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Pine Cones in Plantations as Refuge and Substrate of Lichens and Bryophytes in the Tropical Andes

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Abstract

Deforestation driven by plantations, such as *Pinus patula* Schiede ex Schltdl. et Cham., is a major cause of biodiversity and functional loss in tropical ecosystems. We assessed the diversity and composition of lichens and bryophytes in four size categories of pine cones, small (3–5 cm), medium (5.1–8 cm), large (8.1–10 cm), and very large (10.1–13 cm), with a total of 150 pine cones examined, where the occurrence and cover of lichen and bryophyte species were recorded. Identification keys based on morpho-anatomical features were used to identify lichens and bryophytes. In addition, for lichens, secondary metabolites were tested using spot reactions with potassium hydroxide, commercial bleach, and Lugol's solution, and by examining the specimens under ultraviolet light. To evaluate the effect of pine cone size on species richness, the Kruskal–Wallis test was conducted, and species composition among cones sizes was compared using multivariate analysis. A total of 48 taxa were recorded on cones, including 41 lichens and 7 bryophytes. A total of 39 species were found on very large cones, 37 species on large cones, 35 species on medium cones, and 24 species on small cones. This is comparable to the diversity found in epiphytic communities of pine plantations. Species composition was influenced by pine cone size, differing from small in comparison with very large ones. The PERMANOVA analyses revealed that lichen and bryophyte composition varied significantly among the pine cone categories, explaining 21% of the variance. Very large cones with specific characteristics harbored different communities than those on small pine cones. The presence of lichen and bryophyte species on the pine cones from managed Ecuadorian *P. patula* plantations may serve as refugia for the conservation of biodiversity. Pine cones and their scales (which range from 102 to 210 per cone) may facilitate colonization of new areas by dispersal agents such as birds and rodents. The scales often harbor lichen and bryophyte propagules as well as intact thalli, which can be effectively dispersed, when the cones are moved. The prolonged presence of pine cones in the environment further enhances their role as possible dispersal substrates over extended periods. To our knowledge, this is the first study worldwide to examine pine cones as substrates for lichens and bryophytes, providing novel insights into their potential role as microhabitats within *P. patula* plantations and forest landscapes across both temperate and tropical zones.

Keywords: bryophytes; lichens; pine cone; pine plantations; pine scales; richness

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1. Introduction

Human-induced disturbances, such as deforestation and land-use change, i.e., the conversion of native forests to pasture [1,2] and plantations [3,4], are causing the rapid loss of tropical forests and their ecosystem services. Tree plantations in Ecuador mostly consist of monocultures of fast-growth exotic species to be harvested for commercial purposes [5,6]. In the Andean Region, exotic species such as pine and eucalyptus are commonly used [7,8]. These plantations have been shown to reduce environmental quality and biodiversity [9–11].

Similarly, several studies have pointed out that the conversion of natural forests to plantations has negative effects on the diversity of lichens and bryophytes [12,13]. In pine plantations, these studies have been carried out mainly in temperate, rarely tropical, forests [14–16], with a special emphasis on comparing natural forests and plantations, where lichens have generally been studied more often than bryophytes [17–21]. In pine plantations, the factors of the host tree studied include tree diameter and age of the tree and how species diversity is influenced by these traits [21,22].

Pine cones are very abundant both in natural forests and pine plantations [23–25]. They are one of the most important non-wood forest products that can be obtained from these ecosystems [26,27]. Pine cones play a crucial role in forest ecosystems and plantations, functioning as persistent seed banks that modulate regeneration dynamics and serving as microhabitats and food resources for various organisms [28,29]. Pine cones can be used commercially as an energy resource [30,31], in medicine [32], and in industrial manufacturing [33], but ecologically they also play important roles: their seeds are an important food source for animals (birds, rodents, and insects), which disperse the cones and thus their seeds [29,34,35]. Pine cones generally help protect seeds [36], although insects (e.g., moths and beetles) can cause considerable damage when they consume young seeds and the cone material itself [37,38].

Various compounds have been extracted from pine cones, such as the polysaccharides cellulose and lignin, as well as essential oils [39–42]. Pine cones with winged seeds are often woody and hard, because the tissue of the cone scale is typically lignified [29], which contributes to the long-term persistence of the cones. Thus, the decomposition rates of pine cones are lower than needle litter. Pine cones typically decompose at approximately the same rates as those of wood stems with diameters between 9 and 10 cm [43].

Most studies have analyzed the relationship between pine cone scales and seeds' dispersal, where the scales move in response to changes in relative humidity [36,44–46]. Other studies have focused on colonization processes by fungi [47,48]. Research on epiphytic lichens and bryophytes in tropical regions is generally scarce, with only three studies conducted to date in *P. patula* plantations, none of them on pine cones. For instance, in Ecuador, studies have explored the effects of forest disturbance, including *P. patula* plantations, on the diversity of epiphytic bryophytes and lichens [22]. In Colombia, research has focused on lichen preferences for *P. patula* and *Quercus humboldtii* trees [49]. For Brazil, the authors compared lichen communities in native forests with planted trees, including plantations of *Pinus* [50]. As a consequence, our knowledge on the cryptogam diversity in pine plantations is still insufficient. As far as we know, this is the first study where epiphytes (lichens and bryophytes) have been studied on pine cones in the tropics. Plantations of pine trees are widely distributed in Ecuador [8], the focal area of our research. Considering the paucity of information, we examined (1) how cone size influences richness and diversity and (2) if pine cone size may predict variations in species composition.

2. Materials and Methods

2.1. Study Area

This study was carried out in the city of Loja, located in southern Ecuador, where pine plantations (*P. patula*) were selected inside a radius of 20 km from the provincial capital.

These plantations are approximately 35–40 years old and subject to logging for commercial timber production (Figure 1).

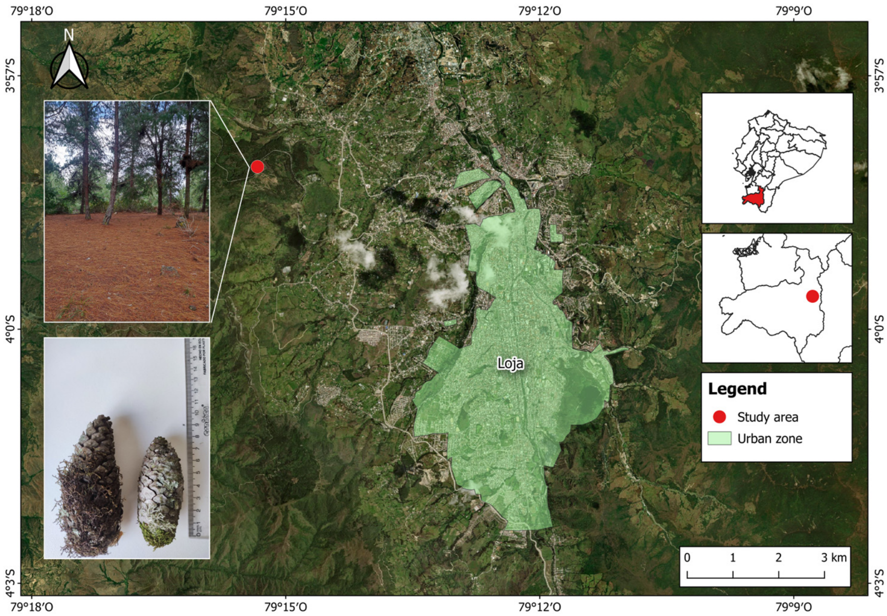


Figure 1. Study area in the city of Loja of southern Ecuador showing the location of *P. patula* plantations.

2.2. Sampling Design and Data Collecting

In the study area, a total of 150 pine cones were randomly collected from the plantation floor during April 2025. In the laboratory, the cones were sorted into four size categories, measured with a ruler, with each category ± 2–3 cm different in size to the next: small (3–5 cm), medium (5.1–8 cm), large (8.1–10 cm), and very large (10.1–13 cm) (Figure 2). Microscopic analyses were conducted within one month after cone collection to minimize the degradation of bryophyte and lichen structures and ensure the accuracy of the morphological and anatomical identification.

(**A**) (**B**) (**C**)

Figure 2. Sampling and collected pine cones by Kristhel Ángeles Benítez-Arévalo (**A**); pine cones divided into four size categories (**B**); several samples of pine cones with lichens and bryophytes (**C**).

Lichen and bryophyte presence and cover (Figure 2) were recorded using a Zeiss Stemi DV4 stereoscope (Carl Zeiss, Göttingen, Germany). Lichens and bryophytes were identified with a ZEISS Axiocam 212 camera (Carl Zeiss, Oberkochen, Germany) microscope and a Zeiss Stemi DV4 stereoscope, using the available keys for bryophytes [51–53] and lichens [54–57]. Specific keys were used for the identification of several tropical lichen species [58–64]. Secondary compounds were inferred by spot testing, using reactions with potassium hydroxide (K), commercial bleach (C), and Lugol's solution (I), as well as observing specimens under ultraviolet (UV) light. Specimens are deposited at the herbarium HUTPL. For bryophyte nomenclature, we mainly followed *The Liverworts and Hornworts of Colombia and Ecuador* [53] and the World Checklist of Hornworts and Liverworts [65]. For lichen nomenclature, we followed the checklist of lichen-forming, lichenicolous, and allied fungi of Ecuador [66].

2.3. Data Analysis

The effects of pine cone size on species richness and diversity (as expressed by the Shannon–Weaver and Simpson indices) were analyzed using the Kruskal–Wallis test. The Shapiro–Wilk test was used to assess the normality of the data distribution. The Shapiro–Wilk test indicated that the response variables were not normally distributed ($p < 0.05$). Species composition data for the four pine cone size categories were subjected to principal component analysis (PCA) to determine the relationships among the cryptogams and pine cone size. For the PCA, a correlation plot was made using the "corrplot ()" function from the "corrplot" package [67]. We performed a permutational multivariate analysis of variance (PERMANOVA) to detect the effects of pine cone size on the composition of lichen and bryophyte species. For these analyses, the Bray–Curtis distance and 1000 permutations were used to analyze our data [68]. Violin plots and PCA were generated using the "ggplot2" package (R version 3.2.2) [69] and PERMANOVA with the "vegan" statistical package [70]. All analyses were calculated utilizing the statistical software R 3.2.2 [71].

3. Results and Discussion

A total of 48 taxa were recorded on pine cones, including 41 lichens and 7 bryophytes (Table A1, Figure A1), with a predominance of crustose lichens (23 species), followed by foliose (13) and fruticose (5) ones. The richness of the lichen species was similar to that found by Calviño-Cancela et al. [17], who reported 40 species of epiphytic lichens in *P. patula* plantations, and higher than the 31 species reported by Käffer et al. [50] from *Pinus* spp. Therefore, the species found in our study on pine cones of *P. patula* are similar to the species richness of epiphytic lichens on bark reported from forests and plantations of various pine tree species. For example, Calviño-Cancela et al. [21] reported 42 species on the bark of *P. pinaster*, Wagner et al. [18] reported 43 lichen species from *P. resinosa*, Sevgi et al. [20] reported 33 species on *P. nigra*, and Bäcklund et al. [19] reported 31 species for *P. contorta* and 37 species for *P. sylvestris*. In this context, pine cones of *P. patula* can be considered a refuge rivaling the richness of epiphytic lichens on bark. Conversely, the overall low species richness of bryophytes (only 7 liverwort species found) is comparable to the equally low numbers of bryophytes (13–16 species) typically found in these forests growing on the bark of *P. sylvestris* [72,73].

The violin plots indicated that species richness and diversity did not vary significantly across the four pine cone size categories (Figure 3). This pattern was confirmed by the Kruskal–Wallis test, where species richness (KW = 1.228, p-value = 0.746), the Shannon–Weaver index (KW = 2.941, p-value = 0.400), and Simpson index (KW = 14.61, p-value = 0.061) of the species were not significantly affected by cone size. Although *P. patula* plantations support a high diversity of lichens, their open canopy structure and leaf form (needles) favor better light availability [22,50,74]. As a result, lichens are generally more common in these plantations; they are better adapted to tolerate drier conditions and higher UV radiation compared to bryophytes, which overall need higher humidity and more shaded conditions.

The large and very large pine cones have a larger area available for colonization and species assemblage of lichens and bryophytes compared to smaller pine cones. This pattern reflects a positive response between tree diameter on lichen and bryophyte diversity and species composition, with a significant increase in species diversity towards large trees [75–80]. The larger cones thus provide more surface area for species establishment. In this context, the numbers of pine cone production reported by Brockway [81] and Paterson [82] are relevant: 10–53 cones per tree are typically reported, which represents a significant surface area available for the presence of lichens and bryophytes. However, it also suggests that large and very large cones reflect a more advanced age of the cone. This means that pioneering lichens (e.g., small crustose taxa) could have been replaced by late-successional taxa (e.g., foliose and fruticose lichens), or they could coexist with the latter. Thus, the age of the cone is a key factor that will be considered in future research on lichen and bryophyte community dynamics.

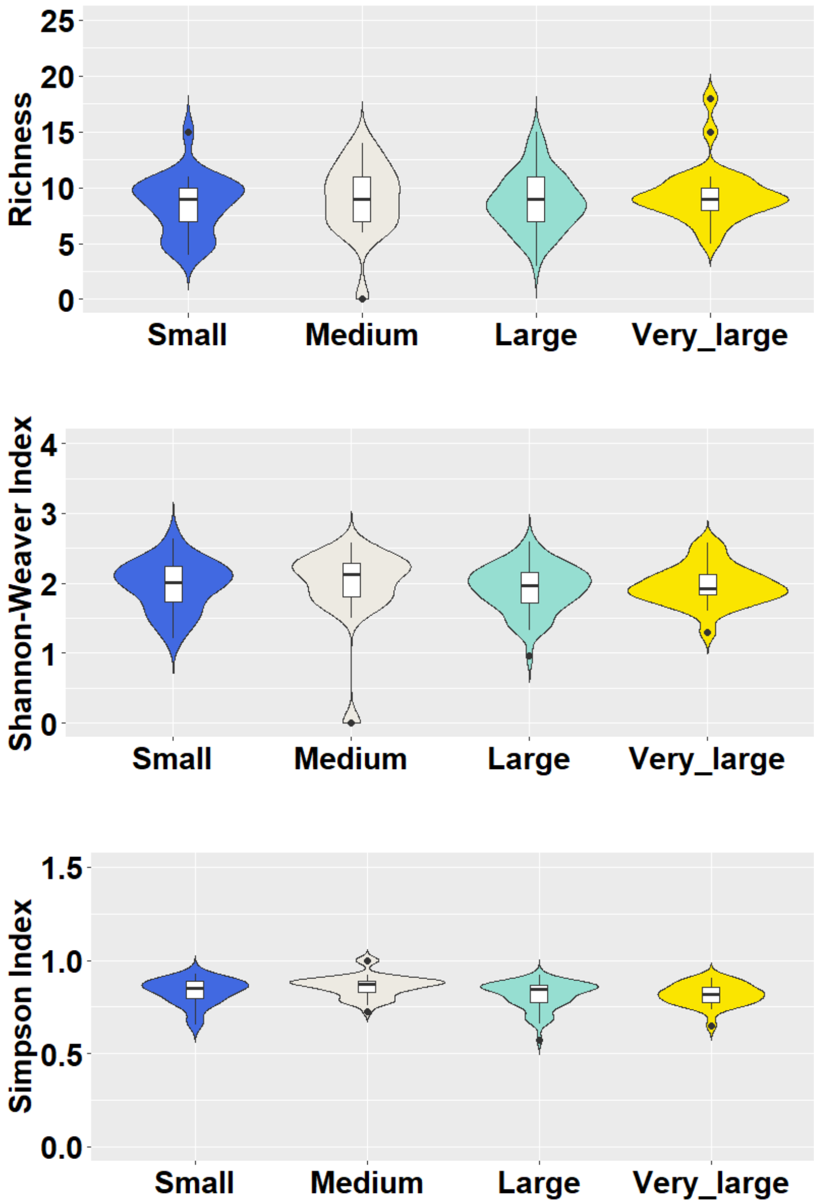


Figure 3. Violin plot for species richness and diversity indices (Shannon–Weaver and Simpson) of lichens and bryophytes related to pine cone size in *P. patula* plantations. Boxes span the first to third quartiles; the horizontal line inside the boxes represents the median.

The PCA showed species grouping according to pine cone size (Figure 4), where PCA 1 explains most of the variability in the species composition (6.9%) and PCA 2 explains less than 6%. Confirming these patterns, multivariate statistical analyses showed that lichen and bryophyte composition was structured according to the different pine cone categories with 21% explained variance (F = 12.917, *p*-value = 0.001, r^2 = 0.21).

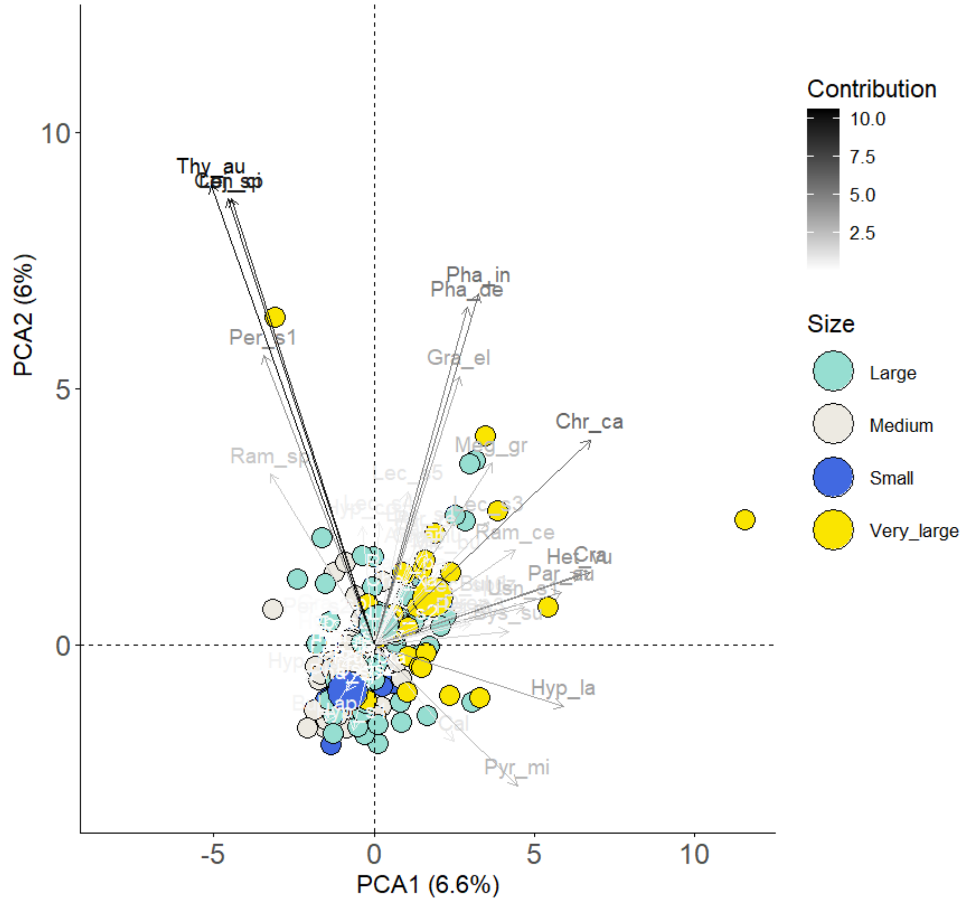
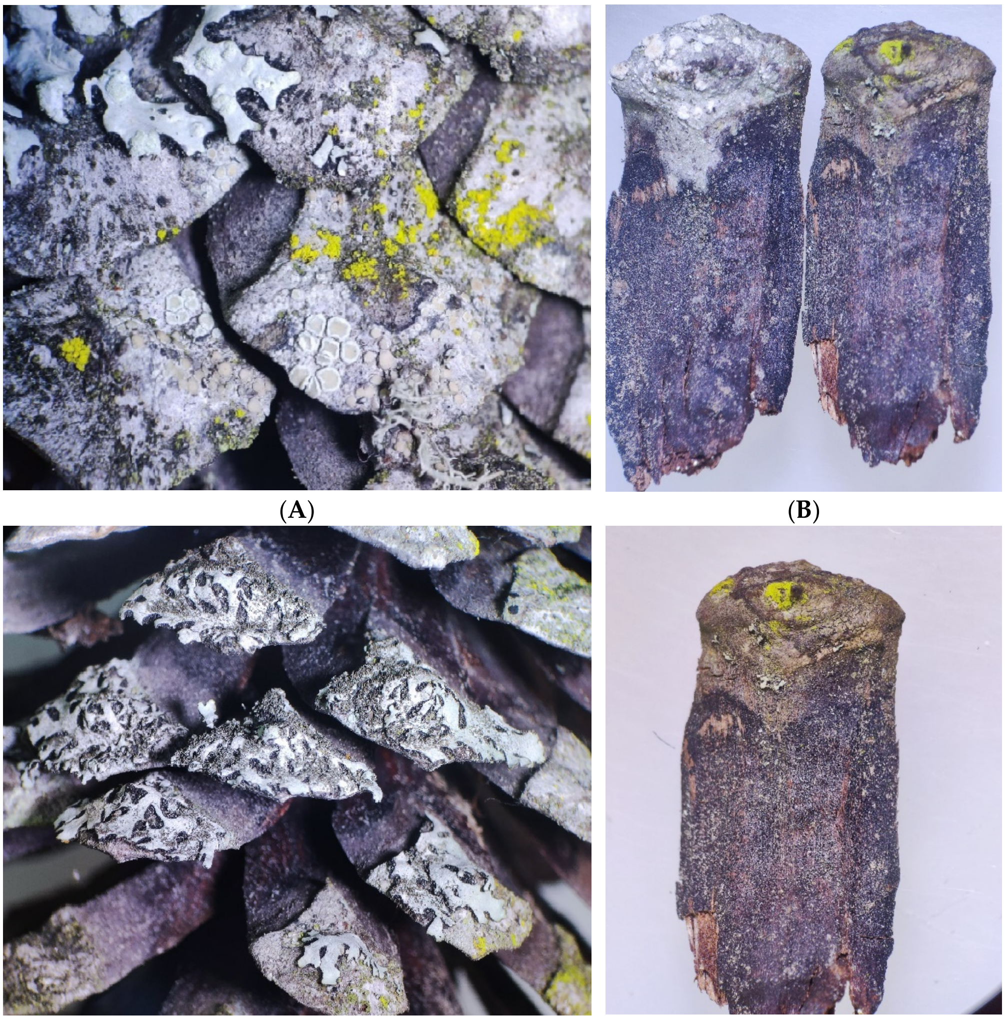


Figure 4. Principal component analysis biplot ordination of the species associated with pine cone size categories in *P. patula* plantations.

Apart from substantially contributing to the available surface area for establishing communities on pine cones, these cones potentially also contribute to the dispersal of lichens and bryophytes to other areas. Different sized cones generally also differ in the number of scales (on average, 102 scales in small, 125 scales in medium, 140 scales in large, and 210 scales in very large cones). Each pine cone scale typically contains several propagules and/or whole or parts of lichens and/or bryophytes thalli (Figure 5). Previous studies have documented seed dispersal when pine cones or their parts (scales) are moved by birds and rodents [29]. It can be assumed that these processes also aid in the indirect dispersal of lichens and bryophytes and their propagules when the cones or scales are moved. Some studies have documented that pine cones have a relatively long lifespan; in dry conditions in particular, the scale usually becomes detached [36], so these then potentially serve to facilitate the dispersal of lichens and bryophytes as "meta-propagules", i.e., entire scales or even whole cones with their lichens and bryophytes attached are distributed to other areas, both other forests and plantations.

This research provides new and important insights into substrates ignored by previous studies, namely pine cones. Unlike previous studies, we document that pine cones might be equally as important as the substrate typically studied, potentially also additionally acting as meta-dispersal agents in native forests and *P. patula* plantations of the tropics [17,39]. Kasai et al. [43] showed that the decomposition rates of pine cones were lower than that of needle litter and the same level as trees stems and branches 9–10 cm in diameter. The pine cones of *Picea abies* (L.) H. Karst., a species that produces cones analogous to those of other pine species, exhibited a 60% reduction in dry mass while maintaining morphological integrity still after 13 years [83]. This long time period that pine cone decomposition takes place over is related to lignin and cellulose presence in the cone [39–42], both polysaccharides that take time to decompose. According to Cha and Um [84], pine cones exhibit a relatively elevated lignin content (35.80%) when compared with other lignocellulosic sources.



(**A**) (**B**) (**C**) (**D**)

Figure 5. Pine cones showed several scales with the presence of lichens (**A**,**B**); pine cones showed seven scales with the presence of foliose lichens *Bulbothrix apophysata* (**C**,**D**).

To better understand if this means that lichens on these cones also manage to persist after the cones have fallen off the tree, more extensive studies are necessary, but our preliminary research suggests that at least on most cones of different ages that we collected, both lichens and bryophytes were still present as healthy thalli.

Here, we documented several lichen species, such as *Bulbothrix*, *Chrysotrix*, *Graphis*, *Parmotrema*, *Leucodermia*, *Hypotrachyna*, *Lecanora*, *Phaeographis*, *Ramalina*, and *Usnea*, and bryophytes such as *Frullania* and *Cheilolejeunea*, that are widely reported as epiphytes on bark. Fernandez-Prado et al. [22], Simijaca et al. [49], and Käffe et al. [50] reported *Chrysothrix candelaris*, *Hypotrachyna costaricensis*, *Hypotrachyna horrescens*, *Hypotrachyna laevigata*, *Leucodermia leucomelos*, *Parmotrema austrosinense*, *Parmotrema cristiferum*, *Phaeographis inconspicua*, and *Parmotrema reticulatum* from pine plantations in tropical regions. These are all species that we have also reported in our study to grow on cones. Lichen and bryophyte communities on cones are largely dominated by photophilous taxa (e.g., *Parmotrema*, *Hypotrachyna*, *Graphis*, *Phaeographis*, *Frullania*), which produce secondary metabolites that may enhance their tolerance to the characteristic of plantations of there being lots of light available in their environments. A similar trend has been documented on tree bark in tropical *P. patula* plantations, where drought-tolerant species prevail, in contrast to the dominance of moisture-sensitive taxa in native *Quercus* forests in Colombia [49], *Araucaria* forests in Brazil [50], and secondary montane forests in Ecuador [22]. However, the occurrence of *Byssoloma subdiscordans*, a species typically restricted to humid, shaded environments, indicates that certain microhabitats within the plantations may still maintain environmental conditions for the presence of sensitive lichen species [49].

We recommend the performance of further research to evaluate lichen and bryophyte development in pine cones across different successional stages of *P. patula* plantations. Studying not only the age of the cone since it has fallen from the tree but also if the difference in cone size is related to the age of the tree and potentially the age of the plantation will help us to understand not only successional processes' impact on species diversity and composition but possibly the role that the cones play as meta-propagules, aiding in the dispersal of lichens and bryophytes, and thus potentially the recovery of natural forests. Species growing on pine cones thus have an underexplored potential to contribute to restoration in southern Ecuador, an aspect not previously anticipated and, until now, not investigated.

4. Conclusions

Our results indicate that pine cones in Andean *P. patula* plantations support a high diversity of cryptogams, which can be compared in species richness with lichens and bryophytes growing as epiphytes on bark. Very large pine cones harbored different communities than those on small cones; the large surface area is apparently more suitable for substrates and also potentially indirectly contributes to the dispersal of lichens and bryophytes when the cones are moved by birds and rodents. The presence of lichen and bryophyte species on the pine cones of managed Ecuadorian *P. patula* plantations thus may serve as refugia for the conservation of biodiversity. Our results suggest that leaving the cones in place will contribute to the conservation of these organisms in pine plantations. Pine cones should not be commercially harvested since they may function as meta-dispersal units, persisting for long periods, composed of numerous scales (102–210). These cones serve a much underappreciated role in these semi-natural to artificial environments, potentially playing a significant role in the recovery of natural environments.

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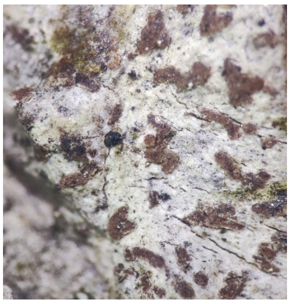
Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

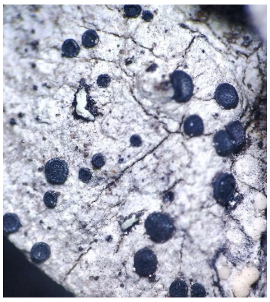
Table A1. Species of bryophytes and lichens occurring on pine cones.

Family	Species	Small	Medium	Large	Very Large	Total	Growth Form
Lichens							
Arthoniaceae	*Arthonia* sp.	0	2	2	2	6	Crustose
Arthoniaceae	*Coniocarpon cinnabarinum* DC.	0	0	1	0	1	Crustose
Caliciaceae	*Cratiria* sp.	13	28	25	17	83	Crustose
Chrysotrichaceae	*Chrysothrix candelaris* (L.) J. R. Laundon	21	42	53	25	141	Crustose
Graphidaceae	*Allographa nuda* (H. Magn.) Lücking & Kalb	6	23	22	11	62	Crustose
Graphidaceae	*Graphis elegans* (Borrer ex Sm.) Ach.	11	28	27	12	78	Crustose
Graphidaceae	*Graphis* sp.	0	6	2	0	8	Crustose
Graphidaceae	*Phaeographis dendritica* (Ach.) Müll.Arg	14	26	28	18	86	Crustose
Graphidaceae	*Phaeographis inconspicua* (Fée) Müll.Arg	13	28	33	18	92	Crustose
Graphidaceae	*Phaeographis* sp.	0	1	0	0	1	Crustose
Lecanoraceae	*Lecanora* sp1	0	1	3	1	5	Crustose
Lecanoraceae	*Lecanora* sp2	0	0	2	0	2	Crustose
Lecanoraceae	*Lecanora* sp3	14	31	31	19	95	Crustose
Lecanoraceae	*Lecanora* sp4	0	8	5	1	14	Crustose
Lecanoraceae	*Lecanora* sp5	9	24	20	9	62	Crustose
Lecanoraceae	*Lecanora* sp6	7	7	4	6	24	Crustose
Parmeliaceae	*Bulbothrix apophysata* (Hale & Kurok.) Hale	8	29	22	7	66	Foliose
Parmeliaceae	*Bulbothrix isidiza* (Nyl.) Hale	0	3	19	7	29	Foliose
Parmeliaceae	*Hypotrachyna costaricensis* (Nyl.) Hale	0	1	4	4	9	Foliose
Parmeliaceae	*Hypotrachyna horrescens* (Taylor) Krog & Swinsc.	4	4	4	1	13	Foliose
Parmeliaceae	*Hypotrachyna laevigata* (Sm.) Hale	19	30	42	20	111	Foliose
Parmeliaceae	*Hypotrachyna* sp1	1	3	2	1	7	Foliose
Parmeliaceae	*Hypotrachyna* sp2	0	3	0	0	3	Foliose
Parmeliaceae	*Parmotrema austrosinense* (Zahlbr.) Hale	10	18	20	9	57	Foliose
Parmeliaceae	*Parmotrema cristiferum* (Taylor) Hale	0	1	2	0	3	Foliose
Parmeliaceae	*Parmotrema reticulatum* (Taylor) M. Choisy	0	4	5	4	14	Foliose
Parmeliaceae	*Parmotrema subisidiosum* (Müll. Arg.) Hale & Fletcher	0	1	0	0	1	Foliose
Parmeliaceae	*Usnea* sp1	9	7	21	10	47	Fruticose
Parmeliaceae	*Usnea* sp2	4	11	6	4	25	Fruticose
Pertusariaceae	*Pertusaria* cf. amara (Ach.) Nyl.	0	3	15	1	19	Crustose
Pertusariaceae	*Pertusaria* sp1	0	1	0	0	1	Crustose
Pertusariaceae	*Pertusaria* sp2	0	0	0	1	1	Crustose
Physciaceae	*Heterodermia vulgaris* (Vain.) Follman & Redón	0	0	0	1	1	Foliose
Physciaceae	*Leucodermia leucomelos* (L.) Kalb	1	1	0	0	2	Foliose
Pilocarpaceae	*Byssoloma subdiscordans* (Nyl.) P. James.	1	3	0	1	5	Crustose
Pyrenulaceae	*Pyrenula* aff. *microcarpa* Müll.Arg.	12	17	27	8	64	Crustose
Ramalinaceae	*Megalaria* aff. *grossa* (Pers. ex Nyl.) Hafellner.	1	4	8	4	17	Crustose
Ramalinaceae	*Ramalina peruviana* Ach.	0	0	1	2	3	Fruticose
Ramalinaceae	*Ramalina celastri* (Sprengel) Krog & Swinscow	1	2	2	4	9	Fruticose
Ramalinaceae	*Ramalina* sp.	5	12	9	0	26	Fruticose
Teloschistaceae	*Caloplaca* sp.	1	5	7	3	16	Crustose
Bryophytes							
Frullaniaceae	*Frullania brasiliensis* Raddi	0	0	0	1	1	Foliose
Frullaniaceae	*Frullania riojaneirensis* (Raddi) Spruce	2	5	1	2	10	Foliose
Lejeuneaceae	*Cheilolejeunea xanthocarpa* (Lehm. & Lindenb.) Malombe	0	3	4	0	7	Foliose
Lejeuneaceae	*Drepanolejeunea* sp.	0	0	2	2	4	Foliose
Lejeuneaceae	*Lejeunea* sp.	0	0	1	1	2	Foliose
Lejeuneaceae	*Microlejeunea bullata* (Taylor) Steph.	0	2	1	2	5	Foliose
Lejeuneaceae	*Thysananthus auriculatus* (Wilson & Hook.) Sukkharak & Gradst.	0	0	3	1	4	Foliose

Appendix B


Arthonia sp.


Coniocarpon cinnabarinum


Cratiria sp.


Chrysothrix candelaris


Allographa nuda


Graphis elegans


Graphis sp.


Phaeographis dendritica


Phaeographis inconspicua

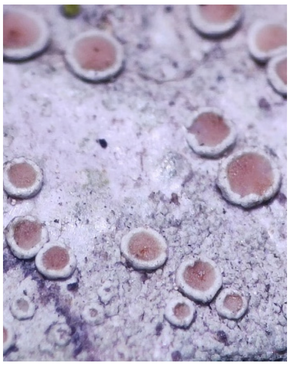

Phaeographis sp.


Lecanora sp1


Lecanora sp2


Lecanora sp3


Lecanora sp4


Lecanora sp5


Lecanora sp6

Figure A1. *Cont*.

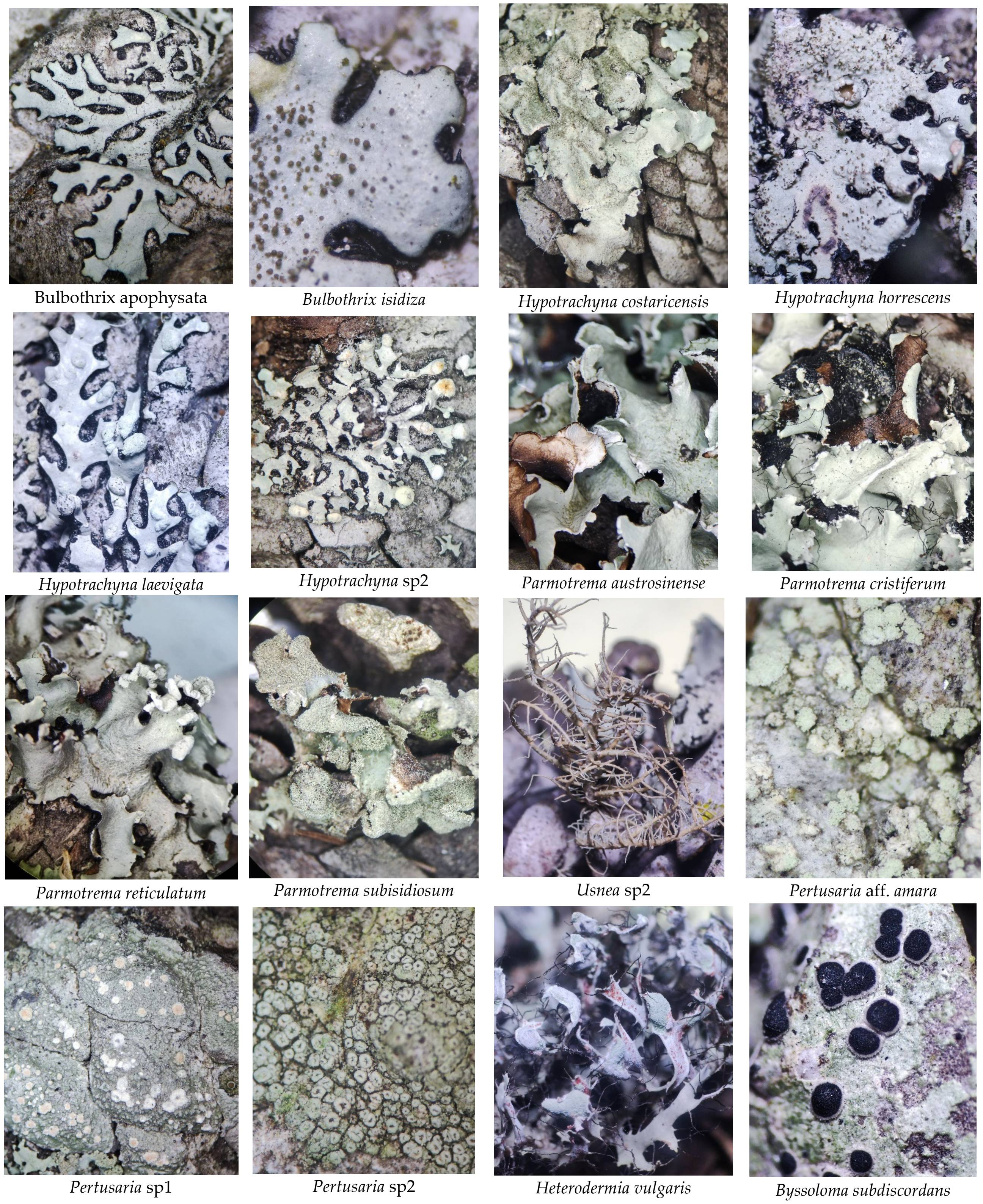


Figure A1. *Cont*.

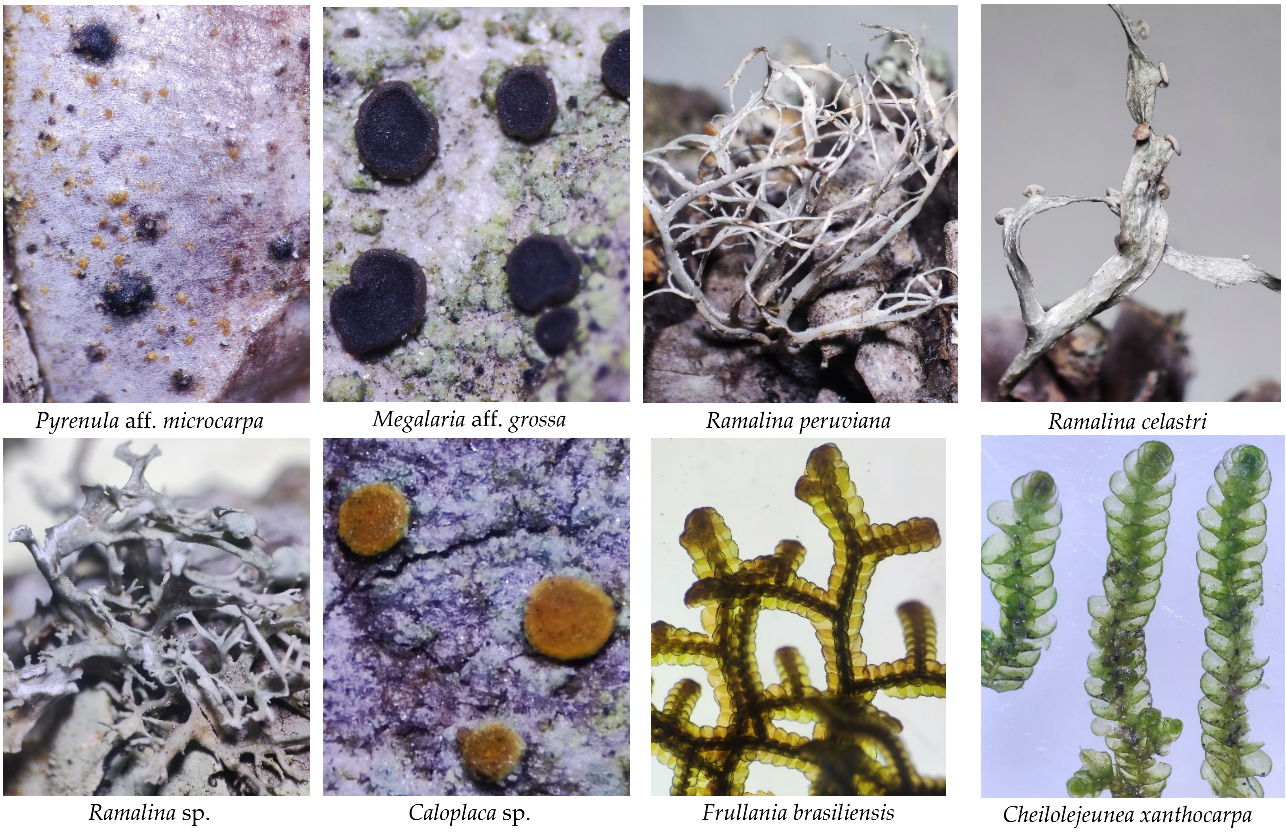


Figure A1. Species of lichens and bryophytes occurring on pine cones.

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