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# Lichen Responses to Disturbance: Clues for Biomonitoring Land-use Effects on Riparian Andean Ecosystems

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**Abstract:** The transformation of natural ecosystems due to anthropogenic land use is considered one of the main causes of biodiversity loss. Lichens, due to their poikilohydric nature, are very sensitive to natural and anthropogenic disturbances. Therefore, lichen communities have been widely used as bioindicators of climatic and environmental changes. In this study, we evaluated how the species richness and community composition of epiphytic lichens respond to land-use intensity in riparian ecosystems of the Andes in southern Ecuador. Additionally, we evaluate how the richness of six functional traits (photobiont type, growth form, and reproductive strategy) changed across the different land-use intensity. We selected 10 trees in twelve sites for a total de 120 trees, equally divided into four riparian land-use intensities (forest, forest-pasture, pasture and urban). We recorded a total of 140 lichen species. Species richness was highest in the forest sites and decreased towards more anthropogenic land uses. Lichen community composition responded to land-use intensity, and was explained by microclimate variables (e.g., precipitation, percentage forested area) and distance to the forest. Richness of functional traits of lichens also differed significantly among the four land-use intensity and decreased from forests to urban land-use. Taxonomic diversity and functional traits can be effectively applied as bioindicators to assess and monitor the effects of land-use changes in the riparian ecosystems of tropical montane regions.

**Keywords:** epiphyte communities; functional traits; bioindicators; riparian land-use; tropical Andes

## 1. Introduction

Ecosystem transformation due to anthropogenic disturbances such as land-use change is considered one of the main drivers of biodiversity loss [1–4]. Several studies state that current land-use practices will generate major impacts on the structure and functioning of ecosystems at different geographic scales [5–7], modifying biotic and abiotic conditions, increasing replacement rates and affecting local extinction [4–8]. Most of the tropical primary forests (e.g., montane Andean forests) were transformed to secondary forests, pastures, cropland, and urbanized areas to satisfy human needs [2,6,9]. In consequence, the diversity of plants, lichens, birds, arthropods, fish, reptiles and mammals has been diminished because of land use [4,10–12].

Epiphytic lichens are an essential component of tropical humid forests because of their important role in water and nutrient cycles [13]. Therefore, they are key organisms facilitating crucial ecosystem processes [10,14,15]. Epiphytic lichens are poikilohydric, thus they lack an active regulation of the loss and absorption of water [16], which in turn increases their sensitivity to environmental disturbances [17,18]. For these reasons, several biological traits of lichens as such as photobiont type, growth, reproduction, and development can be affected by environmental changes [19–22]. In this manner, these functional traits can be used as a complementary approach to better understand ecosystems because they allow us to assess the biodiversity and their relationship with ecosystem functioning [23,24].

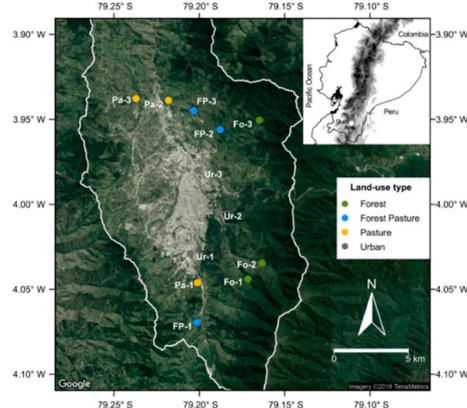
As a general pattern, microclimatic variables (e.g., light, humidity, and temperature) that change in response to ecosystem transformation have been considered as constraining factors over the taxonomic and functional diversity of epiphytic lichens [21,25]. Therefore, several studies have used both taxonomic and functional diversity (e.g., richness of each functional trait) as indicators of land-use change [20,22,26,27], forest disturbance [14,21,28], global warming [29] and air quality [19,30–32].

In temperate ecosystems, most of the research has been focused on assessing the effects of different land uses on taxonomic and functional diversity of lichens [5,20,26,27]. Whereas in the tropics, studies have been restricted to determine the effects of disturbance and atmospheric pollution on lichen diversity [21,25,33,34]. This research is the first in Ecuador to quantify the response of taxonomic diversity and functional traits of epiphytic lichens to different land-use intensities along the riparian ecosystems of southern Andean streams. This area is affected by rapid forest transformation [9,35] and its riparian zones present a high degree of alteration [12,36,37]. Furthermore, we demonstrate, as in other regions (e.g., [20]), the complementary application of lichen's taxonomic and functional traits to detect and monitor changes in the structure and functioning of tropical Andean ecosystems. We predicted that intensive land-use can decrease the taxonomical diversity of species (richness and composition) and functional traits, and that these changes are related to alterations in the microclimate. Specifically, we addressed the following questions: 1) how does the species richness and community composition respond to land-use intensity? And 2) how does the richness of each functional trait respond to land-use intensity?

## 2. Materials and Methods

### 2.1. Study Area

This study was conducted around the city of Loja (180,000 inhabitants) in the southern Ecuadorian Andes, at altitudes between 2200 and 2400 masl (Figure 1). The climate is humid tropical with a mean annual temperature between 7–20 °C, and annual rainfall between 800–2500 mm [38].



**Figure 1.** Location of the study area and 12 sampling sites equally distributed in four riparian land uses of Andean streams in southern Ecuador. Codes indicate the land-use intensity (Fo = forest, FP = forest-pasture, Pa = pasture, Ur = urban).

Since the 1960s, these native forests have been transformed into agricultural and urbanized land [31,36,37]. In this study, we distinguished four different land uses, i.e., forest, a combination of forest and pasture, pasture, and urban land use, where we established 12 sampling sites located in riparian margins influenced by those land uses mentioned before. Forest sites (Fo) are characterized by a dense canopy layer of evergreen montane tropical vegetation (ca. 72%–78% coverage). The upper canopy is composed of native trees of the genera *Croton*, *Hedyosmum*, *Clusia*, *Morella*, and *Juglans*. Forest-Pasture sites (FP) are characterized by a semidense canopy layer (ca. 52%–60% coverage). The disturbed forests are mixed with pastures dominated by planted trees of *Alnus acuminata* and *Eucalyptus globulus*. Pasture sites (Pa) are affected by deforestation. The canopy layer is ca. 31%–34% in coverage, mainly composed of planted trees of the genera *Inga* and *Eucalyptus*. Urban sites (Ur) are characterized by a very uniform structure and dominate sections of grassland with planted trees of *Salix* spp. The open canopy layer is ca. 31%–34% in coverage.

## 2.2. Data Collection

In each site ( $n = 12$ ), we selected 10 mature trees with similar bark structure and diameter at breast height (DBH) over 20 cm within each site (120 trees total). They were selected about five meters from the river bank. We determined the occurrence of epiphytic lichens on 120 trees in total (10 trees per site). We used 20 × 50 cm quadrat on the bark of each selected tree, at the cardinal point with the most lichen abundance to 1.5 m above the ground. The sampling quadrat (20 × 50 cm) was divided into ten grids of a 10 cm × 10 cm, and the cover of each species in each grid was estimated as the proportion of the ten grids occupied by it. Lichen species cover was used as a surrogate of species abundance. For species identification, we used taxonomic and floristic papers [39–42]. In addition, we tested for specific secondary compounds using spot tests based on thallus fluorescence under ultraviolet light, with K (10% water solution of potassium hydroxide), Cl (bleach) and para-phenylenediamine (Pd). For the nomenclature of the species we followed mainly MycoBank. Finally, the specimens are stored in the Herbarium of Universidad Técnica Particular de Loja (HUTPL).

We evaluated six traits to perform the analysis of functional traits: (1) photobiont type; (2) growth form; (3) size; (4) reproduction type; (5) type of reproductive structure; and (6) thallus color (Table 1). The functional traits were selected based on previous studies, due to their relation to ecosystem functioning and land uses [5,19,21,22,25]. For instance, photobiont type and growth form (thallus morphology) are related with light, temperature and water requirements for the processes of photosynthesis and respiration [23,43–45], and with water uptake and loss [21,44]. Finally, reproductive strategy and reproductive structure are related to dispersion ability and establishment [22,25].

**Table 1.** List of the six functional traits and their categories of the epiphytic lichen community in four riparian land uses of Andean streams in southern Ecuador.

Functional Trait	Categories
Photobiont type	C = Chlorococcoid; CY = Cyanobacteria; T = Trentepohlia
Growth form	CR = Crustose; F = Filamentose; FB = Foliose with broad lobes; FN = Foliose with narrow lobes; FR = Fruticose; G = Gelatinose
Thallus size	MA = Macrolichens; MI = Microlichens
Thallus colour	L = Light; D = Dark
Reproduction type	A = Asexual; S = Sexual; AS = Asexual and sexual
Reproductive structure	AP = Apothecia; I = Isidia; L = Lirellae; P = Perithecia; SO = Soredia

## 2.3. Environmental Variables

We quantified aerial forests cover (%) for each site from a 2016 land uses map obtained in other study from high-resolution (0.30–2 m) imagery (pers. comm.). Land use was classified into forest, pasture, crops, urban, bare surface. In a GIS, we extracted the land use information for all sites, and the area (m<sup>2</sup> and %) covered by forest was calculated. Also, we calculated the distance to forests

for each site. Forest cover and distance to forests were obtained using the open source GIS software Quantum GIS 1.7.4 (QGIS). Light conditions were recorded by measuring canopy openness (%) using four digital hemispherical photographs per site. Digital photographs were always taken on overcast days and at breast height (1.3 meter), with a horizontally leveled digital camera and using a fish-eye lens. Photographs were analyzed using the software Gap Light Analyzer ver. 2.0 [46]. In addition, the following variables were measured: mean precipitation (mm) from the interpolated data of the meteorological stations located around the study area and tree diameter (DBH).

#### 2.4. Data Analysis

Species richness of epiphytic lichens was defined as the total number of species found in each tree. We calculated sampling completeness with the rarefaction curves (95 % confidence intervals) and the Chao 2 species richness estimator. For the calculation of the rarefaction curves and species richness estimators, we used the R package 'vegan'. Similarly, the species richness of each functional trait category was calculated as the total number of species with each trait category found in each tree. Thus, the effects of land use, % forests, distance to forest, precipitation, DBH and tree high on the species richness and the richness of each functional trait at the tree level were modeled by generalized linear mixed models (GLMMs) using Poisson distribution [47]. This modeling approach was chosen because our data present a hierarchical structure with sites nested within land use and trees nested within sites. Predictors were included as explanatory variables (fixed factors), and sites were included as random sources of variation. We used a logistic transformation for canopy openness and % forests variables [48]. Following this, we performed a stepwise best-model selection using a stepwise regression backwards, with predictors variables scaled and centered (mean = 0, SD = 1). Canopy openness was omitted in the model selection due to collinearity with % forests and precipitation. For GLMMs, the minimal adequate model was selected based on Akaike's Information Criterion (AIC) provided for the model selection procedure. We used the package 'nlme' with *lme* function [49] for the mixed-effect model analyses in R environment [50].

Shifts in lichen species composition were evaluated through a canonical correspondence analysis (CCA) based on chi-square distances. CCA analysis was applied to an abundance matrix square-root transformed. Land-use intensity was established as the covariate and remaining variables were used as explicative variables. Prior to the analysis, we applied a logistic transformation to explanatory variables % forest and distance to the forest; and a square-root transformation to precipitation.

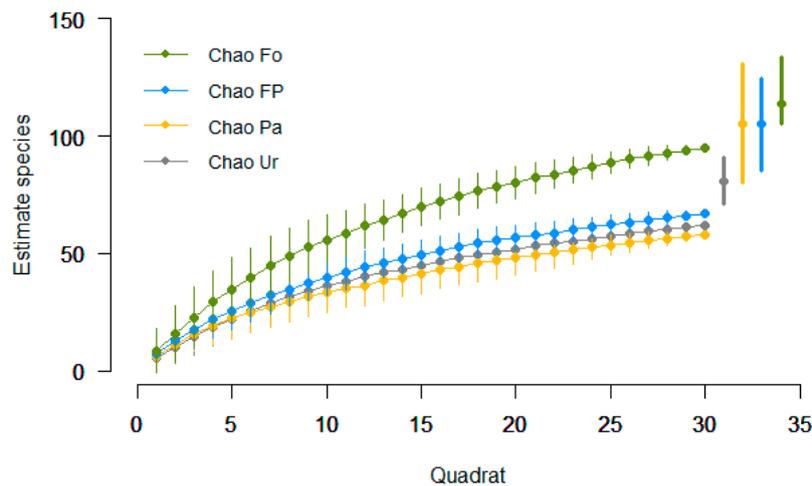
Variation in lichen species composition at the tree level in relation with measured environmental variables was explored by constrained ordinations [51]. As the first step, our data set (120 trees × 140 species) was subjected to a detrended correspondence analysis (DCA) to determine the most appropriate constrained ordination. Due to the length of the first DCA axis was 7.84 standard deviation units, we used a canonical correspondence analysis (CCA) to test the null hypothesis that species composition is independent of environmental variables [52]. CCA analyses were conducted between environmental variables and the epiphytic lichens abundances (square-root transformed). Land-use intensity was established as a covariate and remaining variables were used as explicative variables. Prior to the analysis, we applied a logistic transformation to explanatory variables % forest and distance to a forest; and a square-root transformation to precipitation. The model selection for the ordination was determined with a stepwise procedure based on a permutation test (using the *ordistep* function and 999 permutations). Then, the significance of explanatory variables on ordination was evaluated with ANOVA-like permutation test for Canonical Correspondence Analysis (using *anova.cca* function and 999 permutations). Additionally, the Pearson correlation coefficient of the explanatory continuous variables with the first two axes of the ordination (CCA1 and CCA2) was calculated. Also, in order to identify characteristic species in each ordination axis and relate them to predictor variables, we extracted the scores of the lichen species that were found at the end of the axes. For ordination analysis we used the 'vegan3d' package [53].

The IndVal function in the labdsv package [54] were used for indicator species analysis (ISA) [55] to determine individual species that are mainly associated with one land-use intensity. The indicator value ranges from 0 (one species was absent from one land-use intensity) to 1 (one species occurred in all trees of one land-use intensity and was absent from other trees). The significance was tested using a Monte Carlo permutation test with 1000 replicates.

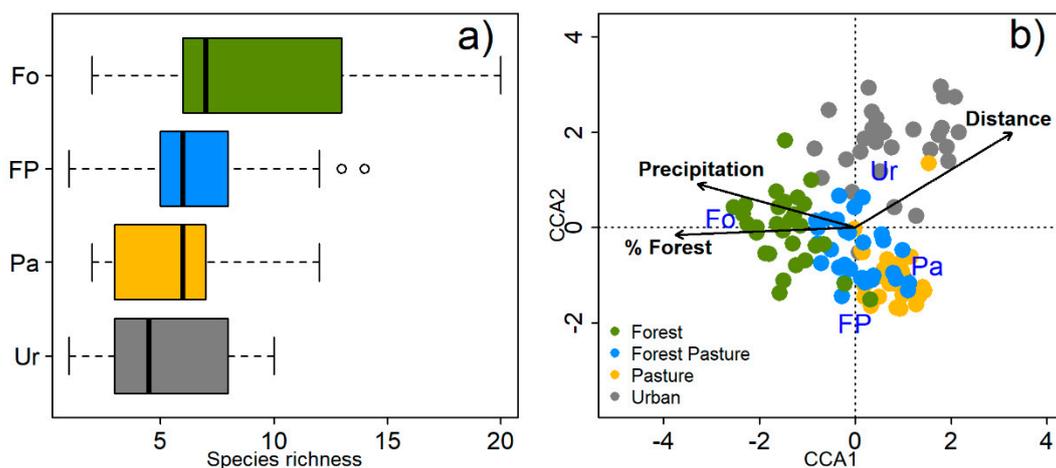
### 3. Results

#### 3.1. Species Richness and Community Composition

We recorded a total of 140 species of epiphytic lichens on 120 trees, distributed in 36 genera and 22 families. A total of 94 species were found in forest sites, 66 species in forest-pasture, 57 species in pasture, and 61 in urban sites. The Chao-2 richness estimator, confirming a high number of species estimated in forest, followed by forest-pasture, urban and pasture (Figure 2). Species richness of epiphytic lichen decreased along the land-use intensity, i.e., from forest to urban (Table 2; Figure 3a).



**Figure 2.** Rarefaction curves with 95 % confidence intervals and Chao 2 estimator (points in the right of figure) of four study land-use intensity. Forest (Fo); Forest-pasture (FP); Pasture (Pa); and Urban (Ur).



**Figure 3.** (a) Variation in species richness of epiphytic lichens in four riparian land uses of Andean streams in southern Ecuador. (b) CCA ordination plot of the lichen community using abundance data per tree and land-use intensity (covariate) precipitation, distance to forest and percentage of forest (predictors). Fo = Forest, FP = Forest Pasture, Pa = Pasture, Ur = Urban.

**Table 2.** Summary of the GLMM applied on species richness in four riparian land uses of Andean streams in southern Ecuador. Significant differences at  $p$ -value < 0.05. DBH: diameter at breast height.

Source of Variation	Coefficient	Standard Error	Z-value	$p$ -value
Forest	2.651	0.297	8.908	<0.001
Forest-Pasture	−0.663	0.286	−2.313	0.020
Pasture	−0.976	0.336	−2.899	0.003
Urban	−1.661	0.537	−3.093	0.001
Distance to forest	0.445	0.160	2.767	0.005
DBH	−0.004	0.056	0.078	0.937

Results GLMMs showed that lichen richness was lower in land uses with more intensity, i.e., forest-pasture, pasture and urban sites had a negative correlation with lichen richness. Conversely, distance to forests and forest land use showed a positive correlation (Table 2). The mean tree diameter (DBH) was not significant in any case (Table 2).

CCA indicated that precipitation, distance to forest and % forest were important factors to distinguish the taxonomic composition of the epiphytic lichen community among land uses (Figure 3b; Table 3). Together, these variables explained a total variation of 10%. The % forest and precipitation were negatively correlated to axis 1, while distance to forest was positively correlated (Figure 3b, Table S1). Only distance to forest and precipitation were positively correlated to CCA axis 2. Across CCA axis 1, the lichen species *Heterodermia leucomela*, *Dirinaria picta*, *Parmotrema arnoldi* and *Physcia aipolia* showed more preference for disturbed sites (pasture and urban site) with less canopy cover, low humidity and more light availability. Conversely, lichen species such as *Leptogium millegranum*, *Leptogium diffractum*, *Puntelia rudedta*, *Sticta fuliginosa* and *Sticta tomentosa* preferred the conditions of more humidity and closed canopy provided by the forest sites. Similarly, across CCA axis 2 the lichen species *Cococarpia palmicola*, *Leptogium coralloideum*, *Leptogium laceroides*, *Lobaria subexornata* and *Sticta fuliginosa* were related to sites with closed canopy and high humidity; whereas, *Heterodermia diademata*, *Heterodermia leucomela*, *Physcia aipolia*, *Physcia crispa*, *Telochistes exilis* and *Ramalina celastri* were related to open canopy sites and less humidity (Figure 3b).

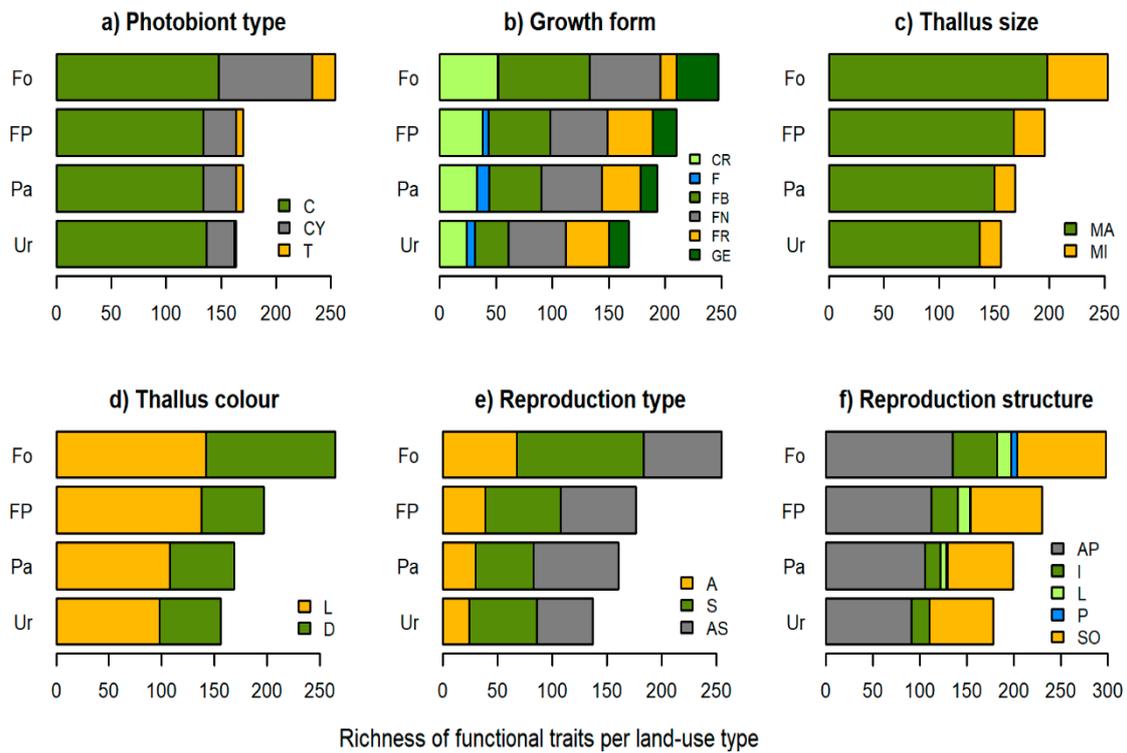
**Table 3.** Shift in lichen species composition in relation to predictor variables, measured with ANOVAlike permutation test in four riparian land uses of Andean streams in southern Ecuador. Significant differences at  $p$ -value (<0.05) are shown in bold. DBH: diameter at breast height.

Source of Variation	Degrees of Freedom	Chi Square	F-statistic	$p$ -value
Land use	3	1.196	2.316	<b>0.001</b>
Precipitation	1	0.242	1.410	<b>0.003</b>
Distance to forest	1	0.283	1.6477	<b>0.001</b>
% Forest	1	0.245	1.423	<b>0.014</b>

Eighteen species were the best indicators of forests land-use intensity, followed by forest-pasture with seven species and six and four species for urban and pasture respectively (Appendix A).

### 3.2. Functional Traits

Species richness of lichens with cyanobacteria and trentepohlia decreased from forest sites to urban sites (Figure 4a). A similar pattern was observed in the growth form, thus, crustose, foliose with broad lobes and gelatinose lichen species decreased along the land-use intensity (Figure 4b). Macrolichens with dark thallus decreased in pasture or urban sites (Figure 4b–d). Conversely, lichen with fruticulose growth form were more abundant in disturbed sites (Figure 4b). Lichens with sexual and asexual reproduction; and with apothecia, isidia and soredia as reproductive structure decreased in land use gradient (Figure 4e–f).



**Figure 4.** Variation in the richness of functional traits of the epiphytic lichen community in four riparian land uses of Andean streams in southern Ecuador. Functional trait and categories evaluated are indicated as follows. Photobiont type (a): C = Chlorococcoid; CY = Cyanobacteria; T = *Trentepohlia*. Growth form (b): CR = Crustose; F = Filamentose; FB = Foliose with broad lobes; FN = Foliose with narrow lobes; FR = Fruticose; G = Gelatinose. Thallus size (c): MA = Macrolichens; MI = Microlichens. Thallus color (d): L = Light; D = Dark. Reproduction type (e): A = Asexual; S = Sexual; AS = Asexual and sexual. Reproductive structure (f): AP = Apothecia; I = Isidia; L = Lirellae; P = Perithecia; SO = Soredia. Fo = Forest; FP = Forest Pasture; Pa = Pasture; y Ur = Urban.

The GLMMs models showed that the most relevant predictor for richness of functional traits of lichens was land-use intensity (Table 4). The land-use intensity forest, % forests, and distance to forest (correlated with canopy cover and precipitation) showed a positive correlation on lichen species with cyanobacteria as photobiont, and gelatinose and foliose with broad lobes growth forms and macrolichens (Table 4). Conversely, forest-pasture, pasture and urban land use showed positive correlation with lichens species with fruticose thallus. Lichens with dark colour, apothecia, soredia and isidia reproductive structure were correlated positively with forest (Table 4). The tree diameter (DBH) showed a positive effect on isidia as reproductive structure (Table 4).

**Table 4.** Summary of the GLMM applied on the functional traits of the epiphytic lichen community in four riparian land uses of Andean streams in southern Ecuador. Coefficient of variation with differences at  $p$ -value ( $<0.05$ ) are indicated in brackets. DBH: diameter at breast height. Fo = Forest; FP = Forest-Pasture; Pa = Pasture; y Ur = Urban. DBH = diameter at breast height, Dist-F = distance to forest; %Fo = percentage of forest.

Functional Traits	Land-use Intensity				DBH	Dist-F	%Fo
	Fo	FP	Pa	Ur			
<b>Photobiont type</b>							
Chlorococcoid	1.883 (0.004)						
Cyanobacteria	0.927 (0.001)	−0.871 (0.01)	−0.953 (0.01)	−1.195 (0.002)			
Trentepohlia				−1.969 (0.03)			
<b>Growth form</b>							
Crustose	1.033 (0.005)	−0.704 (0.04)	−0.977 (0.02)	−1.847 (0.01)			
Filamentose				−6.699 (0.04)	2.347 (0.02)		
Foliose with broad lobes	1.277 (0.002)			−2.064 (0.01)	0.789 (0.04)		
Foliose with narrow lobes	0.911 (0.003)						
Fruticose	−0.844 (0.02)	1.007 (0.03)		1.013 (0.04)			
Gelatinose		−1.028 (0.02)	−2.211 (0.01)	−2.13 (0.02)			
<b>Thallus size</b>							
Macrolichens	2.112 (0.009)						
Microlichens					1.553 (0.01)	1.368 (0.006)	
<b>Thallus colour</b>							
Light	1.519 (0.001)						
Dark	1.818 (0.001)	−1.091 (0.02)	−1.17 (0.03)				
<b>Reproduction type</b>							
Asexual	1.539 (0.001)	−1.263 (0.004)	−1.929 (0.002)	−2.226 (0.001)			
Sexual	1.298 (0.001)		−0.818 (0.01)	−0.622 (0.04)			
Asexual and sexual	0.775 (0.001)						
<b>Reproductive structure</b>							
Apothecia	1.769 (0.001)						
Isidia	0.502 (0.006)	−0.492 (0.03)	−0.98 (0.005)	−1.281 (0.008)	0.271 (0.02)		
Lirellae							
Perithecia							
Soredia	1.099 (0.03)						

## 4. Discussion

### 4.1. Species Richness, Functional Traits and Community Composition

Our findings reveal a negative effect of land-use intensity on several metrics of taxonomic diversity and functional traits of the epiphytic lichen communities across riparian buffers in the

Andes of southern Ecuador. There was a decrease in species richness and changes in community composition from forest to urban sites, as in other studies [5,20,56–59]. Similarly, the richness of functional traits such as photobiont type and growth form of epiphytic lichens diminished along the land-use intensity. Other studies have also demonstrated that land-use change has affected the functional traits of lichens [5,15,19,21,22,25,27,60]. Following this pattern for richness of functional traits Pinho et al. [20], Benitez et al. [21] and Koch et al. [22], showed that forest disturbance and urbanization have a strong correlation on the richness of functional traits of the epiphytic lichen communities. This phenomenon associated with species richness and functional traits can be explained by the ecological and physiological requirements related to water availability. Thus, a greater richness of sensitive species (e.g., *Leptogium*), species with cyanobacteria and gelatinose growth were present in forest sites with a closed canopy [5,14,18,19,61–64] than in pasture and urban sites. This is because they are intolerant to light and strongly depend on atmospheric humidity, in some cases they even need liquid water to do photosynthesis [65].

On the other hand, the highest occurrence of heliophytic lichen species with green algae and cortical pigments, microlichens, lichens with narrow lobes, light and fruticose thallus were related to sites with a more anthropogenic land use (e.g., forest-pasture, pasture and urban zones). These species show a higher tolerance to lower humidity and more light intensity promoted positively by an open canopy [5,14,18–20,23,63,64]. In our case, heliophytic lichen species (e.g., *Parmotrema*, *Teloschistes*, and *Usnea*), species with narrow lobes such as *Physcia*, *Heterodermia* and *Hypotrachyna*, and fruticose species (e.g., *Usnea* and *Teloschistes*) were present in more anthropogenic areas because these sites present high levels of solar radiation and water stress [22,63]. These lichen species can hydrate very fast, as well as rapidly lose water, because they occupy more surface and have a broad fixation structure to substrate [25,56]. In addition, most of the recorded species present secondary metabolites (i.e., atranorine or usnic acid) that provide protection against solar radiation typical in altered zones [21,22]. In the disturbed sites we also observed an increase of lichen species with chlorococcoid green algae. An explanation to this finding is that green algae species are better adapted to open forests because they avoid the photoinhibition by using a minimum amount of water in their thallus during photosynthesis [5,20–22,56,63].

Epiphytic lichen community composition was also influenced by the differences in land-use intensity. A forest cover reduction leads to less humidity and more intensity of light, thus lichen species restricted to undisturbed forests (shade epiphytes) are more affected [10,19,63]. In our study, the forest sites were dominated by species of the genera *Leptogium*, *Sticta* and *Lobaria*, which are species with cyanobacteria as a photobiont with high needs of water and forest cover [26,62,66]. These species are strictly associated with forest and can be considered good indicators of land-use intensity. On the other hand, another group of species were favored by the disturbance gradient, because they are capable of tolerating more light intensity and low humidity [10,14]. Thus, forest-pasture, pasture, and urban sites were dominated by xerophytic species (sun epiphytes) of the genera *Heterodermia*, *Parmotrema*, *Physcia*, *Teloschistes* and *Usnea* [15,22,59]. The adaptive advantage of sun epiphytes against shade epiphytes is their secondary metabolites that make them tolerant to high levels of radiation [21]. Both indicators and some non-indicator species have important ecological implications in the riparian ecosystems of the southern Ecuadorian Andes. For instance, most species of the genus *Leptogium* (e.g., *L. burgesii*, *L. cochleatum*, *L. coralloideum*, *L. corticola*, *L. laceroides* and *L. marginellum*), *Lobaria* (*L. subexornata*) and *Sticta* (*S. ferax*, *S. fuliginosa* and *S. tomentosa*); are associated with forest land use intensity and can be considered as good indicators of riparian forests with closed canopy and higher humidity [10]. *Heterodermia hypoleuca*, *H. leucomela*, *Physcia aipolia* and *Ramalina celastri* are the best indicators for urbanization, whereas that *Dirinaria picta* and *Flavopunctelia flaventior* for pasture. In accordance with other studies, the presence of these species indicates exposed conditions and can be considered a good indicator of the effects of land-use changes [10,20–22,28].

#### 4.2. Application in Biomonitoring

Along our disturbance gradient, our measures of epiphytic lichen species richness, community composition, and functional traits richness, performed well when detecting the negative effect of land use intensity. However, functional traits have an advantage over community structure and species richness, of providing evidence of potential alterations in the biodiversity-ecosystem functioning relationships [21,22,24]. In this context, photobiont type and growth form of epiphytic lichens are easily measured and could be suitable indicators for detecting land-use intensity along riparian margins in Andean ecosystems. Likewise, growth form is a more sensitive indicator to changes in canopy cover facilitating a quantification of the effects of riparian forest disturbance, and potentially to assess the success of forest management in riparian buffers that promote and enhance the ecosystem health of Andean streams [36]. This first study in Ecuador, which assesses the suitability of a set of taxonomic and functional metrics of the epiphytic lichen community could be used as a complementary approach to understand the structure and functioning of riparian ecosystems in the tropical Andes. Therefore, these metrics could be effective indicators of land-use transformation in tropical Andes. Furthermore, the information provided here can contribute to better management practices in riparian margins of montane ecosystems in general.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/1424-2818/11/5/73/s1>, Table S1: Lichen species contribution to CCA axes using abundance data per tree and land-use intensity (covariate) precipitation, distance to forest and percentage of forest (predictors).

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#### Appendix A

**Table A1.** Indicator species analysis found in forest, forest-pasture, pasture and urban.

Taxa	Land-use Intensity	Indicator Value	p-value
<i>Bacidia</i> sp.	Forest	3.3	1.000
<i>Bacidia</i> sp. 1	Pasture	1.7	1.000
<i>Bacidia</i> sp. 2	Forest	3.3	1.000
<i>Bacidia</i> sp. 3	Forest-pasture	3.3	1.000
<i>Byssoloma subdiscordans</i> (Nyl.) P. James	Pasture	4.8	0,3211
<i>Candelaria concolor</i> (Dickson) Stein	Urban	6.7	0.2438
<i>Candelaria</i> sp.	Forest	3.6	0.6059
<i>Canomaculina pilosa</i> (Stizenb.) Elix & Hale	Pasture	6.2	0.2464
<i>Chapsa</i> aff. <i>dilatata</i> (Müll. Arg.) Kalb	Forest	1.9	1.00
<i>Chapsa</i> aff. <i>diploschistoides</i> (Zahlbr.) Frisch	Forest	3.3	1.000
<i>Chapsa</i> sp.	Forest-pasture	5.3	0.4695
<i>Chrysothrix candelaris</i> (L.) JR Laundon	Urban	10.7	0.0494
<i>Cladonia coniocraea</i> (Flörke) Sprengel	Forest	23.3	0.0008
<i>Coccocarpia palmicola</i> (Spreng.) Arv. & D.J. Galloway	Forest	3.3	1.000
<i>Coccocarpia pellita</i> (Ach.) Müll. Arg.	Forest	6.7	0.2368
<i>Coenogonium linkii</i> Ehrenb	Forest	20	0.0016
<i>Coenogonium pineti</i> (Ach.) Lücking & Lumbsch	Forest-pasture	3.3	1.000
<i>Dirinaria picta</i> (Sw.) Clem. & Schear	Pasture	10	0.0444
<i>Flavopunctelia flaventior</i> (Stirt.) Hale	Pasture	31.7	0.0012
<i>Graphis</i> sp.	Forest	6.7	0.2272
<i>Graphis</i> sp. 1	Forest	3.3	1.000
<i>Graphis</i> sp. 2	Forest	3.3	1.000
<i>Graphis</i> sp. 3	Forest	3.3	1.000
<i>Heterodermia albicans</i> (Pers.) Swinscow & Krog	Forest-pasture	3.3	0.7986
<i>Heterodermia andina</i> Moberg	Urban	5.7	0.2745
<i>Heterodermia comosa</i> (Eschw.) Follmann & Redón	Pasture	3.3	1.000
<i>Heterodermia corallophora</i> (Taylor) Skorepa	Pasture	15.1	0.0162
<i>Heterodermia diademata</i> (Taylor) D.D. Awasthi	Forest	3.3	1.000
<i>Heterodermia galactophylla</i> (Tuck.) W.L. Culb.	Pasture	5.4	0.4147
<i>Heterodermia hypoleuca</i> (Mühl.) Trevis.	Urban	18	0.0026
<i>Heterodermia isidiophora</i> (Nyl.) D.D. Awasthi	Forest	14.1	0.0468

Table A1. Cont.

Taxa	Land-use Intensity	Indicator Value	p-value
<i>Heterodermia japonica</i> (M. Satô) Swinscow & Krog	Pasture	12.2	0.0714
<i>Heterodermia leucomela</i> (L.) Poelt	Urban	15.5	0.0084
<i>Heterodermia pseudospeciosa</i> (Kurok.) Culb.	Forest	3	0.6067
<i>Heterodermia sitchensis</i> Goward & Noble	Pasture	14.8	0.2697
<i>Heterodermia squamulosa</i> (Degel.) Culb.	Forest-pasture	13	0.0086
<i>Heterodermia spathulifera</i> Moberg & Purvis	Forest	21.8	0.0006
<i>Heterodermia speciosa</i> (Wulfen) Trevisan	Pasture	2	1.000
<i>Heterodermia</i> sp.	Forest	3.3	1.000
<i>Hypotrachyna costaricensis</i> (Nyl.) Hale	Forest-pasture	6.7	0.2446
<i>Hypotrachyna revoluta</i> (Flörke) Hale	Forest	4.6	0.2931
<i>Hypotrachyna rockii</i> (Zahlbr.) Hale	Forest	34	0.0002
<i>Hypotrachyna reducens</i> (Nyl.) Hale	Pasture	15.7	0.1236
<i>Hypotrachyna sinuosa</i> (Sm.) Hale	Forest	2.2	1.000
<i>Lecanora chlorotera</i> Nyl.	Urban	10	0.0566
<i>Lecanora helva</i> Stizenb.	Urban	3.3	1.000
<i>Lecanora</i> sp.	Urban	3.3	1.000
<i>Lepraria</i> sp.	Forest	3.8	0.7365
<i>Leptogium austroamericanum</i> (Malme) CW Dodge	Forest	6.3	0.1882
<i>Leptogium azureum</i> (Sw.) Mont.	Urban	7.4	0.2442
<i>Leptogium burgesii</i> (L.) Mont.	Forest	20	0.0004
<i>Leptogium burnetii</i> Dodge	Forest-pasture	3.3	1.000
<i>Leptogium cochleatum</i> (Dicks.) P.M. Jørg. & P. James	Forest	24.1	0.0002
<i>Leptogium coralloideum</i> (Meyen & Flot.) Vain.	Forest	11.1	0.0388
<i>Leptogium corticola</i> (Taylor) Tuck.	Forest	15.9	0.0036
<i>Leptogium cyanescens</i> (Rabh.) Körb.	Forest-pasture	5.7	0.3835
<i>Leptogium diaphanum</i> (Sw.) Nyl.	Forest-pasture	20.3	0.019
<i>Leptogium laceroides</i> B. de Lesd.	Forest	10	0.0466
<i>Leptogium marginellum</i> (Sw.) Gray	Forest	10	0.0468
<i>Leptogium millegranum</i> Sierk	Urban	9.8	0.0558
<i>Leptogium olivaceum</i> (Hook.) Zahlbr.	Forest	6.7	0.2388
<i>Leptogium phyllocarpum</i> (Pers.) Mont.	Urban	6.7	0.2442
<i>Leptogium</i> sp.	Forest	13.3	0.025
<i>Lobaria erosa</i> (Eschw.) Nyl.	Forest	2.8	1.000
<i>Lobaria subexornata</i> (Yoshim.) Yoshim.	Forest	16.7	0.0024
<i>Megalospora melanoderma</i> (Müll. Arg.) Zahlbr.	Forest	13.3	0.0134
<i>Normandina pulchella</i> (Borrer) Nyl.	Forest	13.3	0.0134
<i>Parmotrema arnoldii</i> (Du Rietz) Hale	Forest-pasture	4.6	0.8822
<i>Parmotrema austrosinense</i> (Zahlbr.) Hale	Pasture	13.8	0.067
<i>Parmotrema chinense</i> (Osbeck) Hale y Ahti	Urban	5.6	0.3569
<i>Parmotrema conferendum</i> Hale	Forest-pasture	7	0.2651
<i>Parmotrema cristiferum</i> (Taylor) Hale	Forest	8.1	0.1466
<i>Parmotrema exquisitum</i> (Kurok.) DePriest & B.W. Hale	Forest-pasture	4.7	0.5609
<i>Parmotrema peralbidum</i> (Hale) Hale	Forest-pasture	3.1	1.000
<i>Parmotrema subinctorium</i> (Zahlbr.) Hale	Forest	2.5	0.6121
<i>Parmotrema</i> sp.	Forest-pasture	12.4	0.0242
<i>Pannaria conoplea</i> (Ach.) Bory	Forest-pasture	21.3	0.0042
<i>Pertusaria</i> sp.	Forest	3.3	1.000
<i>Pertusaria</i> sp. 1	Forest	6.7	0.242
<i>Pertusaria</i> sp. 2	Urban	6.8	0.1912
<i>Pertusaria</i> sp. 3	Forest	6.7	0.2442
<i>Pertusaria</i> sp. 4	Forest	6.7	0.232
<i>Pertusaria</i> sp. 5	Forest-pasture	3.3	1.000
<i>Pertusaria</i> sp. 6	Forest-pasture	1.7	1.000
<i>Phaeographis brasiliensis</i> (A. Massal.) Kalb & Matthes-Leicht	Forest	8.8	0.0598
<i>Phaeographis decipiens</i> Müll. Arg.	Pasture	3.3	1.000
<i>Phaeographis dendritica</i> (Ach.) Müll. Arg.	Forest-pasture	2.3	1.000
<i>Phaeographis intricans</i> (Nyl.) Vain.	Forest	6.7	0.2476
<i>Phaeographis inusta</i> (Ach.) Müll. Arg.	Pasture	3.3	1.000
<i>Phaeographis quadrifera</i> (Nyl.) Staiger	Forest-pasture	15.4	0.0052
<i>Phaeographis punctiformis</i> (Eschw.) Müll. Arg.	Forest	3.3	1.000
<i>Phaeographis subtigrina</i> (Vain.) Zahlbr.	Forest-pasture	2.3	0.9884
<i>Phaeophyscia</i> aff. <i>limbata</i> (Poelt) Kashw.	Pasture	9.2	0.1222
<i>Phaeophyscia</i> sp.	Forest	11.1	0.2202
<i>Phyllopsora isidiotyla</i> (Vain.) Riddle	Pasture	30.9	0.0002
<i>Physcia aipolia</i> (Ehrh. Ex Humb.) Fürnr.	Urban	12	0.0372
<i>Physcia atrostriata</i> Moberg	Pasture	3.3	1.000
<i>Physcia crispa</i> Nyl.	Urban	10.9	0.0638
<i>Physcia endochrysea</i> (Nyl.) Hampe	Urban	14.9	0.0088
<i>Physcia poncinsii</i> Hue	Urban	6.7	0.2446
<i>Physcia solediosa</i> (Vain.)	Urban	6.7	0.248
<i>Physcia</i> sp.	Urban	3.3	0.6163
<i>Physcia</i> sp. 1	Urban	3.3	1.000
<i>Physcia</i> sp. 2	Pasture	5.2	0.2494
<i>Pseudocyphellaria aurata</i> (Ach.) Vain.	Forest-pasture	11.9	0.0144
<i>Pseudocyphellaria crocata</i> (L.) Vain.	Pasture	10.3	0.0998
<i>Punctelia</i> aff. <i>crispa</i> Marcelli, Jungbluth & Elix	Forest-pasture	3.3	1.000

Table A1. Cont.

Taxa	Land-use Intensity	Indicator Value	p-value
<i>Punctelia reddenda</i> (Stirt.) Krog	Forest-pasture	10	0.0616
<i>Punctelia rudecta</i> (Ach.) Krog	Forest	4.2	0.6065
<i>Punctelia subrudecta</i> (Nyl.) Krog	Forest	14.9	0.0088
<i>Punctelia</i> sp.	Forest	2.0	1.000
<i>Punctelia</i> sp. 1	Forest	3.3	1.000
<i>Punctelia</i> sp. 2	Forest-pasture	2.1	0.912
<i>Pyrenula</i> sp.	Forest-pasture	10.0	0.053
<i>Pyrenula</i> sp1.	Forest-pasture	11.9	0.0932
<i>Pyxine cocoëns</i> (Sw.) Nyl.	Forest	10.0	0.0616
<i>Ramalina celastri</i> (Spreng.) Krog & Swinscow	Urban	12.8	0.0132
<i>Ramalina cochlearis</i> Zahlbr.	Urban	2.2	1.000
<i>Ramalina peruviana</i> Ach.	Forest-pasture	4.0	0.6189
<i>Rimelia reticulata</i> (Taylor) Hale	Forest-pasture	2.1	1.000
<i>Rimelia subsidiosa</i> (Müll. Arg.) Hale	Pasture	3.7	0.7261
<i>Rinodina</i> sp.	Forest	11.4	0.033
<i>Sticta andensis</i> (Nyl.) Trevis.	Forest	3.3	1.000
<i>Sticta ferax</i> Müll. Arg.	Forest	16.7	0.0028
<i>Sticta fuliginosa</i> (Dicks.) Ach.	Forest	39.8	0.0002
<i>Sticta humboldtii</i> Hook. f.	Forest	6.7	0.2488
<i>Sticta tomentosa</i> (Sw.) Ach.	Forest	20	0.0008
<i>Sticta</i> sp.	Pasture	13.3	0.015
<i>Teloschistes flavicans</i> (Sw.) Norman	Urban	6.9	0.1842
<i>Teloschistes chrysoththalmus</i> (L.) Beltr.	Pasture	2.5	0.8224
<i>Teloschistes exilis</i> (Michaux) Vain.	Forest-pasture	9.6	0.5153
<i>Teloschistes hypoglaucus</i> (Nyl.) Zahlbr.	Urban	1.7	1.000
<i>Usnea</i> sp.	Forest-pasture	14.9	0.0336
<i>Usnea</i> sp. 1	Urban	2.4	1.000
<i>Usnea</i> sp. 2	Pasture	8.2	0.3405
<i>Usnea</i> sp. 3	Urban	16.4	0.0188
<i>Usnea</i> sp. 4	Urban	9.0	0.1246
<i>Usnea</i> sp. 5	Urban	5.3	0.4397
<i>Usnea</i> sp. 6	Forest-pasture	3.9	0.6755
<i>Usnea</i> sp. 7	Urban	6.0	0.2809

## References

- Turner, W.; Nakamura, T.; Dinetti, M. Global Urbanization and the Separation of Humans from Nature. *BioScience* **2004**, *54*, 585. [[CrossRef](#)]
- Gibson, L.; Lee, T.M.; Koh, L.P.; Brook, B.W.; Gardner, T.A.; Barlow, J.; Sodhi, N.S. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* **2011**, *478*, 378. [[CrossRef](#)] [[PubMed](#)]
- Cui, L.; Shi, J. Urbanization and its environmental effects in Shanghai, China. *Urban Clim.* **2012**, *2*, 1–15. [[CrossRef](#)]
- Newbold, T.; Hudson, L.N.; Hill, S.L.; Contu, S.; Lysenko, I.; Senior, R.A.; Day, J. Global effects of land use on local terrestrial biodiversity. *Nature* **2015**, *520*, 45. [[CrossRef](#)]
- Stofer, S.; Bergamini, A.; Aragon, G.; Carvalho, P.; Coppins, B.J.; Davey, S.; Lököš, L. Species richness of lichen functional groups in relation to land use intensity. *Lichenologist* **2006**, *38*, 331–353. [[CrossRef](#)]
- Liira, J.; Sepp, T.; Parrest, O. The forest structure and ecosystem quality in conditions of anthropogenic disturbance along productivity gradient. *For. Ecol. Manag.* **2007**, *250*, 34–46. [[CrossRef](#)]
- Gowda, J.H.; Kitzberger, T.; Premoli, A.C. Landscape responses to a century of land use along the northern Patagonian forest-steppe transition. *Plant Ecol.* **2012**, *213*, 259–272. [[CrossRef](#)]
- Mckinney, M. Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *Bioscience* **2002**, *52*, 883–890. [[CrossRef](#)]
- Tapia-Armijos, M.F.; Homeier, J.; Espinosa, C.I.; Leuschner, C.; de la Cruz, M. Deforestation and forest fragmentation in South Ecuador since the 1970s—losing a hotspot of biodiversity. *PLoS ONE* **2015**, *10*, e0133701. [[CrossRef](#)]
- Benítez, Á.; Prieto, M.; González, Y.; Aragón, G. Effects of tropical montane forest disturbance on epiphytic macrolichens. *Sci. Total Environ.* **2012**, *441*, 169–175. [[CrossRef](#)] [[PubMed](#)]
- Alberti, M. Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol. Evol.* **2015**, *30*, 114–126. [[CrossRef](#)] [[PubMed](#)]
- Iñiguez-Armijos, C.; Hampel, H.; Breuer, L. Land-use effects on structural and functional composition of benthic and leaf-associated macroinvertebrates in four Andean streams. *Aquat. Ecol.* **2018**, *52*, 77–92. [[CrossRef](#)]

13. Holz, I.; Gradstein, R.S. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica—species richness, community composition and ecology. *Plant Ecol.* **2005**, *178*, 89–109. [[CrossRef](#)]
14. Nöske, N.M.; Hilt, N.; Werner, F.A.; Brehm, G.; Fiedler, K.; Sipman, H.J.; Gradstein, S.R. Disturbance effects on diversity of epiphytes and moths in a montane forest in Ecuador. *Basic. Appl. Ecol.* **2008**, *9*, 4–12. [[CrossRef](#)]
15. Hauck, M.; Lkhagvadorj, D. Epiphytic lichens as indicators of grazing pressure in the Mongolian forest-steppe. *Ecol. Indic.* **2013**, *32*, 82–88. [[CrossRef](#)]
16. Gauslaa, Y.; Solhaug, K.A.; Longinotti, S. Functional traits prolonging photosynthetically active periods in epiphytic cephalolichens during desiccation. *Environ. Exp. Bot.* **2017**, *141*, 83–91. [[CrossRef](#)]
17. Giordani, P. Variables influencing the distribution of epiphytic lichens in heterogeneous areas: A case study for Liguria, NW Italy. *J. Veg. Sci.* **2006**, *17*, 195–206. [[CrossRef](#)]
18. Benítez, Á.; Prieto, M.; Aragón, G. Large trees and dense canopies: Key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. *For. J. For. Res* **2015**, *88*, 521–527. [[CrossRef](#)]
19. Giordani, P.; Brunialti, G.; Bacaro, G.; Nascimbene, J. Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecol. Indic.* **2012**, *18*, 413–420. [[CrossRef](#)]
20. Pinho, P.; Bergamini, A.; Carvalho, P.; Branquinho, C.; Stofer, S.; Scheidegger, C.; Maguas, C. Lichen functional groups as ecological indicators of the effects of land-use in Mediterranean ecosystems. *Ecol. Indic.* **2012**, *15*, 36–42. [[CrossRef](#)]
21. Benítez, A.; Aragón, G.; González, Y.; Prieto, M. Functional traits of epiphytic lichens in response to forest disturbance and as predictors of total richness and diversity. *Ecol. Indic.* **2018**, *86*, 18–26. [[CrossRef](#)]
22. Koch, N.M.; Matos, P.; Branquinho, C.; Pinho, P.; Lucheta, F.; de Azevedo Martins, S.M.; Vargas, V.M.F. Selecting lichen functional traits as ecological indicators of the effects of urban environment. *Sci. Total Environ.* **2019**, *654*, 705–713. [[CrossRef](#)]
23. Merinero, S.; Martínez, I.; Rubio-Salcedo, M.; Gauslaa, Y. Epiphytic lichen growth in Mediterranean forests: Effects of proximity to the ground and reproductive stage. *Basic. Appl. Ecol.* **2015**, *16*, 220–230. [[CrossRef](#)]
24. Giordani, P.; Rizzi, G.; Caselli, A.; Modenesi, P.; Malaspina, P.; Mariotti, M.G. Fire affects the functional diversity of epilithic lichen communities. *Fungal Ecol.* **2016**, *20*, 49–55. [[CrossRef](#)]
25. Koch, N.M.; de Azevedo Martins, S.M.; Lucheta, F.; Müller, S.C. Functional diversity and traits assembly patterns of lichens as indicators of successional stages in a tropical rainforest. *Ecol. Indic.* **2013**, *34*, 22–30. [[CrossRef](#)]
26. Hauck, M.; de Bruyn, U.; Leuschner, C. Dramatic diversity losses in epiphytic lichens in temperate broad-leaved forests during the last 150 years. *Biol. Conserv.* **2013**, *157*, 136–145. [[CrossRef](#)]
27. Zarabska-Bozejewicz, D.; Kujawa, K. The effect of land use on taxonomical and functional diversity of lichens in an agricultural landscape. *Fungal Ecol.* **2018**, *33*, 72–79. [[CrossRef](#)]
28. Aragón, G.; Martínez, I.; Hurtado, P.; Benítez, Á.; Rodríguez, C.; Prieto, M. Using Growth Forms to Predict Epiphytic Lichen Abundance in a Wide Variety of Forest Types. *Diversity* **2019**, *11*, 51. [[CrossRef](#)]
29. Gauslaa, Y. Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *Lichenologist* **2014**, *46*, 1–16. [[CrossRef](#)]
30. Llop, E.; Pinho, P.; Matos, P.; Pereira, M.J.; Branquinho, C. The use of lichen functional groups as indicators of air quality in a Mediterranean urban environment. *Ecol. Indic.* **2012**, *13*, 215–221. [[CrossRef](#)]
31. Ochoa, D.; Cueva, A.; Prieto, M.; Aragón, G.; Benítez, A. Cambios en la composición de líquenes epifitos relacionados con la calidad del aire en la ciudad de Loja (ECUADOR). *Caldasia* **2015**, *37*, 333–343. [[CrossRef](#)]
32. Benítez, Á.; Medina, J.; Vásquez, C.; Loaiza, T.; Luzuriaga, Y.; Calva, J. Lichens and Bromeliads as Bioindicators of Heavy Metal Deposition in Ecuador. *Diversity* **2019**, *11*, 28. [[CrossRef](#)]
33. Kääfer, M.I.; de Azevedo, S.M.; Alves, C.; Pereira, V.C.; Fachel, J.; Vargas, V.M.F. Corticolous lichens as environmental indicators in urban areas in southern Brazil. *Ecol. Indic.* **2011**, *11*, 1319–1332. [[CrossRef](#)]
34. Koch, N.M.; Branquinho, C.; Matos, P.; Pinho, P.; Lucheta, F.; Martins, S.M.; Vargas, V.M. The application of lichens as ecological surrogates of air pollution in the subtropics: A case study in South Brazil. *Environ. Sci. Pollut. Res.* **2016**, *23*, 20819–20834. [[CrossRef](#)] [[PubMed](#)]
35. Tapia-Armijos, M.F.; Homeier, J.; Draper-Munt, D. Spatio-temporal analysis of the human footprint in South Ecuador: Influence of human pressure on ecosystems and effectiveness of protected areas. *Appl. Geogra.* **2017**, *78*, 22–32. [[CrossRef](#)]

36. Iñiguez-Armijos, C.L.; Frede, H.G.; Hampel, H.; Breuer, L. Deforestation and benthic indicators: How much vegetation cover is needed to sustain healthy Andean streams? *PLoS ONE* **2014**, *9*, e105869.
37. Iñiguez-Armijos, C.; Rausche, S.; Cueva, A.; Sánchez-Rodríguez, A.; Espinosa, C.; Breuer, L. Shifts in leaf litter breakdown along a forest–pasture–urban gradient in Andean streams. *Ecol. Evol.* **2016**, *6*, 4849–4865. [[CrossRef](#)] [[PubMed](#)]
38. Rollenbeck, R.; Bendix, J. Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. *Atmos. Res.* **2011**, *99*, 277–289. [[CrossRef](#)]
39. May, P.F.; Brodo, I.M.; Esslinger, T.L. *Identifying North American lichens: A Guide to the Literature*; Farlow Herbarium, Harvard University: Cambridge, MA, USA, 2002.
40. Sipman, H.J.M. Identification Key and Literature Guide to the Genera of Lichenized Fungi (Lichens) in the Neotropics, Provisional Version. Botanical Garden & Botanical Museum Berlin-Dahlen, Free University of Berlin, 2003. Available online: <http://www.bgbm.fu-berlin.de/sipman/keys/neokeyA.htm> (accessed on 10 January 2018).
41. Cáceres, M.E.S.; Lücking, R.; Rambold, G. Phorophyte specificity and environmental parameters as determinants for species composition, richness and area cover in corticolous crustose lichen communities in the Atlantic rainforest of northeastern Brazil. *Mycol. Progr.* **2007**, *6*, 117–136. [[CrossRef](#)]
42. Moncada, B.; Lücking, R.; Suárez, A. Molecular phylogeny of the genus *Sticta* (lichenized Ascomycota: Lobariaceae) in Colombia. *Fungal Divers.* **2014**, *64*, 205–231. [[CrossRef](#)]
43. Lange, O.L.; Kilian, E.; Ziegler, H. Water vapor uptake and photosynthesis of lichens: Performance differences in species with green and blue-green algae as phycobionts. *Oecologia* **1986**, *71*, 104–110. [[CrossRef](#)]
44. Lakatos, M.; Rascher, U.; Büdel, B. Functional characteristics of corticolous lichens in the understory of a tropical lowland rain forest. *New Phytol.* **2006**, *172*, 679–695. [[CrossRef](#)] [[PubMed](#)]
45. Marini, L.; Nascimbene, J.; Nimis, P.L. Large-scale patterns of epiphytic lichen species richness: Photobiont-dependent response to climate and forest structure. *Sci. Total Environ.* **2011**, *409*, 4381–4386. [[CrossRef](#)] [[PubMed](#)]
46. Frazer, G.W.; Canham, C.D.; Lertzman, K.P. *Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation*; Simon Fraser University: Burnaby, British Columbia; The Institute of Ecosystem Studies: Millbrook, NY, USA, 1999; Volume 36.
47. McCullagh, P.; Nelder, J.P. *Generalized Linear Models*, 2nd ed.; Chapman and Hall: London, UK, 1989; p. 511.
48. Warton, D.I.; Hui, F.K. The arcsine is asinine: The analysis of proportions in ecology. *Ecology* **2011**, *92*, 3–10. [[CrossRef](#)]
49. Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D.; Team, R.C. nlme: Linear and Nonlinear Mixed Effects Models. R Package Vers 1.3-5. 2017. Available online: <http://CRAN.R-project.org/package=nlme> (accessed on 10 January 2018).
50. R Core Team. *R: A Language Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2015; Available online: <https://www.r-project.org/> (accessed on 10 January 2018).
51. Hill, M.O.; Gauch, H.G. Detrended correspondence analysis: An improved ordination technique. In *Classification and Ordination*; Springer: Berlin/Heidelberg, Germany, 1980; pp. 47–58.
52. Legendre, P.; Anderson, M.J. Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.* **1999**, *69*, 1–24. [[CrossRef](#)]
53. Oksanen, J.; Kindt, R.; Simpson, G.L. Package ‘vegan3d’. 2018. Available online: <http://CRAN.R-project.org/package=vegan3d> (accessed on 10 January 2018).
54. Roberts, D.W. Labdsv: Ordination and Multivariate Analysis for Ecology. Version 1.4-1. 2012. Available online: <http://CRAN.R-project.org/package=labdsv> (accessed on 10 January 2018).
55. Dufréne, M.; Legendre, P. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* **1997**, *67*, 345–366. [[CrossRef](#)]
56. Ellis, C.J.; Coppins, B.J. 19th century woodland structure controls stand-scale epiphyte diversity in present-day Scotland. *Divers. Distrib.* **2007**, *13*, 84–91. [[CrossRef](#)]
57. Baniya, C.B.; Solhøy, T.; Gauslaa, Y.; Palmer, M.W. The elevation gradient of lichen species richness in Nepal. *Lichenologist* **2010**, *42*, 83–96. [[CrossRef](#)]
58. Aragón, G.; Martínez, I.; Izquierdo, P.; Belinchón, R.; Escudero, A. Effects of forest management on epiphytic lichen diversity in Mediterranean forests. *Appl. Veg. Sci.* **2010**, *13*, 183–194. [[CrossRef](#)]

59. Ellis, C.J.; Coppins, B.J. Partitioning the role of climate, pollution and old-growth woodland in the composition and richness of lichen epiphytes in Scotland. *Lichenologist* **2010**, *42*, 601–614. [[CrossRef](#)]
60. Chongbang, T.B.; Keller, C.; Nobis, M.; Scheidegger, C.; Baniya, C.B. From natural forest to cultivated land: Lichen species diversity along land-use gradients in Kanchenjunga, Eastern Nepal. *Ecol. Mont* **2018**, *1*, 46–60. [[CrossRef](#)]
61. Moning, C.; Werth, S.; Dziock, F.; Bässler, C.; Bradtka, J.; Hothorn, T.; Müller, J. Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *For. Ecol. Manag.* **2009**, *258*, 745–751. [[CrossRef](#)]
62. Aragón, G.; Martínez, I.; García, A. Loss of epiphytic diversity along a latitudinal gradient in southern Europe. *Sci. Total Environ.* **2012**, *426*, 188–195. [[CrossRef](#)] [[PubMed](#)]
63. Matos, P.; Pinho, P.; Aragon, G.; Martínez, I.; Nunes, A.; Soares, A.M.; Branquinho, C. Lichen traits responding to aridity. *J. Ecol.* **2015**, *103*, 451–458. [[CrossRef](#)]
64. Leppik, E.; Jueriado, I.; Liira, J. Changes in stand structure due to the cessation of traditional land use in wooded meadows impoverish epiphytic lichen communities. *Lichenologist* **2011**, *43*, 257–274. [[CrossRef](#)]
65. Lange, O.; Büdel, A.; Meyer, A.; Kilian, E. Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *Lichenologist* **1993**, *25*, 175–189. [[CrossRef](#)]
66. Kiebacher, T.; Keller, C.; Scheidegger, C.; Bergamini, A. Epiphytes in wooded pastures: Isolation matters for lichen but not for bryophyte species richness. *PLoS ONE* **2017**, *12*, e0182065. [[CrossRef](#)] [[PubMed](#)]



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