

Article

The Reproductive Strategy as an Important Trait for the Distribution of Lower-Trunk Epiphytic Lichens in Old-Growth vs. Non-Old Growth Forests

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Abstract: (1) Research Highlights: The work studied the beta diversity patterns of epiphytic lichens as a function of their reproductive strategies in old-growth and non-old growth forests from the Mediterranean area. (2) Background and Objectives: The reproductive strategies of lichens can drive the dispersal and distribution of species assemblages in forest ecosystems. To further investigate this issue, we analyzed data on epiphytic lichen diversity collected from old-growth and non-old growth forest sites (36 plots) located in Cilento National Park (South Italy). Our working hypothesis was that the dispersal abilities due to the different reproductive strategies drove species beta diversity depending on forest age and continuity. We expected a high turnover for sexually reproducing species and high nestedness for vegetative ones. We also considered the relationship between forest continuity and beta diversity in terms of species rarity. (3) Materials and Methods: we used the Bray–Curtis index of dissimilarity to partition lichen diversity into two components of beta diversity for different subsets (type of forest, reproductive strategy, and species rarity). (4) Results: The two forest types shared most of the common species and did not show significant differences in alpha and gamma diversity. The turnover of specific abundance was the main component of beta diversity, and was significantly greater for sexually reproducing species as compared to vegetative ones. These latter species had also the least turnover and greater nestedness in old-growth forests. Rare species showed higher turnover than common ones. (5) Conclusions: Our results suggest that sexually reproducing lichen species always have high turnover, while vegetative species tend to form nested assemblages, especially in old-growth forests. The rarity level contributes to the species turnover in lichen communities. Contrary to what one might expect, the differences between old-growth and non-old growth forests are not strong.

Keywords: sexual reproduction; vegetative propagules; forest management; functional traits; beta diversity



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1. Introduction

Reproductive strategies widely affect the species distribution of vascular plants, bryophytes, and lichens. A tradeoff between dispersion and establishment abilities is the key to the success of most of the species of plants. Relying on different dispersal vectors such as wind, water, or animals, vascular plants have evolved a broad range of dispersal modes or strategies [1,2], using generative (such as spores, seeds, or fruits) and vegetative (such as fragments of stems, stolons, rhizomes, or bulbils) diaspores [3].

Lichens are symbiotic organisms in which fungi and algae and/or cyanobacteria form an intimate biological union [4] and both partners must be present for their successful reproduction and dispersal [5]. Lichen propagules (diaspores) contain cells from both partners and represent an essential evolutive solution to this problem [6]. This vegetative

reproduction grants a reasonable survival rate and success for the establishment of new lichen thalli [7]. Still, it is characterized by a low dispersal ability [8]. Some authors have shown that diaspores usually have a dispersal range of about 10–100 m for *Lobaria pulmonaria* [9–12], and up to 30 m for *Evernia prunastri*, *Ramalina farinacea* [13], and *Hypogymnia physodes* [14].

Sexual reproduction in lichens only involves the mycobiont partner, through spore production and propagation. To germinate and give rise to a new individual, the spore must find a compatible photosynthetic partner on a suitable substrate to colonize [4]. Sexual spores are generally smaller than vegetative structures and they are also actively discharged (except those of *Caliciales*), so they are likely to be dispersed over longer distances [6]. Further, this propagation form allows the genetic turnover of the populations, which is extremely important for adaptation to environmental changes [15]. For example, even in the hostile environments of Antarctica, Seymour et al. [6] reported that many lichens produced sexual structures, often in abundance.

In forest ecosystems, the distribution of lichen species is driven both by landscape and stand-level factors [16–19]. In this paper we focus on these latter aspects. In particular, the structural characteristics of the stand (e.g., basal area, tree height) and the availability of tree substrates suitable for lichen colonization (e.g., old trees) and of micro-habitats can be the main limiting factors conditioning the most appropriate reproductive strategies to obtain better species dispersal abilities [16–19].

So far, most studies have focused on the effect of reproductive strategies on the dispersal ability and distribution of species assemblages (see e.g., [18]) or on single forest-dwelling species (see e.g., the studies on the umbrella and flagship species *Lobaria pulmonaria*; [11,12,19]). Only a few papers have explored this issue in terms of beta diversity and species turnover [20]. Furthermore, no previous study, to our knowledge, has addressed the topic comparing what happens to lichen communities in old-growth (hereafter OG) and non-old growth (NOG) forests, especially in Mediterranean oak and beech forests.

In the present study, we assess the hypothesis that the dispersal abilities for the different reproductive strategies drive the species turnover and nestedness (beta diversity) depending on forest age and continuity. To address this question, we used the data from a study on epiphytic lichen diversity carried out in OG and NOG forest stands in a national park in Southern Italy [21,22].

The details of the study hypothesis are illustrated in Figure 1, where possible patterns of species dispersion with different reproductive strategies in OG and NOG forests are reported. We expect sexually reproducing species to be characterized by a high turnover regardless of forest type (Figure 1b,d). This hypothesis is based on the observation that spores have a potentially very high spatial range of dispersion, but, at the same time, they may encounter more difficulties than vegetative species in the formation and establishment of new thalli. These biological characteristics would lead to strong discontinuities (turnover) in the floristic compositions of the various sites. On the other hand, we hypothesize that the beta diversity of vegetative species is mainly determined by a high nestedness between sites of the same forest types and that this pattern is more evident in OG forests than in NOG ones (Figure 1a,c). This assumption is based on the fact that vegetative species are particularly favored in the colonization of contiguous sites which would tend to host a similar set of species, especially in conditions of ecological continuity such as those found in OG forests.

Additionally, we also considered the relationship between forest continuity and lichen beta diversity in terms of species rarity. Since diversity may be influenced by dispersal ability, we expect that rare species spread more easily in OG forests.

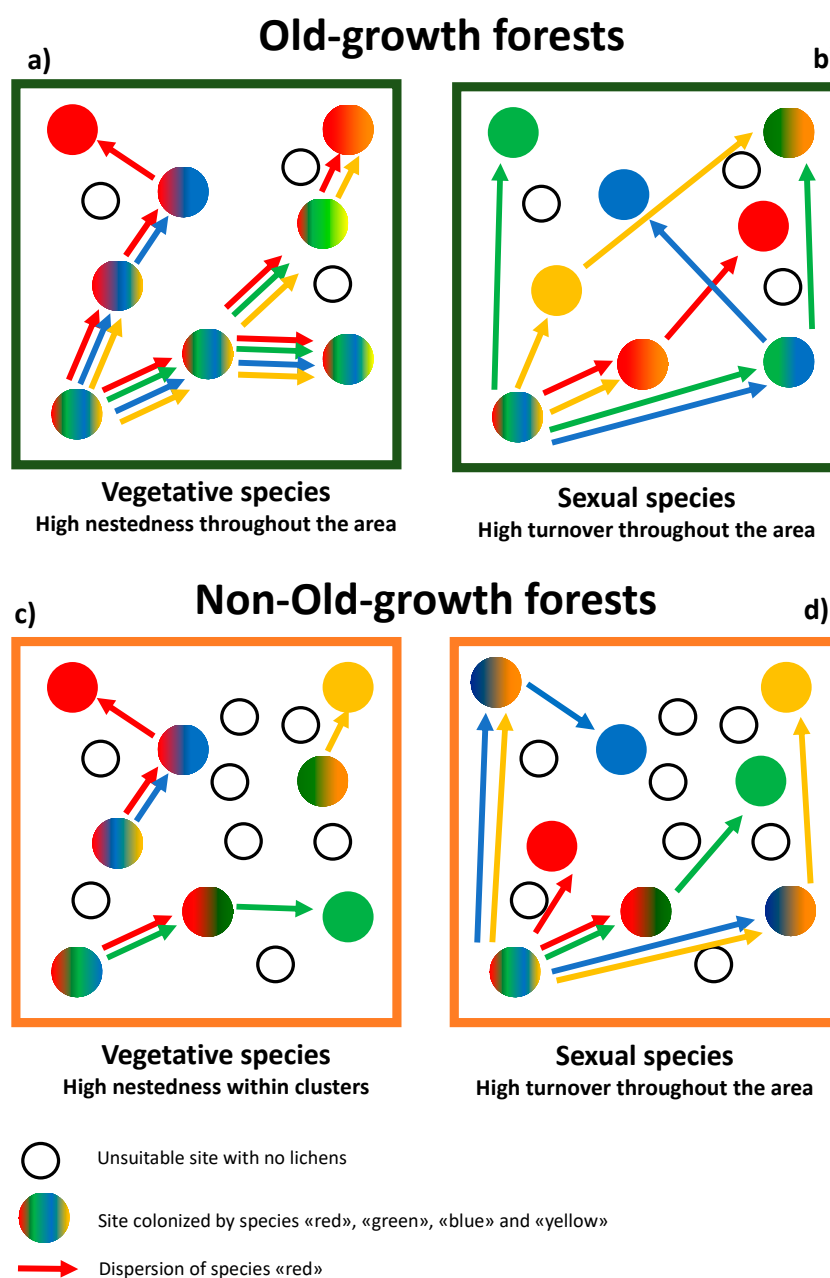


Figure 1. Schematic representation of the hypotheses tested in the study on the beta diversity patterns of lichen species with contrasting reproductive strategies in old-growth (OG) and non-old growth (NOG) forests. The squares represent the areas with different types of forest. We report the possible dispersion flows (arrows) of the different species (colors) between sites (circles) that determine the colonization and are the basis of the potential compositional differences: (a) vegetative species in OG forests; (b) sexual species in OG forests; (c) vegetative species in NOG forests; (d) sexual species in NOG forests.

2. Materials and Methods

We analyzed lichen diversity data collected within a long-term monitoring project focused on old-growth forests of The Cilento, Vallo di Diano e Alburni National Park, in Southern Italy (see the results here: [21–26]).

2.1. Study Area

The Cilento, Vallo di Diano e Alburni National Park extends over 181,000 ha, stretching between the Tyrrhenian coast and the margin of the Lucania mountains, in the Campania Region (southern Italy). This study was carried out in the interior forest habitats, from

300 to 1696 m, in a survey area of 30 × 42 km (Figure 2). The hilly substrates mainly develop on flysch formations; the inner mountains are carbonate massifs predominantly constituted by carbonate and dolostone [27]. Native forests are mostly represented by turkey oak (*Quercus cerris* L.) woodlands of the hilly and sub-montane belts (from 450 to 850 m in altitude), mesophilous mixed forests dominated by turkey oak mostly on the north-facing slopes (between 800 and 1000 m in altitude), and beech (*Fagus sylvatica* L.) woodlands (thermophilous and microthermal coenoses) in upland areas. Chestnut (*Castanea sativa* Mill.) coppices and holm oak (*Quercus ilex* L.) woods are less common. In this area, bioclimatic characteristics range from Mediterranean to temperate with a cooler and more humid climate, and inland areas are usually subject to a temperature lower than 10 °C for three months per year. Rainfall increases along with altitude from 730 to 1700 mm year⁻¹.

2.2. Sampling Design

Thirty-six plots (50 × 50 m) were randomly selected, taking into account structural attributes, “old-growths”, and forest types, in proportion to their area within the park (Figure 2). They represented a sub-sample of the 132 sites investigated during a preliminary extensive survey on forest structural attributes (systematic survey, grid dimension 500 m; see [28]). The selected plots were classified as old-growth (OG) or non-old growth (NOG) forests according to their structural attributes. In particular, OG stands were considered to be structurally more heterogeneous than younger ones in relation to the following criteria: (1) the presence of OG individual trees (individuals with DBH >50 cm); (2) weak or no human disturbance; (3) multi-layered canopy; (4) large volumes of standing and fallen deadwood; and (5) decaying ancient and veteran trees (standing dead trees). OG forest sites significantly differed (Wilcoxon test, $p < 0.05$) from NOG forests with regard to higher tree circumference (median: 113 vs. 72 cm), number of diameter classes (median: 11 vs. 9), and volume of fallen deadwood (median: 1.394 vs. 0.0 vol ha⁻¹). The other structural variables were similar between the two forest types (Table 1).

The sampling plots represented overall five forest types as follows: (1) beech woodlands (10 NOG, 7 OG plots); (2) turkey oak woodlands (7 NOG, 4 OG plots); (3) mixed broadleaf forests (2 NOG, 2 OG plots); (4) chestnuts woods (2 NOG plots); and (5) holm oak woods (2 OG plots). The dominant tree species of each forest type were considered as tree substrate for lichen sampling. In each plot, three sampling trees were considered within one randomly selected circular sub-plot (7-m radius). In mixed broadleaf forests we sampled different tree species (*Alnus cordata* (Loisel.) Desf., *Quercus pubescens* Willd., *Q. cerris*, and *C. sativa*). OG and NOG stands showed moderate differences in the proportion of the sampled tree species composition, with a predominance of beech and turkey oak, as well as seven less frequent tree species (see Table S1).

Table 1. Descriptive statistics of the structural variables included in the models. Results of the Wilcoxon test performed for the two forest types are also reported. n.s.: not significant ($p > 0.05$).

Structural Variables	Abbr.	OG (n:15)		NOG (n:21)		Wilcoxon Test (df:1; n:36)
		Median	Min–Max	Median	Min–Max	
Tree circumference (cm)	TC	113	38–226	72	45–182	W = 219.5, $p < 0.05$
Diameter classes number (n)	DCN	11	3–15	9	4–15	W = 221.5, $p < 0.05$
Number of old trees (n)	OT	7	0–28	1	0–20	W = 213, n.s.
Basal area (m ² ha ⁻¹)	BA	28.0	7.5–48.9	23.4	3.5–44.4	W = 208, n.s.
Standing deadwood (vol ha ⁻¹)	SDW	0.271	0–1.179	0.0	0.0–10.242	W = 162, n.s.
Fallen deadwood (vol ha ⁻¹)	FDW	1.394	0–4.823	0.0	0.0–3.723	W = 256, $p < 0.001$
Tree Species Richness (n)	TSRich	3	1–7	3	1–6	W = 176.5, n.s.
Number of trees (n)	NT	132	56–365	125	50–271	W = 163, n.s.

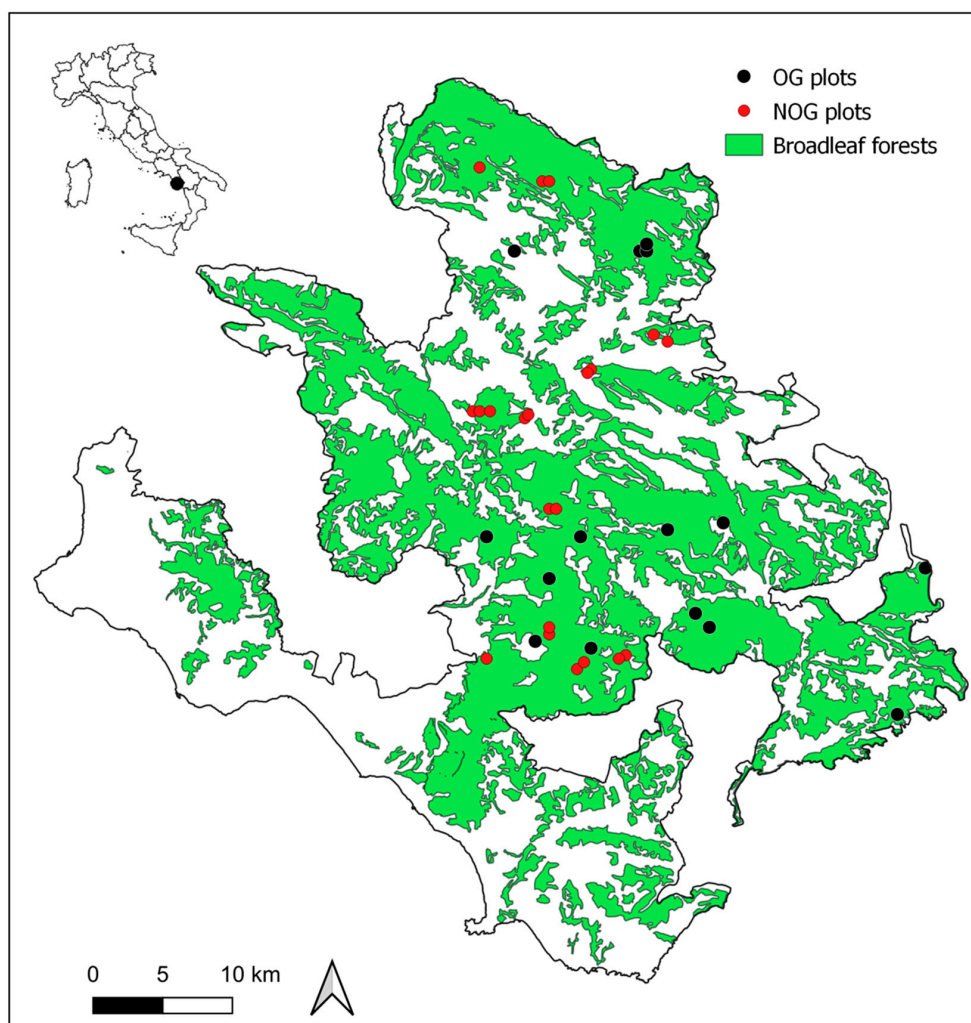


Figure 2. Study area: Cilento National Park (South Italy), with 36 sampling plots.

2.3. Lichen Sampling

To assess epiphytic lichen diversity, on the three trees with a DBH >16 cm and bole inclination <30° closest to the center of each plot, the abundance of each lichen species was recorded on the bole, from 0 to 2 m. According to Tallent-Halsell [29], an abundance score was assigned to each species in relation to its frequency on the recording area: (1) rare = 1–3 thalli in the area; (2) uncommon = 4–10 thalli in the area; (3) common = >10 thalli in area but less than 50% of the considered substrate; and (4) abundant = more than 50% of the considered substrate. In total, 106 trees were sampled.

Nomenclature and author's abbreviations follow Species Fungorum (www.speciesfungorum.org). Dominant reproductive strategy (sexual vs. vegetative) and status follow Nimis [30]. In particular, (1) the rarity of each taxon was obtained using commonness-rarity values calculated for two phytoclimatic units: montane and humid sub-Mediterranean Italy, and (2) threat assessment was performed according to Nascimbene et al. [31].

2.4. Reproductive Strategies in Lichens

Lichens are able to reproduce both sexually and asexually. Sexual reproduction is carried out through sexual spores of the mycobiont reproducing the fungus alone. Vegetative reproduction is carried out through various types of propagules (e.g., conidia, thallus fragments, schizidia, lobules, isidia, soredia). Among them, (1) soredia are more or less granular aggregations of hyphal and algal cells ranging from 20 to 100 µm in diameter or more, and (2) isidia are small thallus outgrowths with varied morphology (e.g.,

cylindrical, clavate, coralloid) containing both symbionts [6,7]. In this work, we define “sexual species” as those species that reproduce mainly sexually through ascospores and “vegetative species” as those that reproduce mainly through vegetative diaspores. Among these latter, we only considered the most representative ones, namely soredia and isidia, while we did not take into account other less frequent types of propagules, such as conidia, thallus fragments, schizidia, and lobules.

2.5. Data Analysis

The Wilcoxon signed-rank non-parametric test has been used for pairwise comparisons among the two types of forest management, OG and NOG.

The beta diversity between site pairs was calculated based on the abundance matrices of the lichen species in the sites following the framework proposed by Baselga [32]. This approach is based on the use of Bray–Curtis dissimilarity and breaks down beta diversity into two components: (1) balanced variation in abundance, accounting for the individuals of some species in one site that are substituted by the same number of individuals of different species in another site (hereafter “turnover”); and (2) abundance gradients, whereby some individuals are lost from one site to the other (hereafter “nestedness”).

To compare the diversity components observed in the different conditions investigated, the beta diversity was calculated for different subsets concerning the type of forest management of the sites (OG vs. NOG), the reproductive strategy (sexual vs. vegetative), and the status of national rarity (common vs. rare) of the species.

Calculations of beta diversity were performed using the *vegan* [33], *ecodist* [34] and *betapart* [35] packages in R environment [36].

3. Results

3.1. The Lichen Biota in the Study Area

In total, 148 lichen species were found in the 106 sampled trees (see Table S2): 89 species with sexual reproduction (60%) and 59 with vegetative reproduction (40%). Of the latter, 43 were sorediate and 16 were isidiate species. Most of the species (106 out of 148) were present in under 20% of the plots, with 34 species (23%) distributed in only one plot, while 16 lichens were present in more than 50% of the plots. Most of the lichens were nationally rare (92 species, 62%; 47 rare and 45 very rare), while common lichens represented 38% of the species pool (56 species; 42 common and 14 very common). Fifteen percent (22 species) of the floristic list was represented by lichens included in the Italian Red List: one Endangered species (*Alyxoria ochrocheila*), 4 Vulnerable species (*Agonimia allobata*, *Solitaria chrysophthalma*, *Sticta limbata*, *Vahliella saubinetii*), 11 Near-Threatened species (*Arthopyrenia salicis*, *Buellia disciformis*, *Caloplaca herbidella*, *Diarthonis spadicea*, *Lobarina scrobiculata*, *Nephroma resupinatum*, *Pachyphiale carneola*, *Pectenium plumbeum*, *Ricasolia amplissima*—chloromorph, *Ricasolia amplissima*—cyanomorph, *Schismatomma ricasolii*), 4 Least Concern species (*Gyalecta liguriensis*, *Lobaria pulmonaria*, *Parmeliella testacea*, *Ramalina subgeniculata*), and two Data-Deficient species (*Leptra slesvicensis*, *Ochrolechia dalmatica*)

3.2. Comparison between OG and NOG Forest Stands

With the exception of the species occurring in only one plot, OG and NOG stands shared most of the common species detected in the study area (83% of the vegetative species and 83% of the sexual ones) and also a significant part of the rare species (58% and 71%, respectively). Further, rare species (both vegetative and sexual) were more exclusive than common ones, above all in NOG stands where they represented more than 20% of the species (Figure 3).

In terms of both alpha and gamma diversity, OG and NOG forest sites did not show statistically significant differences for any combination of groups of species considered (rare vs. common, vegetative vs. sexual) (Table 2, Wilcoxon test, $p > 0.05$).

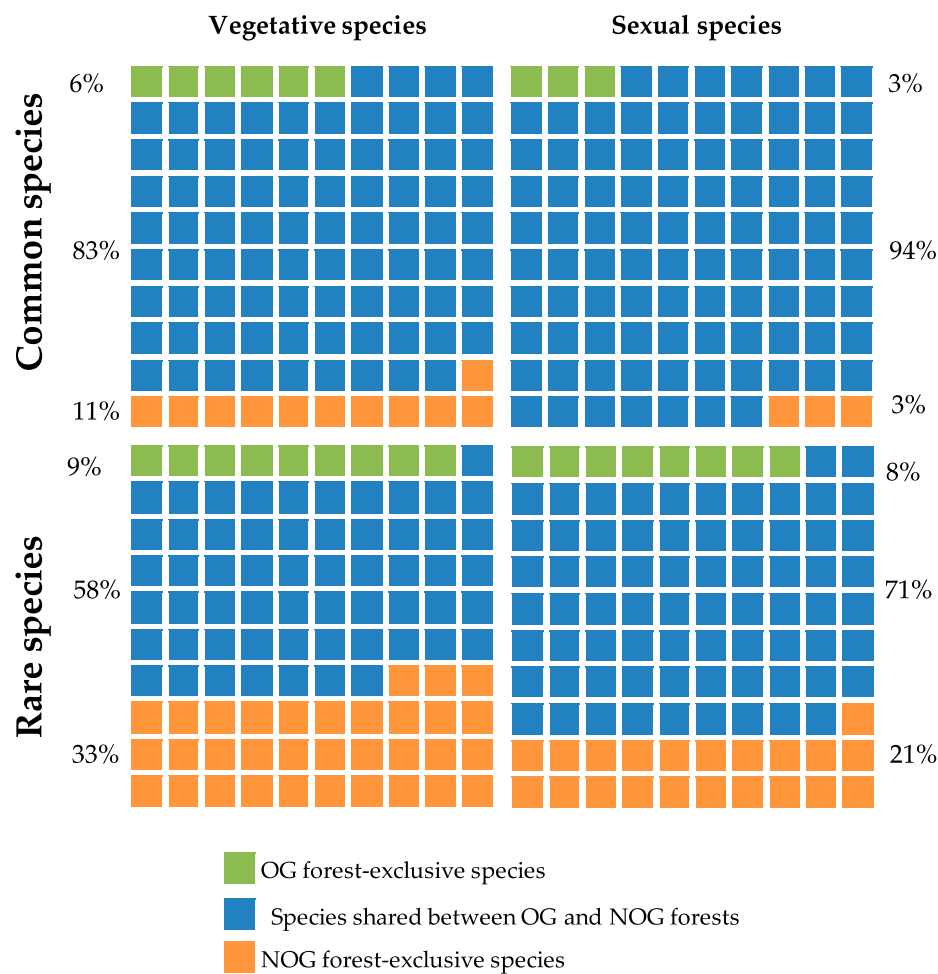


Figure 3. Schematic representation of shared and exclusive species in the OG and NOG forests of the study area (dataset without the species occurring only in a single plot, 34 species). The definition of “common” or “rare” species follows their commonness–rarity values in montane and humid sub-Mediterranean Italy (Nimis 2016).

Table 2. Descriptive statistics of lichen species richness: alpha diversity (average number of species on each tree within a plot) and gamma diversity (average overall number of species within a plot). Results of the Wilcoxon test performed for the two groups of plots are also reported. n.s.: not significant ($p > 0.05$).

Alpha Diversity	OG ($n:15$)		NOG ($n:21$)		Wilcoxon Test ($df:1$; $n:36$)
	Median	Min–Max	Median	Min–Max	
<i>Common species</i>					
Sexual species	5	1–11.7	6.3	3.3–9.3	$W = 116$, n.s.
Vegetative species	6	0–9.7	5.7	3–10.3	$W = 129$, n.s.
<i>Rare species</i>					
Sexual species	5	2.7–8.7	4	1–7	$W = 215.5$, n.s.
Vegetative species	2	0–6	2	0–6.7	$W = 150$, n.s.
Gamma Diversity					
<i>Common species</i>					
Sexual species	7	0–14	9	3–15	$W = 126$, n.s.
Vegetative species	8	2–18	10	4–15	$W = 120$, n.s.
<i>Rare species</i>					
Sexual species	3	0–10	3	0–14	$W = 155.5$, n.s.
Vegetative species	8	3–14	7	1–11	$W = 199$, n.s.

3.3. Beta Diversity within OG and NOG Forest Stands

In all cases considered the turnover of specific abundance was the main component of beta diversity (Table 3). On the other hand, the values of nestedness of specific abundance between two sites always had lower values. In particular, the turnover values were greater for rare species (from 0.805 to 0.879) than for common ones (from 0.594 to 0.842). In general terms, the turnover in sexually reproducing species was always greater than that in vegetatively propagating species. In addition, turnover was greater in NOG than in OG forests. However, considering rare species, regardless of the type of forest stands (OG and NOG), the differences in beta diversity between sexually reproducing vs. vegetative species were smaller than those observed for common species. On the contrary, as far as common species are concerned, the differences in turnover were extremely relevant, both between species with different reproductive strategies and between different types of forest. In particular, the vegetative species had the least turnover (0.594) and greater nestedness (0.232) in OG forests than all other possible combinations of factors.

Table 3. Components of beta diversity in OG and NOG forests of the study area. The results are presented and are disaggregated according to the reproductive strategy and the level of national rarity of the species.

Beta Diversity	OG (n:15)			NOG (n:21)		
	Total	Turnover	Nestedness	Total	Turnover	Nestedness
<i>Common species</i>						
Sexual species	0.877	0.783	0.093	0.886	0.842	0.045
Vegetative species	0.826	0.594	0.232	0.866	0.769	0.098
<i>Rare species</i>						
Sexual species	0.902	0.879	0.023	0.918	0.872	0.045
Vegetative species	0.920	0.805	0.115	0.933	0.846	0.087

4. Discussion

In this work, we investigated the relationship between the reproductive strategy of epiphytic lichen species and their beta-diversity patterns found in OG vs. NOG forests. The acquired results only partially support the hypotheses formulated in the study but provide new insights into the interpretation of the ecology of lichen species in Mediterranean forest ecosystems.

4.1. Sexually Reproducing Lichen Species Had Always High Turnover

The beta diversity analysis confirms the assumption that sexually reproducing species had a high turnover in the forests of the study area, regardless of the type of forest structure, both between old-growth and between non-old growth forests (hypotheses schematized in Figure 1b,d). Our outcomes are consistent with those found by various authors (see [37] for a review), and we can trace back the reasons behind this scenario to several factors:

- (1) The spores are lighter than vegetative diaspores and are potentially able to travel longer distances, reaching more remote sites [38,39].
- (2) Sexually reproducing species could have more problems in the early stages of development and establishment of new thalli because they have to find a photobiont partner [37,40,41].
- (3) Consequently, these species would have less of a tendency to form clusters with homogeneous communities than vegetative species.

4.2. Vegetative Species Tend to Form Nested Communities Especially in OG Forests

Our hypothesis that the vegetative species were distributed in the two types of forest stands (OG and NOG) mainly according to nestedness patterns between sites was only partially supported by the results obtained. Indeed, turnover was always mostly the main component of beta diversity for this group of species. However, in partial support of the

hypothesis depicted in Figure 1a,c, higher nestedness values were recorded for vegetative species than for sexual ones, with particular regard to those found among OG forest sites. The spatial continuity of suitable habitats is undoubtedly the factor that determines these results (Figure 1a), and justifies the (admittedly small) differences with the observed situation between NOG sites (Figure 1c). In addition, our old-growth forest sites are characterized by a high number of old and uneven trees (Table 1) that may represent suitable intermediate substrates (micro-refugia) for the low-range dispersal diaspores [42]. This structural complexity may contribute to this trend of vegetative species. However, the prevalence of turnover between sites suggests that, even in ideal habitat conditions and substrate availability, a limited distance of dispersion strongly conditioned the colonization capacity of vegetative species, as suggested by many authors (see e.g., [19,40,43]). This driver leads to the formation of gaps in the distribution of species within the forest habitat and, consequently, to a high compositional turnover. Although we can imagine considerable differences in the dynamics, range, and success of the establishment depending on the level of rarity, apparently these propagation characteristics limit the distribution not only of rare taxa but also of even highly competitive common species.

4.3. The Rarity Level Determines the Species Turnover in Lichen Communities

We found support for explaining the differences in beta diversity observed as a function of the rarity level of the species. Although the overall beta diversity values were comparable to those observed for common species, the contribution of turnover for rare species in our study area was considerably higher than that observed for common species. The turnover was independent of the forest stand (OG and NOG) and the reproductive strategy of the species. This could be partly affected by the characteristic structure of the species community datasets, where, in the face of a set of highly represented species, there are numerous species with few occurrences, potentially improving turnover values. Nevertheless, we can find possible explanations both in the environmental drivers that shape the distribution of the species and in the autoecological characteristics of the species themselves. With regard to the first aspect, numerous examples in the literature show how the ecological niche of rare species, defined by the interaction of environmental factors, is much more restricted than that of common species [44–47]. The drivers involved in defining the niche of rare species could differ from those decisive for common species. For example, by analyzing the beta diversity patterns of the Lobarion communities, Nascimbene et al. [31] noted that the forest structure variables that influence the distribution of species of conservation interest do not entirely coincide with those that explained communities of common species. For example, the average distance between trees and the age of the stands affected the turnover of rare species much more than that of common ones.

On the other hand, the inadequate dispersal capacity and the low establishment success determined the reduced spatial distribution of rare lichen species (both vegetative and sexual). For example, the effective dispersal range of the large vegetative propagules of *Lobaria pulmonaria* was typically 10 m and rarely reached further than 100 m ([41] and various others). Similarly, Giordani et al. [48] found that sexual reproducing *Seiropora villosa* occupied only a small portion of its colonizable niche because of the minimal propagation ability of its spores.

4.4. The Differences between OG and NOG Are Less Evident than One Might Think

Another aspect that emerges from our results and is worth considering is that concerning the actual differences found between OG and NOG in terms of diversity and composition.

In the case of our study area, OG and NOG shared a high number of species and had no significant differences in terms of both alpha and gamma diversity. Furthermore, contrary to what one might expect, NOG forests were home to the largest number of exclusive species, particularly with regard to rare species. Net of other differences that still exist, it is evident that from a conservation perspective, NOGs play a significant role which cannot

be underestimated. This situation may be for at least two reasons. Firstly, *Castanea sativa* trees represent a substrate that in our dataset is exclusive for NOG stands (chestnut woods and also some individuals in mixed stands). It is well-known that chestnut woods are suitable habitats for mature lichen communities in the Mediterranean area [24,25]. Secondly, sustainable management of NOG forests in the study area may have been subjected, in a more or less conscious way, to management techniques compatible with the maintenance of structured lichen communities [31]. Among others, these techniques include the integration of old trees in commercial stands [49,50], the reduction of the distance between regeneration units and sources of propagules [51], or the prolongation of the rotation cycle [52].

Although there is much evidence showing that epiphytic communities in OG forests are different from those in NOG forests [24], our results highlight some common aspects between the two types of forests. These features should be taken into consideration with greater attention both from a scientific interpretation point of view and from an applicative perspective [31]. This vision is in agreement with [53] who focused on the need to use multiple community-based approaches to interpret the effects of forest management and on the opportunity of an integrated investigation of the dynamics of colonization that persist along gradients of forest use. For example, Brunialti et al. [54] pointed out that many of the methods developed in the past (e.g., [55]) were mainly designed for high forests rather than coppice forests, even though today this management system covers more than 10% of the total European forests.

5. Conclusions

The main highlights of our study can be summarized as follows:

- Sexually reproducing lichen species always had high turnover. This confirms our starting hypothesis based on the long-range dispersal ability of this strategy.
- Vegetative species tend to form nested communities, especially in OG forests. Spatial continuity and structural complexity of our old-growth stands could be the main driver for this result.
- The rarity level determines the species turnover in lichen communities.
- The differences between OG and NOG are less evident than one might think. It is evident that non-old growth stands, when managed with a sustainable approach, can play a significant role in the conservation of well-structured lichen assemblages.

Although our findings only partially support the hypotheses formulated in the study, we believe that they may provide new insights into the interpretation of the ecology of lichen species in Mediterranean forest ecosystems.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1999-4907/12/1/27/s1>, Table S1: Distribution of the sampled tree species in old-growth (OG) and Non old-growth (NO) stands. Table S2: List of the 148 lichen species found on the 106 sampled trees, with their occurrence (number and percentage of plots).

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