

Article

Using Growth Forms to Predict Epiphytic Lichen Abundance in a Wide Variety of Forest Types

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Abstract: Epiphytic richness is continuously declining due to forest fragmentation, logging, burning, agriculture, and livestock. The rate of species loss caused by habitat degradation and loss is more pronounced in Central and South America. Considering the extreme difficulty and time required to identify the more inconspicuous species, rapid diversity assessment methods need to be extrapolated throughout the world. This study correlated lichen growth forms and total epiphytic abundance across 119 forests located in Europe and Central-South America. A total of 54 papers were selected from specific databases focused on lichens. Additionally, data from several unpublished ecological studies were included. Linear regression models showed that epiphytic lichen abundance was highly and positively correlated with the number of growth forms at all geographical levels considered (i.e., Central-South American and European forests, and the combination of both). Thus, the use of growth forms may provide an alternative and complementary way to evaluate epiphytic diversity because most growth forms have cosmopolitan distribution and are easily recognizable.

Keywords: richness; epiphyte; indicator species; forests; Europe; Central-South America

1. Introduction

Well-preserved forests harbor a high diversity of epiphytic lichens, including a high number of species extremely affected by forest logging and deforestation [1,2]. Although forest cover loss is slowing down, deforestation and forest degradation continue throughout some regions of the world, being especially critical in tropical regions. Here, forests are disappearing at alarming rates due to anthropogenic threats [3,4]. This scenario of rapid deforestation has caused the decline of numerous species [2] and the transformation of original landscapes into grasslands, croplands, and plantations with fast-growing species and secondary vegetation to satisfy human needs [5,6].

Species richness is an iconic and useful measure of biodiversity, which allows for easy analysis of the biodiversity loss. However, richness is difficult to quantify in lichens given the substantial effort required for sampling and identification [7]. In many cases, anatomical characters (e.g., cortex and medulla structure, spore size and shape), thin-layer chromatography analyses of secondary metabolites, or even genetic studies (i.e., barcoding) are needed to identify the species [7,8]. The high cost of identification, in terms of financial resources and time, could explain the absence of lichenological studies in many areas of the world.

The strong decline of lichen species due to forest disturbance and the lack of studies focused on lichen diversity have led to the development of rapid assessment methods based on multiple



indicators [9,10] as valuable tools to propose efficient conservation actions. For instance, the abundance of lichen genera and macrolichens has been highly correlated with total species richness [7]. Other studies have evidenced a correlation either between a simplified morphospecies list and lichen diversity values based on total species [9], or between the species abundance of a single family [10] and the total epiphytic richness. However, the use of these proposed indicators is still very restrictive because of the wide taxonomic knowledge that is necessary to apply them, and because their use does not provide advantages in terms of the time and resources used for fieldwork.

One promising alternative is the use of growth forms as an indicator of lichen diversity. Lichen strategies related with growth forms depend on environmental conditions [11,12]. In this regard, previous studies have shown that the abundance of different growth forms is related to microclimatic factors associated with forest structure (canopy cover), such as humidity, light availability, or temperature [2,13]. Moreover, growth forms have been related to the physiology and activity of lichens, such as in the nutrient uptake, photosynthetic performance, or water-use strategy [14,15]. Recent studies have incorporated the use of growth forms for assessing the total species abundance in tropical montane rainforests [2] and in Mediterranean oak forests [16]. Since growth forms are easier to recognize than lichen species, the quantification of growth forms can contribute to the rapid evaluation of areas with high lichen diversity [16].

Despite the a priori usefulness of the proposed method to assess total species abundance, it has only been tested in Mediterranean monospecific oak (*Quercus* spp.) forests. Thus, our main goal was to investigate the feasibility of the method to predict epiphytic lichen abundance based on growth forms, covering a wide variety of forest types and a vast area of Europe and Central-South America. Our first hypothesis was that an increase of the total species abundance involves an increase in the number of growth forms. The second hypothesis was that this correlation between the number of growth forms and species abundance is present both at a global scale and in different forest types. However, the third hypothesis proposed lower correlation values between species abundance and growth forms for Central-South American forests due to their great heterogeneity and diversity.

2. Material and Methods

2.1. Literature Search and Selection

The study area comprised forests located in 13 countries in Europe and 12 countries in Central and South America (Table 1). We conducted a literature search in specific databases available from a website focused on recent literature on lichens (last access on 28 December 2018) (http://nhm2.uio.no/botanisk/lav/RLL/RLL.HTM). We used a combination of the following search strings: "beech, *Fagus*, oak, *Quercus*, conifer, *Picea*, *Pinus*, *Abies*" for Europe. For Central and South America, we used the name of the different countries, such as Ecuador, Bolivia, Cuba, (Table 1) due to the great diversity in the nomenclature of existing forests in these countries (e.g., Chaco, Yungas, Caatinga).

No limitation on the year of publication was used. The search provided more than 500 papers. Fifty-four papers were retained after an accurate screening of titles and abstracts, based on satisfying the following criteria: (i) floristic or ecological studies and (ii) relevant information on lichen diversity for a certain type of forest. Additionally, papers were included from previous literature searches conducted by the authors, as well as from other papers recently accepted and available online. We also included data from four ecological unpublished studies from our own research projects (Table 1). Although forests used for grazing, hunting, farming, etc. are usually poorer in lichen species [17–19], they were included and considered since we were interested in detecting great differences in species richness in order to check our hypotheses.

The selected papers included a large variety of forests at different altitudes and latitudes: Mediterranean (*Quercus* spp.), temperate (*Fagus* spp.), coniferous (*Abies alba, Picea abies, Pinus* spp.), montane (*Nothofagus* spp.), semiarid lowland forests, lowland amazon forests, tropical montane rainforests, tropical dry forests, Atlantic rainforests, riparian forests, etc. (Table 1).

Table 1. Summary of the reviewed studies according to the country (in alphabetical order). Altitude (Alt) and forest type are also included. * refers to four ecological unpublished studies from our own research projects.

Bibliographic Reference	Country	Alt (m)	Forest Type
Central-South America	_ country	Alt (III)	Torest Type
[20]	Argentina	500-1350	Chaco, semiarid lowland forest
[21]	Argentina	1000	Belt of mountain woodland and the transition with the
[22]	Argentina	4	Riverside forest
[23–29]	Bolivia	155-4500	Chiquitano-Chaqueno forest, lowland Amazon forest, Tucumano-boliviano montane forest, Yungas montane
[30]	Brazil	80	Tropical rainforest
[31]	Brazil	130-250	Caatinga vegetation
[32]	Brazil	400-600	Breios and Caatinga
[33]	Brazil	300-800	Atlantic rainforest
[34]	Brazil	240-872	Riparian forest
[35]	Brazil	800-900	Atlantic rainforest
[36]	Brazil	0-800	Atlantic rainforest Caatinga
[00]	Diuzn	0 000	Andean-Patagonian forests and the Andean deciduous
[37]	Chile	1000-1500	forest
[38]	Chile	8–308	Valdivian temperate rainforest (without Nothofagus spp.)
[39]	Chile	1100-1150	Montane coniferous forest (Fitzroya cupressoides)
[40]	Chile	0-349	Valdivian temperate rainforest
[41]	Chile	1100-1150	Temperate forest (<i>Nothofagus dombeyi</i> , <i>N. nitida</i> , and <i>N.</i>
*Rodríguez et al. (in prep.)	Chile	930-1050	Temperate forest (<i>Nothofagus pumilio</i>)
[42]	Colombia	700–4000	Lowland forest, lower montane rainforest, tropical montane rainforest, and <i>Polylevis</i> forest
[43]	Colombia	1900-2000	Premontane forest
[44]	Colombia	2800-3200	High Andean forest
[45]	Costa Rica	2900	Oak forest
[46]	Cuba	1000	Tropical montane rainforest
[47]	Cuba	20	Coastal sclerophyllous forest
[48]	Ecuador	2196–2848	Tropical montane rainforest (primary, secondary, and monospecific <i>Alnus acuminata</i>)
[49]	Ecuador	0–300	Tropical dry forest
[50]	Ecuador	1800–2650	Tropical montane rainforest
*Aragón et al. (in prep.)	Ecuador	80–300	Amazonian forest
[51]	Mexico	2714–2775	Coniferous forest (<i>Pinus ayacahuite, Abies religiosa</i>)
[52]	Panama	0–160	Lowland and coastal forest
[53]	Peru	300-1500	Tropical dry forest
[54]	Venezuela	106-1400	Tropical rainforest
[55]	Venezuela	800-5000	Montane forest (lower and upper) and Polylepis sericea forest
Europe			
*Hurtado et al. (in prep)	Austria	750–1120	Temperate forest (Fagus sylvatica)
[56]	Spain	800	Temperate forest (Fagus sylvatica)
[57]	Spain	870-1100	Mediterranean pine forest (Pinus pinaster, P. nigra)
[58]	Spain	1280-1560	Mediterranean pine forest
[59]	Spain	300-700	Oak forest (Quercus suber)
[60]	Spain	1550	Mediterranean pine forest (Pinus nigra, Ilex, Acer)
[61]	Spain	1000	Oak forest (Quercus ilex, Juniperus oxycedrus)
*Aragón et al. (in prep.)	Spain	710	Oak forest (Quercus faginea)
*Hurtado et al. (in prep)	Spain	856	Temperate forest (Fagus sylvatica)
[62]	Estonia	30-40	Coniferous forest (Picea abies, Pinus sylvestris)
[63]	Estonia	170-200	Coniferous forest (Picea abies, Pinus sylvestris)
[64]	Finland	170	Coniferous forest (Picea abies)
[65]	France	350-500	Oak forest (<i>Quercus ilex</i>)
*Hurtado et al. (in prep)	France	1180–1272	Temperate forest (Fagus sylvatica)

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bibliographic Reference	_ Country	Alt (m)	Forest Type
Europe			
[66]	Greece	570–1210	Oak forest (Quercus cerris, Q. coccifera, Q. frainetto, Q. petraea, Q. pubescens, Q. trojana, Pinus nigra)
[67]	Greece	800-1500	Mediterranean pine forest (Pinus nigra)
[68]	Greece	750-1510	Mediterranean pine forest (Pinus nigra)
[69]	Hungary	250-350	Temperate forest (Fagus, Quercus, Carpinus, Pinus)
[70]	Italy	0-1000	Oak forest (Quercus pubescens)
[71]	Italy	50-390	Oak forest (Quercus ilex, Q. cerris, Q. pubescens)
[72]	Italy	0–900	Oak forest (Quercus pubescens)
[73]	Italy	400-1900	Oak forest (<i>Quercus</i>) and coniferous forest (<i>Pinus</i> sylvestris, Abies alba)
*Hurtado et al. (in prep)	Italy	1077-1213	Temperate forest (Fagus sylvatica)
[74]	Poland	88-150	Oak forest (<i>Quercus rubra</i>)
*Hurtado et al. (in prep)	Slovakia	1233	Temperate forest (Fagus sylvatica)
[75]	Sweden	25-170	Temperate forest (Fagus sylvatica)
[76]	Sweden	260-583	Coniferous forest (<i>Pinus contorta, P. sylvestris, Picea abies</i>)
*Hurtado et al. (in prep)	Sweden	107-161	Temperate forest (Fagus sylvatica)
[77]	Turkey	900-1400	Temperate forest (Fagus orientalis)
[78]	Turkey	21–717	Oak forest (Quercus cerris)
[79]	Ukraine	400-1350	Temperate forest (Fagus sylvatica)

Table 1. Cont.

2.2. Data Analyses

All lichen species from the studied papers were classified according to their thallus growth form (including the ascoma type in the case of crustose species). For that purpose, we followed specific literature [2,14,16,80–83] and the Global Information System for lichenized and non-lichenized ascomycetes (www.lias.net).

In general, thallus morphology is related to specific environmental conditions such as light intensity, temperature, humidity, and wind. For example, fruticose species are well-adapted to enhance air humidity uptake, and they depend on precipitation or water harvesting from fog in high mountains. Fruticose species are further divided by thallus morphology (dorsiventral or cylindrical) and color (light or dark colored), the latter determined by the presence of usnic acids (e.g., *Usnea, Ramalina, Evernia*) or dark melanin (e.g., *Bryoria*). Both features are related to environmental conditions: thallus morphology is related to the capacity for water storage and loss, and thallus color is related to protection against solar radiation. For certain groups (e.g., crustose inconspicuous species) we prioritized a finer division based on ascoma type (e.g., with lirellae, perithecia, or rounded apothecia) over thallus functionality given the reduction in the thallus morphology. Because of the high diversity of crustose inconspicuous species in dry areas (e.g., up to 90% of the species in tropical dry forests), the analysis of these growth forms is essential to make this method applicable to all forest types around the world.

Overall, 31 different growth forms were considered (Table 2). It is important to mention that lichen growth forms are easy to recognize by non-specialists and without knowing the taxonomical identity of the species. Different ascoma types of crustose inconspicuous species are also easily recognized using a field magnifier. Additionally, images can be found for all the types of growth forms sampled (Table 2) on different websites: Consortium of North American Lichen Herbaria (lichenportal.org), Biodiversidad Virtual (biodiversidadvirtual.org), and Pictures of tropical lichens (tropicallichens.net).

Table 2. List of growth forms of epiphytic lichens studied. A lichen species is included as an example of each growth form.

Growth Forms (Examples)	
Leprarioid (Lepraria incana)	
Crustose Conspicuous (<i>Pertusaria albescens</i>) Inconspicuous	
 with rounded apothecia (Buellia disciformis) with lirellae (Arthonia radiata) with perithecia (Pyrenula nitida) Ocellularia-type apothecia (Ocellularia crocea) Chiodecton-type apothecia (Chiodecton leptosporum) Byssoloma-type apothecia (Byssoloma meadii) stalked apothecia (Calicium viride) 	
Granular crustose (<i>Agonimia octospora</i>) Crustose ecorticate (<i>Herpothallon rubrocinctum</i>) Crustose placodioid (<i>Pyxine berteriana</i>)	
Squamulose Flat squamulose (<i>Normandina pulchella</i>) Convex squamulose (<i>Phyllopsora furfuracea</i>) Thallus <i>Psoroma</i> -type (<i>Psoroma hypnorum</i>) Squamulose-foliose (<i>Pannaria rubiginosa</i>)	
Foliose Foliose placodioid (<i>Pectenia plumbea</i>) Foliose umbilicate (<i>Dictyonema glabratum</i>) Foliose narrow-lobed (<i>Physconia venusta</i>) Foliose broad-lobed (<i>Parmelina tiliacea</i>) Large foliose tomentose (<i>Erioderma leylandii</i>) Large foliose glabrae and appressed (<i>Peltigera horizontalis</i>) Large foliose glabrae and ascending (<i>Sticta weigelii</i>) Foliose gelatinous swollen (<i>Collema nigrescens</i>) Foliose gelatinous flat (<i>Leptogium cyanescens</i>)	
Filamentous (Coenogonium linkii)	
Fruticose Fruticose cylindrical light-colored (<i>Usnea glabrescens</i>) Fruticose cylindrical dark-colored (<i>Bryoria implexa</i>) Fruticose dorsiventral light-colored (<i>Ramalina fraxinea</i>) Fruticose dorsiventral dark-colored (<i>Pseudevernia furfuracea</i>)	

We used linear regression models to explore the potential of lichen growth form richness to predict epiphytic lichen richness. Previously, assumptions of the models were checked testing the normality of the residuals. Subsequently, residual graphs were analyzed to check the normality, linearity, and independence of the variables. We tested the use of growth form number as a species richness indicator at different levels: (1) all forests together, (2) forests of Europe and Central-South America independently, (3) each European forest type (Mediterranean, temperate, and coniferous), and (4) unmanaged and managed forests separately. Forest type was not analyzed for Central and South America due to their great variability and the high diversity of tree species in each forest type. All analyses were carried out using the R 3.3.3 environment (R Development Core Team, 2006).

3. Results

A total of 119 forests were considered, covering 25 countries (13 in Europe and 12 in Central-South America) (Table 1), and 43 of which were unmanaged or poorly managed. The number of species in each forest ranged from 263, found in a tropical montane rainforest (Ecuador) [48], to 15 species from a semi-arid lowland rainforest (Argentina) [20]. In Europe, beech forests showed the highest species richness (up to 123 species) [56], while pine forests in Sweden were the least diverse (10–20 species) [76]. In relation to growth forms, crustose inconspicuous species with apothecia, foliose narrow-lobed, and foliose broad-lobed were the most common lichen groups.

Linear regression models showed that the epiphytic lichen abundance was highly and positively correlated with the number of growth forms at all geographical levels considered (Figures 1–3). R² values obtained when all forests were considered together were similar to those obtained after dividing between European and Central-South American forests (Figure 1). When different forest types were considered in Europe, the highest correlation value was found in beech forests (Figure 2). Finally, the lowest correlation values were found in the managed forests (Figure 3B).



Figure 1. Results of the linear models based on the number of growth forms (x-axis) and epiphytic species abundance (y-axis) for: (**A**) All forests together (y = 6.896x - 26.109, n = 119, $R^2 = 0.739$), (**B**) Central-South American forests (y = 7.116x - 23.678, n = 58, $R^2 = 0.742$), and (**C**) European forests (y = 5.297x - 12.543, n = 61, $R^2 = 0.713$); p < 0.0001 in all cases.



Number of growth forms

Figure 2. Results of the linear models based on the number of growth forms (x-axis) and epiphytic species abundance (y-axis) in European forests for: (**A**) Coniferous forests (y = 6.681x - 23.732, n = 22, $R^2 = 0.719$), (**B**) Oak forests (y = 4.839x - 7.124, n = 22, $R^2 = 0.679$), and (**C**) Beech forests (y = 6.597x - 34.437, n = 17, $R^2 = 0.827$); p < 0.0001 in all cases.



Figure 3. Results of the linear models based on the number of growth forms (x-axis) and epiphytic species abundance (y-axis) in: (**A**) Unmanaged forests (y = 7.291x - 27.868, n = 43, $R^2 = 0.695$) and (**B**) Managed forests (y = 3.554x + 4.136, n = 76, $R^2 = 0.486$), where p < 0.0001 in both cases.

4. Discussion

Our results consolidated the potential use of growth forms to assess epiphytic lichen abundance. The most notable result is that lichen growth forms could be used as a surrogate of species abundance in a wide range of forests both in Europe and Central-South America, where an increase in species abundance was always related to an increase in the number of growth forms. These results are similar to those previously obtained in a local study in central Spain developed in three types of oak forests (*Quercus faginea*, *Q. ilex*, *Q. pyrenaica*) [16].

An interesting and unexpected outcome was the relationship found between growth forms and lichen species richness for Central-South American forests, in spite of: (1) the great heterogeneity of forest types, ranging from dry coastal forests to montane tropical rainforests; (2) the large differences in forest structure, including multi-strata forests (tropical montane or Amazonian forests) to mono- or bi-stratified forests such as temperate (*Nothofagus* spp.) or dry forests; and (3) the great diversity of tree species present within a forest (Atlantic, dry, or montane rainforests), when compared against nearly monospecific forests (*Nothofagus* spp.).

The correlation between the number of growth forms and epiphytic abundance was also high for European forests, despite the variability produced by differences in the physical and chemical characteristics of the bark (e.g., pH, roughness) of the different tree species (*Abies, Picea, Pinus, Fagus, Quercus*). The highest correlation was detected in beech forests, whereas in oak forests this correlation was lower, probably as a consequence of the high number of *Quercus* species considered (10 species), including perennial, deciduous, and marcescent species. These species differed in bark roughness, with thick and very rough barks (*Quercus suber, Q. pyrenaica*) or with thin bark cracks (*Quercus ilex*). Furthermore, *Quercus* species in Europe extend along a wide distributional area covering a high climatic variability, from southern Mediterranean to northern temperate forests [84].

Lichens are firmly dependent on environmental conditions and very sensitive to anthropogenic disturbances [17,85–87], meaning that they are excellent indicators of environmental changes [2,12]. Besides, they have some easily detectable traits such as growth form [12,87,88] that are related with ecosystem functioning and whose diversity depends on environmental factors [2,87–90]. Our results showed that unmanaged forests harbored a higher number of epiphytic species and also a high diversity of growth forms. In this sense, different studies have already underlined that mature and unmanaged forests harbored a higher number of epiphytic lichen species, whereas in disturbed forests, epiphytic lichens progressively decreased [1,91,92]. Moreover, lichen species loss in response to environmental changes produced by forest disturbances is clearly correlated with the loss of functional strategies [2,11,12]. It is also important to note that the prediction of total diversity based on the number of growth forms was lower in the managed forests.

Thallus morphology is optimized for the uptake and loss of water [14], and therefore the environmental conditions of a specific location will affect the presence of different morphological types [16]. Sunny morpho-groups such as crustose inconspicuous, foliose narrow-lobed, and foliose broad-lobed are adapted to live in open forests, under high radiation and water stress environmental conditions [3,12,16,93]. Although they appear more frequently in managed forests, species developing these growth forms are also frequent in unmanaged and mature forests [92], specifically in forest clearings or in the most exposed branches of trees. However, species of shaded morpho-groups (e.g., crustose ecorticate, squamulose, squamulose-foliose, large foliose, foliose gelatinous, filamentous) were frequent in more dense and well-preserved forests, and were almost absent in open and managed woodlands [3,11,16,82,93,94]. The higher humidity inside forests benefits the colonization of the species with higher moisture requirements [16,82]. For example, gelatinous lichens (Collema, Leptogium) develop a thin upper cortex that favors an immediate hydration in a very short time [95,96], and they may suffer photoinhibition due to excessive radiation in more open forests [11,95]. Crustose ecorticate species are more frequent inside tropical forests [48,82]. They are well-adapted to remove water excess in two different ways: (1) the medullae hyphae create a hydrophobic layer, and (2) the draining channels of the prothallus exude the water after rain events [82].

As we have already pointed out, previous studies have shown that under stressful conditions the number of species in a specific community should drop. In parallel, the number of functional traits and their variability should also diminish (i.e., functional convergence), at least when environmental filters control the community assembly [97–99]. This positive relationship between species abundance and growth forms diversity may be because a higher number of lichen species could represent a wider range of traits values as a consequence of functional complementarity [100]. In this way, the best well-preserved forests that harbor higher species abundance also harbor a greater diversity of growth forms.

Growth forms are easily recognizable by non-specialists using only a small field magnifier. However, a small likelihood for error (e.g., non-detection or mis-identification of growth forms) may exist, especially in forests with high diversity of epiphytic species and a large number of growth forms. In this case, a direct effect on the number of predictable species may occur because of the linear relationship among growth forms and species abundance. Here, we estimated an average error of 5% when a growth form was not detected. This percentage was calculated based on the case of underestimating a total of seven species per unmanaged forests (higher abundance of epiphytic species), which constitutes an insignificant error. Based on all the results obtained, this proposal provides a valid method for estimating the total lichen richness, especially in South American forests (e.g., tropical rain forests), which show the highest world rates of forest alteration [101].

In conclusion, lichen growth forms may be used to infer total species abundance considering a wide variety of forest types and at a global scale. The use of growth forms will provide an important step for forest conservation, and a promising alternative and complement to evaluate the epiphytic diversity because most growth forms have a cosmopolitan distribution and are easily recognizable in the field.

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