60 YAH stands. This decrease was related to successional processes favouring shade-tolerant tree species such as *L. novocanariensis* (Arévalo et al. 1999; Bermúdez et al. 2007).

Field sampling

A total of 15 upper-canopy trees per host species were randomly chosen within each plot (15 × 3 = 45 total trees). Within each plot, we sampled trees with a basal area similar to the mean basal area calculated for each forest age-class (Bermúdez et al. 2007). The minimum number of sampled trees (15) could not be achieved in the 60 YAH stands, where we could only sample seven trees of *E. arborea*, six of *L. novocanariensis*, and six of *M. faya*.

We employed several sampling strategies. For the three younger forest age-classes (8, 15, and 25 YAH), bryophytes could be directly sampled because the plots had been cut during a previous study to evaluate the recovery of the laurel forest after harvest (Bermúdez et al. 2007). All trees had been cut almost to ground level and carefully felled, thereby minimizing the loss of bryophytic mass. The trees in the oldest forest (60 YAH) had not been cut because their preservation was crucial in such a highly modified landscape and because the age of laurel forests on La Palma is dramatically low (Fernández-López 2001).

Trunks in the 60 YAH were directly sampled using a stepladder from the tree base to a height of 4 m. The canopy was impossible to reach using single-rope climbing techniques because there were no strong upper branches. Therefore, two main branches (i.e., large in diameter) per tree were randomly chosen and then cut and safely lowered; the cuts were made close to the branch bark collar. In total, 54 main branches were collected from the 19 trees sampled in the 60 YAH forest age-class, and 38 (70%) of these branches were sampled. The total number of main branches per tree ranged from 2 to 4 (2.7 ± 0.7); thus, at least 50% of branches on each tree were sampled. The diameter, structure, and epiphytic cover of the branches that were not sampled were very similar to those of the sampled branches (data not shown).

All trees were stratified following Johansson (1974) with modifications. We distinguished five zones within a given tree: tree base (1), trunk (2), inner (3), middle (4), and outer canopy (5). The numbers between brackets indicate how the tree zones were coded for the correlation coefficients (see Data analysis section). Tree bases reached 0.5 m and the remaining vertical zones were delimited following the method described by Johansson (1974). Following González-Mancebo et al. (2004), we divided each tree into two aspect zones that were also coded numerically: the northeastern (1) and southwestern (2) sides of the tree.

Within each aspect zone of a tree, we sampled each tree zone every 0.5 m, from the top of the zone to the bottom. For this reason, older (or larger) trees yielded more samples than did smaller trees. To remove the samples, we used 150 cm^2 rectangles and modified the lengths of sides depending on the tree diameter at the sample zone. For each sample, we recorded forest age, tree species, tree zone, aspect zone, and height above ground. Total cover was visually estimated in the field, and samples were removed intact and brought to the laboratory where bryophytes were identified and percent cover by each species was subsequently calculated; both cover estimates (i.e., numerical percentages of cover) were calculated by the first author to minimize potential bias. All voucher specimens were deposited in the Tenerife Ciencia herbarium of the University of La Laguna (TFC Bry).

Data analysis

To gage the completeness of sampling in relation to differences in sample size (i.e., number of samples) of each forest age-class and host species, we compared observed species richness with predicted species richness using bootstrap, Michaelis Menten, Chao 1, Chao 2, and first- and second-order jackknife (Jackknife 1 and 2) estimators. Such nonparametric estimators represent a lower (bootstrap and Michaelis Menten) and upper (Chao and jackknife) bound of “true” species richness and are useful to determine the degree of sampling representivity (Soberón and Llorente 1993; Hortal et al. 2006). The combination of all estimators was thus useful in determining the extent to which we underestimated bryophyte species richness in each forest age-class and host species. Chao 1 was eventually removed because results were identical to those of Chao 2. These analyses were performed with the software program EstimateS version 8 (Colwell 2006).

One-way analyses of similarity (ANOSIM; Clarke 1993) applying the standard Bray–Curtis coefficient were used to determine whether there were significant differences (1) among the bryophyte assemblages of the three host species within each age of the chronosequence (interhost species) and (2) between paired consecutive forest age-classes (8–15, 15–25, and 25–60 YAH) for each host species separately (intrahost species). ANOSIM is a distribution-free analogue of a one-way ANOVA that compares average rank similarities within preselected groups to average rank similarities between groups. ANOSIM constructs the test statistic (R) that ranges from 0 to 1. An R value that approaches 1 indicates strongly distinct groups (i.e., completely different bryophyte communities on each host tree species within each forest age-class), whereas an R value near 0 indicates that the assemblages are barely distinguishable. The significance level for R was assessed using 999 random permutations of distances between samples. The data were fourth-root transformed before analyses to reduce the weight of common species (Clarke and Warwick 1994). Analyses were carried out with the PRIMER package, version 6 (Clarke and Corley 2006).

Ordination techniques help explain variation in patterns from different plant communities, even through time (Arévalo et al. 1999; González-Mancebo et al. 2004). We used detrended correspondence analysis (DCA) (Hill and Gauch 1980) to examine shifts in species composition along the chronosequence. The analyses were conducted with the CANOCO package (Ter Braak and Šmilauer 1998). Data were entered as mean percent cover of each bryophyte species on each host tree, considering each plot separately. All analyses were carried out with species occurring in more than three samples, and because of the notable differences among epiphytic species, cover data were square-root transformed.

To detect problems of collinearity, correlation coefficients (Spearman rank tests) were initially calculated among all forest structural features considered (i.e., basal area, tree density, and tree height) (see Bermúdez et al. 2007) as well as among the sampling variables measured (i.e., tree zone, aspect zone, sample height). To assist in the ecological interpretation of the DCA axes, Spearman correlation ranks were calculated among the partial-plot ordination scores and a group of variables — basal area (i.e., tree age), tree height, and tree zone. Tree zones and aspect zones were coded numerically (see Field sampling section).

Change in epiphytic bryophyte species composition among host tree species in each forest age-class was evaluated through beta diversity by matched category pairs using the Whittaker index. In these analyses, a matrix of presence data was used, where each plot and host species was considered separately. Then, each plot was grouped into its respective forest age-class. For more details on the calculation of beta diversity, see Pisces Conservation Ltd. (2002). For each forest age-class, two richness measures were provided for each host species: (1) total richness, obtained by totalling all the different species found in the three plots (equivalent to gamma diversity), and (2) species richness, obtained by averaging the number of species in the three plots (equivalent to alpha diversity). All diversity and richness measures were calculated using Species Diversity and Richness software (Pisces Conservation Ltd. 2002).

Kruskal–Wallis tests were used to examine significant differences in number and cover of bryophyte species for each three host species separately, depending on the two main factors under considered (i.e., forest age-classes and vertical tree zones). Prior to running the Kruskal–Wallis tests, richness and cover data were aggregated by averaging them to the plot level; total, liverwort, and moss richness were considered separately. For differences among vertical tree zones, we used 25 and 60 YAH plots because only these plots contained bryophyte colonization over the tree bases. Kruskal–Wallis tests and Spearman correlation rank analyses were carried out using the SPSS package (SPSS 2003).

Results

Sampling adequacy

There were differences in the number of samples (i.e., microplots that contained bryophytes), and these differences were most pronounced among forest age-classes, with the oldest age-class (60 YAH) having a much greater number of samples than the other age-classes (Table 1). The two youngest age-classes (8, 15 YAH) contained many trees without epiphytic bryophytes, and consequently, these stands produced fewer samples (Table 1). Despite these sampling differences, predicted species richness from all nonparametric estimators was similar to observed values of bryophyte richness for all host species through the chronosequence (Table 1), even with the most restrictive estimators of richness like bootstrap. Although the values of completeness varied slightly among calculated estimators, the overall mean percentage of completeness of all estimators considered together ranged from 0.86 to 1.03 (see Table 1).

Biotic parameters of the stand and tree structure

Initially, correlation coefficients were calculated among all forest structural features (i.e., basal area, tree density, tree height) and among sampling variables considered (i.e., tree zone, aspect zone, sample height). Some of these parameters were finally removed from the analyses because they were highly intercorrelated ($P \leq 0.01$; Spearman correlation coefficients not shown). Thereby, because of their apparent independency and the main questions of this study, basal area, tree height, and vertical tree zone were the variables retained for the analyses.

Mean basal area and height for the sampled trees of the three host species (Fig. 1) followed the general pattern described in the Stand description section (Bermúdez et al. 2007). Both basal area and height increased throughout the chronosequence, the exception being mean basal area of *M. faya*, which was strikingly lower in the 60 YAH age-class (Fig. 1).

Composition of epiphytic bryophytes

Forty-seven epiphytic species, consisting of 19 liverworts (40% of all species) and 28 mosses (60%), were found along the chronosequence (Table 2). Only two species, *Hypnum uncinulatum and Frullania teneriffae*, occurred in more than 50% of the samples, while four species of liverworts and five of mosses were recorded three or fewer times. Eighteen species (38%) were exclusive to a single host species (Table 2). Fifteen of these (32%) were exclusive to *L. novocanariensis*, which occurred mainly in 60 YAH forests (e.g., hanging mosses such as *Neckera complanata*, *Neckera intermedia*, *Cryptoleptodon longisetus*, and *Leucodon canariensis*, or the moss turf *Orthotrichum rupestre*; see Table 2). Only two and one species were exclusive to *M. faya* and *E. arborea*, respectively (see Table 2).

The *R* values from ANOSIM used to compare bryophyte assemblages among *E. arborea*, *L. novocanariensis*, and *M. faya* within each forest age-class (i.e., interhost species; Table 3) showed that (1) species composition differed significantly among all host species, but especially between *L. novocanariensis* and the other two host species in 60 YAH stands (also see Table 2), and (2) pairwise comparisons did not reveal any compositional differences between host species in the 8 YAH stands (Table 3). ANOSIM tests between paired consecutive forest age-classes (i.e., 8 vs. 15 YAH, 15 vs. 25 YAH, 25 vs. 60 YAH) for each host species separately (i.e., intrahost species) showed significant differences for all the pairwise comparisons of *L. novocanariensis*, and for 15–25 YAH and 25–60 YAH comparisons of *E. arborea* and *M. faya* (Table 4).

The total beta diversity in the study area was 2.761, and total beta diversity values in each correlative period (i.e., 8 vs. 15 YAH, 15 vs. 25 YAH, 25 vs. 60 YAH) decreased through the chronosequence. However, the highest epiphytic bryophyte species turnover between forest age-classes for an individual host species was for *L. novocanariensis* between 8 and 15 YAH (Table 5); species turnover for this host was also high for the 25 to 60 YAH period. In contrast, the highest values of turnover for *E. arborea* and *M. faya* were detected between 15 and 25 YAH (Table 5).

DCA analysis confirmed that, in general, epiphytic bryophyte communities differed among forest age-class and host species, with the 60 YAH forests showing a marked separation from the three youngest forests along axis 1 (Fig. 2*a*). The two youngest forest age-classes (8 and 15 YAH) were close together along axis 1, indicating similarities between these two age-classes, although the distance between them was greater along axis 2. Additionally, *L. novocanariensis* showed a stronger separation from the other two host species in each cluster performed (i.e., forest age-class), especially along axis 2. In general, these results coincided with those of ANOSIM for intra- and interhost dissimilarity through the chronosequence (Tables 3, 4). However, there was no clear overlap between the ordination of the plots (polygons) and some bryophyte species (see Figs. 2*a* and 2*b*).

The correlation coefficients between the plot ordination scores from DCA ordination and the variables selected (i.e., basal area, tree height, and tree zone; Fig. 2*b*) showed that (1) the scores were positively correlated with basal area (Rho = 0.615; $P \leq 0.001$) and tree height (Rho = 0.470; $P \leq 0.001$) along axis 1, and (2) positively correlated with tree height (Rho = 0.328; $P < 0.001$) and tree zone along axis 2 (Rho = 0.534; $P \leq 0.001$).

Hypnum uncinulatum and *Frullania teneriffae* were notably abundant mats on both *E. arborea* and *M. faya* through

Table 1. Summary table of total bryophyte species richness observed and estimated for each host species over the chronosequence.

	Host species											
	Erica arborea				*Laurus novocanariensis*				*Myrica faya*			
	8 YAH	15 YAH	25 YAH	60 YAH	8 YAH	15 YAH	25 YAH	60 YAH	8 YAH	15 YAH	25 YAH	60 YAH
Observed richness												
No. samples	17	30	240	372	22	33	368	678	27	29	359	364
Bryophyte richness	5	6	16	11	3	15	30	38	6	9	23	19
Liverwort richness	3	3	9	6	3	9	15	14	5	6	12	10
Moss richness	2	3	7	5	0	6	15	24	1	3	11	9
No. uniques	0	0	3	0	0	0	7	0	0	0	2	0
No. duplicates	0	0	2	0	0	1	2	5	0	0	4	0
Richness estimates												
Chao 2	5	6	17	11	3	15	36.98	38	6	9	23.2	19
Jacknife 1	5	6	18.99	11	3	15	36.98	38	6	9	25	19
Jacknife 2	5	6	19.99	11	3	15	41.96	33.02	6	9	23.01	19
Bootstrap	5.03	6.1	17.46	11.20	3	14.09	32.98	38.02	6.12	9.17	24.38	19.09
Michaelis–Menten	5.42	6.67	15.34	10.53	3.34	15.08	27.68	37.03	6.7	10.5	21.74	19.23
% completeness												
Chao 2	**1**	**1**	**0.94**	**1**	**1**	**1**	0.84	**1**	**1**	**1**	**0.99**	**1**
Jacknife 1	**1**	**1**	0.81	**1**	**1**	**1**	0.81	**1**	**1**	**1**	**0.92**	**1**
Jacknife 2	**1**	**1**	0.80	**1**	**1**	**1**	0.71	**1.15**	**1**	**1**	**0.99**	**1**
Bootstrap	**0.99**	**0.98**	**0.92**	**0.98**	**1**	**1.06**	**0.91**	**0.99**	**0.98**	**0.98**	**0.94**	**0.99**
Michaelis–Menten	**0.92**	**0.89**	**1.04**	**1.04**	**0.89**	**0.85**	**1.08**	**1.02**	**0.89**	**0.85**	**1.05**	**0.98**
Mean % completeness	**0.98**	**0.97**	**0.91**	**1**	**0.97**	**0.98**	**0.86**	**1.03**	**0.97**	**0.99**	**0.98**	**0.99**

Note: The percentage of completeness is the ratio of observed to estimated species richness. Significant completeness values are given in bold (values higher than 85%). Observed richness, total number of species; no. samples, microplots that contained bryophytes; uniques, species represented by only one sample; duplicates, species represented by only two samples; YAH, years after harvest. Total richness values observed for liverworts and mosses also are included.

time (Table 2). At 25 and 60 YAH, mat-forming liverworts such as *Lejeunea lamacerina*, *Microlejeunea ulicina* (in many samples but with low cover), and *Radula lindenbergiana*, and the mat moss *Rhynchostegium confertum* (only at 25 YAH) also had a considerable presence on *E. arborea*. On the other hand, mat-forming liverworts such as *Frullania tamarisci*, *Lejeunea lamacerina*, and *Radula lindenbergiana*, and the moss cushion *Ulota calvescens* dominated on *M. faya* (see Table 2). *Frullania tamarisci*, *Frullania teneriffae*, *Ulota calvescens*, and *Orthotrichum lyellii* attained relatively high abundance in upper levels of both tree species (Fig. 2*b*). The transition in dominance of several bryophyte species was therefore barely apparent on *E. arborea* and *M. faya*, while, as is shown below, it was stronger on *L. novocanariensis*, mainly in the 25–60 YAH period (Table 2).

In the three youngest forests, epiphyte communities on *L. novocanariensis* also included *Hypnum uncinulatum* and *Frullania teneriffae* but with a high abundance of particular mat-forming species such as the liverwort *Lejeunea lamacerina*, *Cololejeunea minutissima* (in many samples but with low cover), some *Lophocolea* species, and *Rhynchostegium confertum* (Table 2; Fig. 2*b*). In contrast, other mat-forming species such as *Radula lindenbergiana*, *Frullania polysticta*, and the moss *Homalothecium sericeum*; the fan-forming liverwort *Porella canariensis*; and the hanging mosses *N. intermedia* and *Cryptoleptodon longisetus* were very abundant at 60 YAH (Table 2; Fig. 2*b*). Some turfs of genus *Orthotrichum* and mats of genus *Frullania* or *Pterogonium gracile* showed an increased at 60 YAH (Table 2), which mainly seemed to occur in the upper tree zones of *L. novocanariensis* (see correlations in Fig. 2*b*).

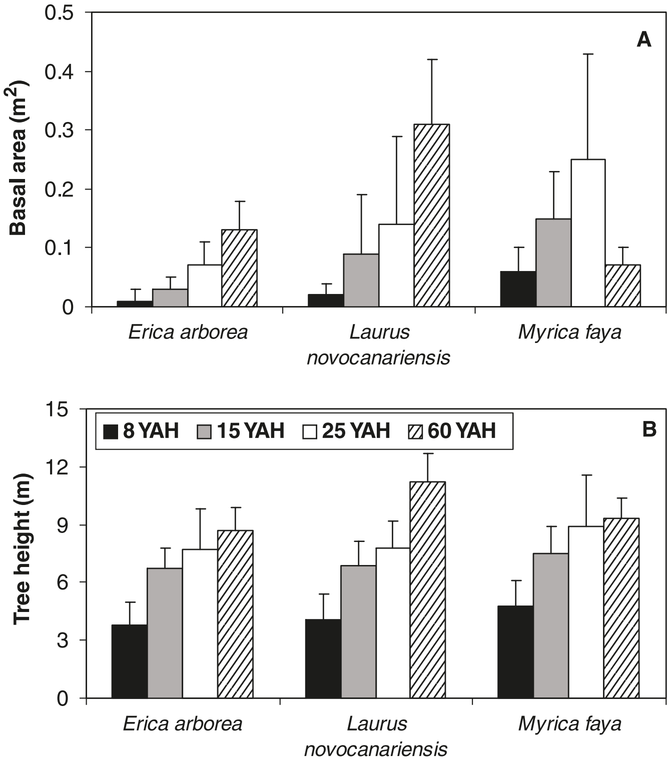
Richness and cover of epiphytic bryophyte groupings

During the chronosequence analysed, there was a gradual increase of species richness (i.e., number of species), at least for *L. novocanariensis* (Table 1; Fig. 3). In contrast, when comparisons were made among all the forest age-classes, *E. arborea* and *M. faya* showed an overall significant increase at 25 YAH and a weak drop in total and liverwort richness at 60 YAH (Table 1; Fig. 3). Moss richness significantly increased for all host species through the chronosequence (Fig. 3). Cover of epiphytic bryophytes followed a more homogeneous pattern through the chronosequence, since total cover and cover of each phylogenetic group significantly increased on all the host species (Fig. 3). Although without statistical support, a markedly higher abundance of mosses was recorded on the 60-year-old trees of the three host species (Fig. 3), and with the exception of the 8 YAH forest age-class, *L. novocanariensis* exhibited higher bryophyte richness measures than *E. arborea* and *M. faya* (Table 1; Fig. 3).

Vertical distribution

In general, when comparing epiphytic bryophyte richness among all five tree zones and analysing each host species separately, two patterns of variation were clear (Fig. 4). At

Fig. 1. Basal area (A) and height (B) for sampled trees per forest age-class throughout the chronosequence (mean + standard deviation). Values are given separately for the three host species (*Erica arborea*, *Laurus novocanariensis*, *Myrica faya*).



25 YAH, there was a gradual decreasing trend of richness from the tree base to the upper colonized zone, although this was significant only for liverwort richness on *L. novocanariensis* and *M. faya* (Fig. 4). In contrast, most of the differences of species richness among tree zones were significant at 60 YAH, where the richest tree level was the trunk (Fig. 4); moss richness peaking in 60 YAH inner canopies of *L. novocanariensis* was the sole exception to this general pattern. *Laurus novocanariensis* was also the only species for which outer canopies were colonized by bryophytes (Fig. 4).

Epiphytic bryophyte cover followed a variation pattern very similar to that of species richness. At 25 YAH, cover measures on each host tree tended to decrease from the tree base to the upper colonized zone (Fig. 5), although without significant differences among tree zones for *E. arborea*. The cover values for each bryophyte grouping were significantly higher on trunks in the 60 YAH (Fig. 5), except for liverworts on *E. arborea*. In this oldest forest class, moss cover was generally higher than liverwort cover on the three host species (see Fig. 5).

Discussion

Clear-cutting has been defined as one of the most dramatic disturbances to bryophytes in managed forests (Fenton and Frego 2005; Dynesius and Hylander 2007) because of tree removal and the resulting abrupt microclimatic changes caused by canopy openings (Lesica et al. 1991; Bardat and Aubert 2007). Accordingly, we were unable to detect bryophytes on bark up to 8 years following the last clearcut; remnant species had even disappeared from tree bases of cleared forest patches.

Sampling adequacy

Several tropical and subtropical studies have suggested that sampling of four to five trees, from tree base to outer canopy, may yield over 75% of the epiphytic species richness of a homogeneous forest stand (e.g., Acebey et al. 2003). We sampled at least six complete trees of each host species within each forest stand. In the present study, most species richness estimators showed values of ca. 90% completeness. Therefore, we conclude that the differences in the sampling sizes among host species and among forest age-classes (see Table 1) were not significant because the sampling method yielded a good representation of the actual richness of epiphytic bryophytes that occurs in each laurel forest stand analysed (on average, more than 85%).

Species composition of epiphytic bryophytes

According to the host-tree structural features, microclimatic particularities, and, consequently, epiphytic bryophyte composition, the three tree species analysed in the current study can be assembled into two groups. The first consists of *Laurus novocanariensis*, which is shade tolerant and presents higher stemflow values (i.e., funnelling ratios) in addition to greater leaf size (Aboal et al. 1999; Arévalo et al. 1999). The second group is represented by *Erica arborea* and *Myrica faya*; these species develop drier bark owing to their lower stemflow values and smaller leaves (Aboal et al. 1999; Ohsawa et al. 1999). Thus, compositional divergences between epiphytic floras and the generally higher bryophyte richness on *L. novocanariensis* than on *M. faya* and *E. arborea* (detected after 15 years of regrowth and clearly manifested at 60 YAH; see Tables 2, 3) are clearly related to those structural differences. This finding has been previously documented (González-Mancebo et al. 2003, 2004).

Our results suggest that both species turnover rate and abundance shifts of mosses versus liverworts varied over time, depending on host species. As shown by beta diversity and similarity analyses (Tables 4, 5), the highest level of epiphytic species turnover on *L. novocanariensis* between consecutive forest age-classes was found between 8 and 15 YAH. This host species also showed significantly high species replacement rates between 15 and 25 YAH and even more so between 25 and 60 YAH (Tables 2, 4, 5). Conversely, *E. arborea* and *M. faya* showed one replacement peak in the 15–25 YAH period, and then turnover rates and compositional differences between forest age-classes decreased (see Tables 2, 4, 5).

Temporal species turnover on *L. novocanariensis* was therefore significant between 8 and 15 YAH. However, it was not until 60 YAH that this host species showed a significant replacement of species and an increase in the abundance of shade-tolerant species (e.g., the mat *Frullania polysticta* and the fans *Cryptoleptodon longisetus* and *Porella canariensis*). At this age, the number of exclusive species also peaked; of these, the hanging mosses *Leucodon canariensis* and *N. intermedia* have previously been associated with old-growth forests of moist environments (González-Mancebo et al. 2003, 2004). Nonetheless, com-

Table 2. List of epiphytic bryophyte species and their percentage of cover on each tree species and in the four forest age-classes: 8, 15, 25, and 60 years after harvest (YAH).

			Host species											
			Erica arborea				*Laurus novocanariensis*				*Myrica faya*			
	Acronyms	Growth form	8 YAH	15 YAH	25 YAH	60 YAH	8 YAH	15 YAH	25 YAH	60 YAH	8 YAH	15 YAH	25 YAH	60 YAH
Liverworts														
*Calypogeia fissa**	Calyfiss	Mat										0.2		
Cephaloziella baumgartneri	Cephbaum	Mat									1.1			
*Cephaloziella divaricada**	Cephdiva	Mat											0.5	
Cololejeunea minutissima	Colominu	Mat			0.4	0.3		0.7	0.8	0.7			0.8	1.3
Frullania dilatata	Fruldila	Mat				3			1.4	2.6			1.6	4
*Frullania microphyla**	Frulmicr	Mat							1.2	2.5				
*Frullania polysticta**	Frulpoly	Mat							1.5	**8**				
Frullania tamarisci	Frultama	Mat							1.2	2.6				**19**
Frullania teneriffae	Frultene	Mat	**4.2**	**2.2**	**2.6**	**5.5**		0.6	1.3	6.1	**1.7**	**1.9**	**4.9**	**16.6**
Lejeunea eckloniana	Lejeeckl	Mat			0.4			0.6	1.2	1			1.1	
Lejeunea lamacerina	Lejelama	Mat			0.9	2	**1.25**	0.6	1.5	2.4	**2.2**	1	1.4	9.9
*Lejeunea mandonii**	Lejemand	Mat								1				
Lophocolea bidentata	Lophbide	Mat	0.7		1.4		**0.5**	1	**2.4**	2	1.5	1.5	2.2	1
Lophocolea fragans	Lophfrag	Mat	0.7	**1.5**				0.7	0.4			1	0.6	
Lophocolea heterophylla	Lophhete	Mat			0.9			**1.2**	1.5		1.1	**1.7**	2.2	
Metzgeria furcata	Metzfurc	Mat							1.2	1.3				7.6
Microlejeunea ulicina	Micrulic	Mat			0.7	1.1			0.4	0.5			2	2.5
Porella canariensis	Porecana	Fan			0.5		**0.7**	1.1	1.2	**10.9**			0.7	9.5
Radula lindenbergiana	Radulind	Mat		0.7	0.7	**5**		0.9	1.1	2.7			1	4.9
Mosses														
Brachytecium rutabulum	Bracruta	Weft								4.5			0.5	0.5
*Brachytheciastrum velutinum**	Bracvelu	Weft		0.75										
*Cryphaea heteromala**	Cryphete	Mat								2.2				
*Cryptoleptodon longisetus**	Cryplong	Fan							0.7	7				
Dicranoweissa cirrata	Dicrcirr	Turf			0.8				1	0.7			1.5	0.5
Fissidens bryoides	Fissbryo	Turf							0.5			0.7		
*Fissidens taxifolius**	Fisstaxi	Turf						0.5	0.5	1				
Homalothecium sericeum	Homaseri	Mat							0.7	7.3				2.4
Hypnum cupressiforme	Hypncupr	Mat		1	2								0.7	
Hypnum uncinulatum	Hypnunci	Mat	**2.5**	**1.6**	1.9	**32.3**		0.4	0.8	3	**1.6**	**3.4**	**3.6**	**14.9**
Isothecium myosuroides	Isotmyos	Weft							2	4.5			**7.1**	
Kindbergia praelonga	Kindprae	Weft			**3.4**			**1.6**	**2.6**	4.9				
*Leucodon canariensis**	Leuccana	Tail								1				
Neckera cephalonica	Neckceph	Fan				1			0.5	4.3				1.7
*Neckera complanata**	Neckcomp	Fan								3				
*Neckera intermedia**	Neckinte	Pendant								7.8				
Orthotrichum acuminatum	Orthacum	Turf							0.5	3			1.5	
Orthotrichum lyellii	Orthlyel	Turf			0.5	2				1.9			0.9	2.6

Table 2 (*concluded*).

			Host species											
			Erica arborea				*Laurus novocanariensis*				*Myrica faya*			
	Acronyms	Growth form	8 YAH	15 YAH	25 YAH	60 YAH	8 YAH	15 YAH	25 YAH	60 YAH	8 YAH	15 YAH	25 YAH	60 YAH
*Orthotrichum rupestre**	Orthrupe	Turf								2.1				
Orthotrichum sp.	Orthsp	Turf							1	3.1			1	
*Oxyrrhynchium pumilum**	Oxyrpumi	Weft						0.4	0.5	0.7				
*Plasteurhynchium meridionale**	Plasmeri	Weft								2.5				
*Pterogonium gracile**	Ptergrac	Mat								3.7				
*Rhynchostegiella litorea**	Rhynlito	Weft						0.4						
Rhynchostegium confertum	Rhynconf	Mat	**1.7**		**3**			**2.7**	**3.1**	**8**		1.5	2.7	2.9
Scleropodium touretii	Scletour	Weft				1				5.5				2.5
Ulota calvescens	Ulotcalv	Cushion			1	1.7			0.8	2.6			1.6	2.2
Zygodon rupestris	Zygorupe	Turf							0.4	2			0.7	

Note: The three highest values for each category and the exclusive species for each host species are marked in bold and with an asterisk, respectively. Although frequency data and standard deviation of cover were calculated, they were not included to facilitate visualization of the table. Acronyms used in the ordination analysis and growth forms of each species are also included.

Table 3. Similarity values for bryophyte species composition among the three host species through the chronosequence according to results from one-way analyses of similarity (*R* values).

	Erica vs. Laurus		Erica vs. Myrica		Laurus vs. Myrica	
	R	*P*	*R*	*P*	*R*	*P*
8 YAH	–0.075	0.325	0.058	0.178	0.148	0.063
15 YAH	**0.325**	0.002	**0.321**	0.002	**0.425**	0.001
25 YAH	**0.745**	0.001	**0.278**	0.007	**0.786**	0.001
60 YAH	**0.997**	0.001	**0.623**	0.002	**0.926**	0.001

Note: Significant differences ($P < 0.05$) between host species within a pair are shown in bold. YAH, years after harvest; Erica, *Erica arborea*; Laurus, *Laurus novocanariensis*; Myrica, *Myrica faya*.

Table 4. Similarity values for bryophyte species composition between paired consecutive of forest age-classes according to the results from one-way analyses of similarity (*R* values).

	8 vs. 15 YAH		15 vs. 25 YAH		25 vs. 60 YAH	
	R	*P*	*R*	*P*	*R*	*P*
Erica	0.123	0.052	**0.962**	>0.001	**0.851**	0.001
Laurus	**0.908**	0.001	**0.882**	0.001	**0.984**	>0.001
Myrica	0.113	0.093	**0.975**	>0.001	**0.907**	0.001
Total	**0.316**	0.003	**0.807**	0.001	**0.905**	0.001

Note: Significant differences ($P < 0.05$) between forest age-classes within a pair are shown in bold. "Total" values are for the three host species together. YAH, years after harvest; Erica, *Erica arborea*; Laurus, *Laurus novocanariensis*; Myrica, *Myrica faya*.

Table 5. Epiphytic bryophyte beta diversity values for paired consecutive forest age-classes according to Whittaker index.

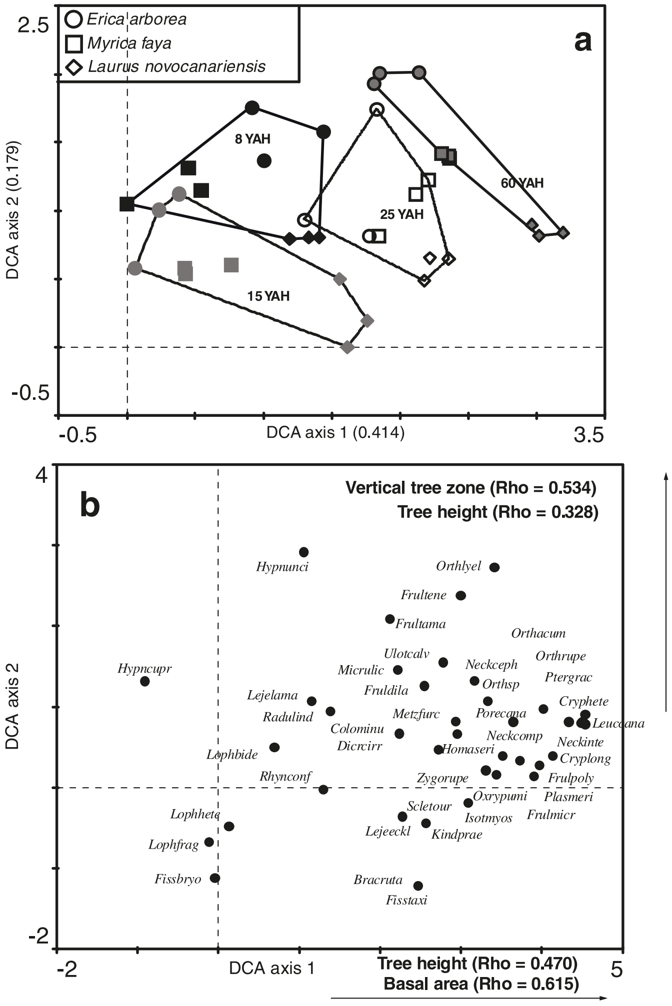
	Years after harvest		
	8–15	15–25	25–60
Erica	0.646	1.348	0.538
Laurus	1.374	0.754	1.143
Myrica	0.666	1.143	0.557
Total	2.462	2.001	1.329

Note: "Total" values are for the three host species together. Erica, *Erica arborea*; Laurus, *Laurus novocanariensis*; Myrica, *Myrica faya*.

pared with other undisturbed laurel forests (Zippel 1998; González-Mancebo et al. 2008), the abundance of these later-successional species that could be characteristic of old-growth formations is extremely low in the present study area.

During the 8–15 and 25–60 YAH periods, epiphytic communities on *E. arborea* and *M. faya* showed lower temporal turnover rates than those on *L. novocanariensis* and were dominated by mat-forming liverworts characteristic of early-successional stages (e.g., *Cololejeunea minutissima*, *Frullania teneriffae*, *Lejeunea lamacerina*, *Microlejeunea ulicina*, *Radula lindenbergiana*) as well as drought-tolerant competitive mosses (e.g., the mat *Hypnum uncinulatum*); *Hypnum uncinulatum* was also a component of the epiphytic community at 15–25 YAH. Such an overall lower species turnover on *E. arborea* and *M. faya* may be at least in part related to those generally drier conditions presented by their bark, because the prevalence of highly competitive mat species growing adpressed to bark likely reflects more arid mi-

Fig. 2. Detrended correspondence analysis (DCA) ordination of epiphyte communities occurring in the plots selected. Square-root transformed percent cover data of bryophytes were used in the analysis; the analysis included those species occurring in more than three samples (microplots). Ordination of the plots (points) distinguishing forest age-class and host species is shown in Fig. 2*a*; eigenvalues are indicated between brackets along axes 1 and 2. Species ordination (points) and Spearman correlation coefficients (Rho) between the main variables considered and respective ordination axes scores are presented in Fig. 2*b*. Trees are identified to species but are also presented in groups based upon forest age-classes. Black symbols show the 8 years after harvest (YAH) age-class; grey symbols show 15 YAH; open symbols show 25 YAH; and grey symbols with a dark contour show 60 YAH. Bryophyte species are indicated by the first four letters of the genus and the species (see acronyms in Table 2).



croclimates (e.g., Holz et al. 2002; Acebey et al. 2003; González-Mancebo et al. 2003; Andersson and Gradstein 2005).

However, the drier microclimate is likely to be only one factor contributing to the slower species replacement rate, because other species (e.g., the turf *Dicranum canariense* and the weft *Isothecium myosuroides*) have been found to dominate the epiphytic communities on *E. arborea* and *M. faya* in old-growth laurel forests with mesoclimates similar to those of the forests in this study (González-Mancebo et al. 2008). When late-successional bryophytes are locally extirpated as a result of tree harvesting, their reestablishment may be slow, at least in part because of the poor dispersal abilities exhibited by many of these species (Miles and Longton 1992; Pohjamo et al. 2006; Pharo and Zartman 2007). Poor dispersal abilities may be an important limiting factor in clearcuts, where the potential propagule bank (i.e., bark on old trees) disappears completely. Although dispersal limitations for the species sampled in this study have not been surveyed, several studies have suggested that many bryophytes can overcome dispersal problems posed by disturbed landscapes if appropriate habitats or substrates are available (Moen and Jonsson 2003; Kantvilas and Jarman 2004; Pharo et al. 2004; Åström et al. 2005; Hylander et al. 2005).

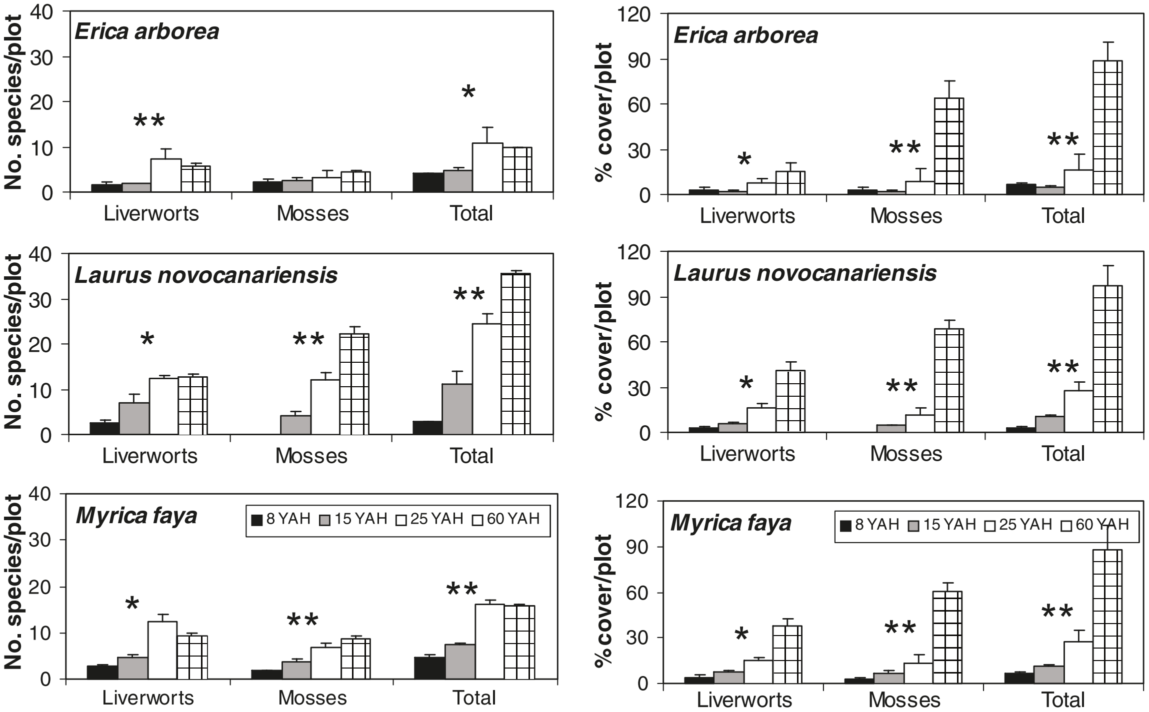
Succession over time has been largely regarded as being caused by changing habitat conditions (i.e., microenvironmental gradients) as harvested forests progressively recover (Lesica et al. 1991; McGee and Kimmerer 2002; Vanderpoorten et al. 2004; Bardat and Aubert 2007). Our study shows that the chronological availability of suitable habitats after harvesting varies depending on host identity. Because turnover on *E. arborea* and *M. faya* was relatively lower than that on *L. novocanariensis*, we suggest that the occurrence and (or) increase in availability of appropriate habitats for bryophytes with inherently restricted ecological niches is faster on *L. novocanariensis* (e.g., *Cryptoleptodon longisetus*, *Leucodon canariensis*, and *N. intermedia*; Zippel 1998; González-Mancebo et al. 2004) than on *E. arborea* and *M. faya*, both of which showed a clear predominance of early-successional species (e.g., *Frullania teneriffae* and *Hypnum uncinulatum*).

Despite several important aspects of the successional dynamics of epiphytic bryophyte communities after clear-cutting that we observed, the present study has some shortcomings. Probably the most important limitation is related to the low number of stands (only one stand per age-class); this limitation affects the strength of our conclusions on species turnover through time and space because unmeasured climatic factors (e.g., temperature, humidity) may have an exacerbating effect. However, although we acknowledge this limitation, a substantial number of studies comparing bryophyte communities among small-scale stands (e.g., Wolf 1995; Acebey et al. 2003; González-Mancebo et al. 2004; Andersson and Gradstein 2005; Fenton and Frego 2005) have obtained useful data for the management and conservation of non-vascular communities that inhabit forest ecosystems.

Species richness of epiphytic bryophytes

In terms of all measures of epiphytic bryophyte richness (Fig. 3, but see Table 1), variation in the number of species was again dependent on host species. There was an interesting drop in the number of species for *E. arborea* and *M. faya* between 25 and 60 YAH. Thus, while the highest richness values for *L. novocanariensis* were reached at 60 YAH, the only richness measure that peaked in the 60 YAH forest age-class for *E. arborea* and *M. faya* was moss richness; the other measures peaked at 25 YAH (Table 1; Fig. 3). Therefore, contrary to our prediction, only *L. novocanariensis* showed a gradual increase in the number of species and had the highest bryophyte species richness in the oldest forest stand. However, there is a certain probability

Fig. 3. Number of species and cover (mean + standard deviation) per plot through the chronosequence, considering both phylogenetic groupings together (total) and individually (liverworts and mosses). The three host species (*Erica arborea*, *Laurus novocanariensis*, *Myrica faya*) are showed separately. Asterisks indicate significant differences between forest age-classes for each bryophyte grouping: **, $P \leq 0.01$; *, $P \leq 0.05$.



that the observed decrease in species richness between 25 and 60 YAH may be a sampling artifact that resulted from the lack of true replication and not a general feature of harvested laurel forests.

There are two possible explanations for this richness drop (in addition to the lack of true replication): (1) because microclimatic conditions on both host species are putatively more challenging to bryophytes (i.e., smaller leaf size and lower funnelling ratios) and important structural forest changes took place through this chronosequence, increased light availability and microclimatic moderation may have interacted to the detriment of some shade species at 60 YAH, in particular certain liverworts (e.g., *Lophocolea heterophylla*; see Table 2) and pleurocarpous mosses (e.g., *Rhynchostegium confertum*); (2) because of the increasing prevalence of highly competitive species on the 60 YAH bark of *E. arborea* and *M. faya*, the drop in the species richness could be a clear case of competitive exclusion.

Although many studies have shown that factors regulating the colonization and establishment of bryophytes are likely of greater significance to community composition and richness, competition among species has been also stressed as major factor (Barkman 1958; Wolf 1995; Andersson and Gradstein 2005; Bardat and Aubert 2007).

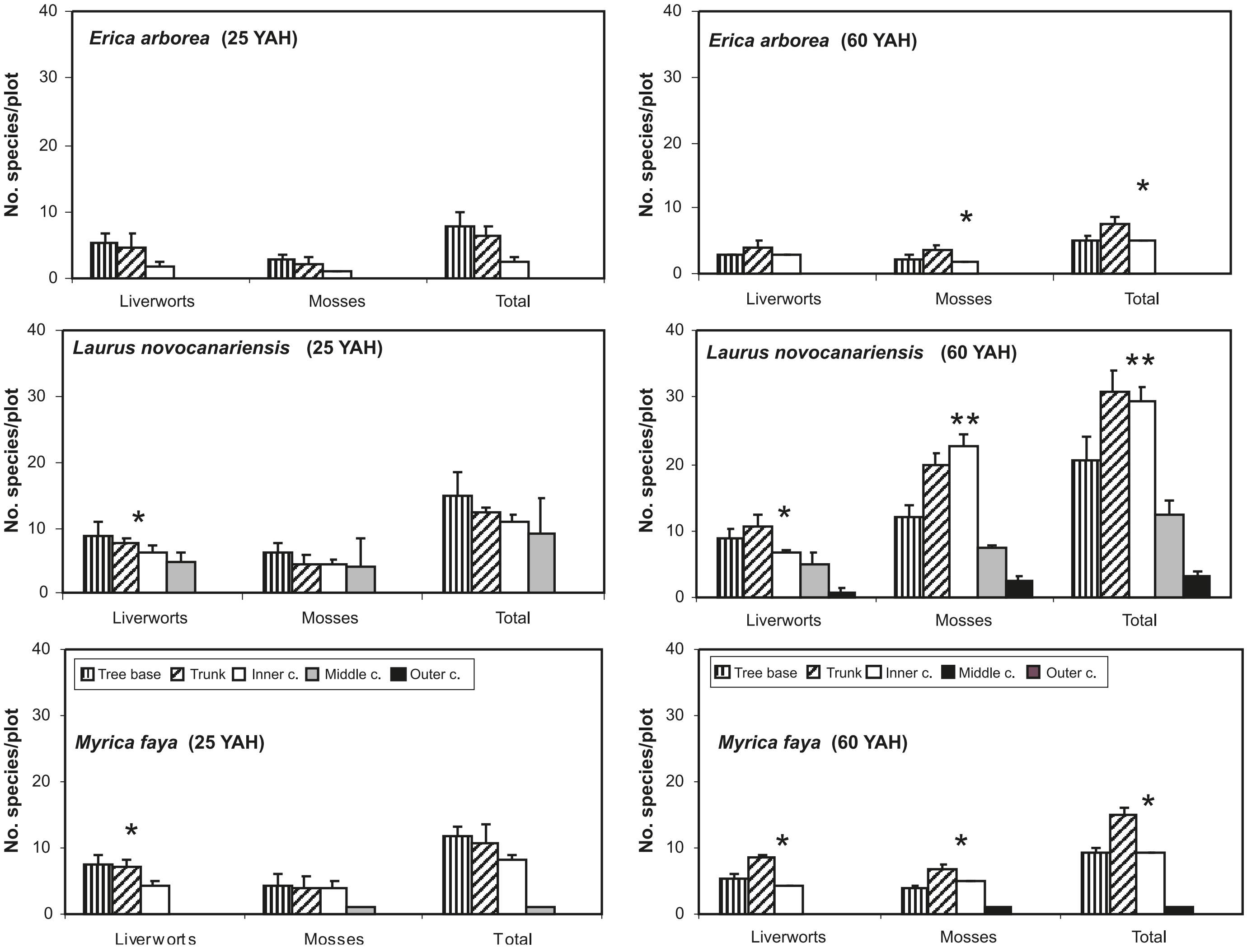
Vertical distribution

Our results also showed that successional trends and species richness of epiphytic bryophytes through the vertical tree gradient differed significantly among host species. In the vertical pattern of distribution of bryophyte communities, three important observed changes indeed showed individual characteristics according to the host species: (1) "incipient phase" (from 8 to 15 YAH; not shown), where bryophytes colonized tree bases almost uniquely; (2) "early phase" (25 YAH; Figs. 4, 5), where richness and abundance of liverworts and mosses were very similar, mainly concentrated at tree bases, but with the initiation of colonization of the upper tree levels; and (3) "middle phase" (60 YAH; Figs. 4, 5), where there was a massive movement of epiphytic bryophyte richness and abundance from tree bases to trunks, moss cover was higher than liverwort cover, and there were differences among host species regarding vertical distribution of bryophytes.

During the middle phase bryophytes on *L. novocanariensis* colonized the youngest branches (i.e., twigs), moss richness peaked in the inner canopies, and mosses were more abundant and diverse than liverworts (see Figs. 4, 5). This last observation may be related to the significant increase of hanging moss species (Table 2). For both *M. faya* and *E. arborea*, upward migration was apparently more limited; mosses also dominated, but only in terms of abundance. In the case of *M. faya*, this dominance was only detected on the trunks. In both cases, a drier microclimate on their bark and the competitive interaction among species could explain the prevalence of particular mat mosses with broad ecological requirements.

Furthermore, the abundance of some pioneer species (e.g., particular leafy liverwort species and *Orthotrichum* spp.) increased with forest age (Table 2; but see Fig. 2*b*), mainly on *L. novocanariensis*. This increase shows the upward movement of pioneer species that occupied the youngest and most exposed upper branches of the trees (Ruchty et al.

Fig. 4. Number of species (mean + standard deviation) per plot along the five vertical tree zones, considering both phylogenetic groupings together (total) and individually (liverworts and mosses). This analysis was performed with those forest age-classes showing notable colonization by bryophytes (25 and 60 years after harvest (YAH)). The three tree species (*Erica arborea*, *Laurus novocanariensis*, *Myrica faya*) are analysed separately. Asterisks indicate significant differences between vertical tree zones for each bryophyte grouping: **, $P \leq 0.01$; *, $P \leq 0.05$.



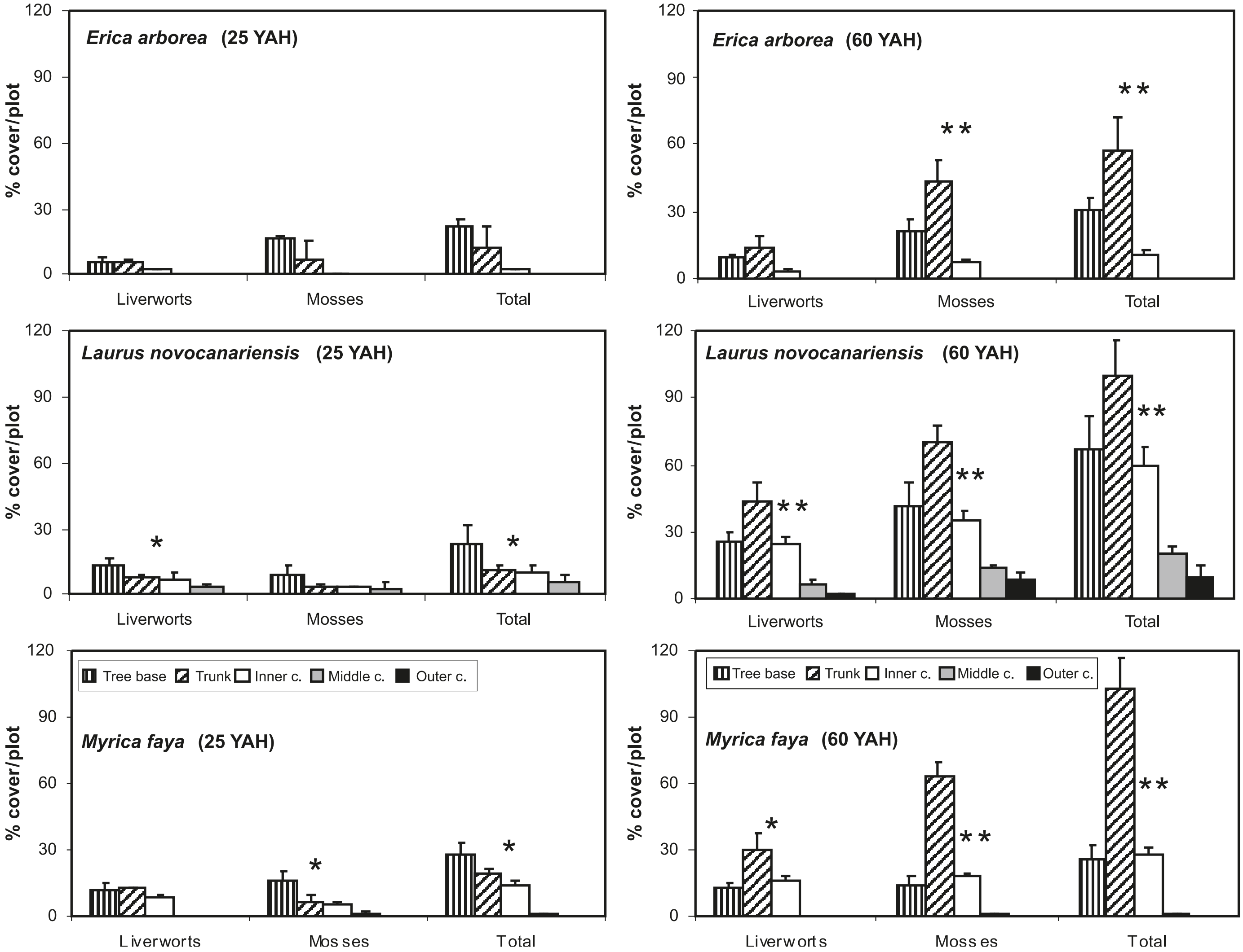
2001). Therefore, the present study is consistent with the classic views that (1) species richness diminishes downwards with increasing tree diameter (i.e., substrate age), likely as a result of increasing competition (Wolf 1995), and (2) successional processes in vertical gradients (i.e., from canopy to trunk) favour the gradual replacement of species, from pioneer species to those that characterize old-growth forests (Barkman 1958; Ruchty et al. 2001; Acebey et al. 2003).

Conclusions and management implications

Our results suggest that some liverworts prevail during early-successional stages and are gradually replaced by mosses during later-successional stages; this contrasts with the low resistance to disturbance of liverworts in other studies (e.g., Pharo et al. 2004; Nelson and Halpern 2005). Moss dominance is a common characteristic of Canarian undisturbed laurel forests (González-Mancebo et al. 2008), especially in the inner canopy. Because moss cover did not peak at the inner canopies of *L. novocanariensis* (presumably the most favourable vertical tree level in rain forests; Veneklaas et al. 1990; Wolf 1995; Acebey et al. 2003) and because there was a clear dominance of pioneer liverworts and early-successional mosses on *E. arborea* and *M. faya*, we suggest that within the silvicultural cycle analysed, these forests are at a secondary successional stage, even the oldest forest age-class (60 YAH).

In addition, because peak species richness was achieved at intermediate stages of the clearcut regime (mainly for *E. arborea* and *M. faya*), we conclude that our case study may support the intermediate disturbance hypothesis (Connell 1978; Roxburgh et al. 2004). This hypothesis posits that the trade-off between early- and later-successional species allows both groups to coexist indefinitely if intermediate disturbances are maintained. This hypothesis is still intensively debated (see Roxburgh et al. 2004). Because early- and later-successional bryophytes performed best (i.e., presence and

Fig. 5. Cover (mean + standard deviation) per plot along the five vertical tree zones, considering both phylogenetic groupings together (total) and individually (liverworts and mosses). This analysis was performed with those forest age-classes showing notable colonization by bryophytes (25 and 60 years after harvest (YAH)). The three tree species (*Erica arborea*, *Laurus novocanariensis*, *Myrica faya*) are analysed separately. Asterisks indicate significant differences between vertical tree zones for each bryophyte grouping: **, $P \leq 0.01$; *, $P \leq 0.05$.



abundance) at different postdisturbance stages and on different host species (i.e., the competitively early-successional species occupied the most recently disturbed stands and the harshest host species) and, consequently, the highest richness values were detected in different microhabitats (i.e., host species vs. tree zones) and at different intermediate scales of disturbance (i.e., at 25 YAH for *E. arborea* and *M. faya*, and at 60 YAH for *L. novocanariensis*), our study provides additional support to this hypothesis.

Management implications

Although this is the first direct study of epiphytic bryophytes growing on whole trees in the Macaronesian region, and there are no data for old-growth forests for comparison, our results permit us to suggest that most of the clear-cutting effects on species richness, cover, and composition of both phylogenetic bryophyte groups (moss and liverwort) persist for at least 60 years. This time span by far exceeds the current silvicultural regime of 7–8 years (Bermúdez et al. 2007). This short rotation is due to changes in products demanded from laurel forests. The recommended harvesting periods of greater than 100 years (Kantvilas and Jarman 2004; Holz and Gradstein 2005) may be difficult to carry out in the social context in question. Therefore, this study urgently calls for the maintenance of permanent patches of old-growth formations across managed laurel forest environments. This practice has been advised in conservation surveys for different forest ecosystems (Hazell and Gustafsson 1999; McGee and Kimmerer 2002) but virtually ignored in the Canarian laurel forests.

Conserving old-growth forest stands may provide refuge for sensitive forest-dwelling species. Therefore, these undisturbed patches may act as spore sources for the recolonization of clear-cut stands. Such patches have added value because many bryophytes are characterized as dispersal limited at local scales because spore deposition usually follows a strong leptokurtic pattern, where a majority of spores are deposited very close to the parent sporophyte (Miles and

Longton 1992; Hedenâs et al. 2003). Further, long-distance dispersal might be impeded by climatic barriers (Ozinga et al. 2004), for instance, those created by clearcuts. Pohjamo et al. (2006) and Pharo and Zartman (2007) recently suggested that many bryophytes do not usually disperse further than a few tens of metres.

To summarize, the present study suggests that after clearcutting, the temporal availability of suitable habitats for bryophyte species with strict environmental requirements may vary depending on host species. Our data illustrate the importance of considering both time since disturbance and host identity for the adequate maintenance and management of overall biodiversity of epiphytic bryophytes. Although management recommendations should be evaluated at a regional scale and more studies on minimum sizes of high-quality, old-growth forest patches are necessary, preserving mature stands including trees of selected host tree species can contribute greatly to the survival of epiphytic bryophytes that inhabit heavily managed subtropical montane cloud forests.

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