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To cite this article: Daniela Mellado-Mansilla, Carolina A. León, Gabriel Ortega-Solís, Javier Godoy-Güinao, Ricardo Moreno & Iván A. Díaz (2017): Vertical patterns of epiphytic bryophyte diversity in a montane *Nothofagus* forest in the Chilean Andes, *New Zealand Journal of Botany*, DOI: [10.1080/0028825X.2017.1364273](https://doi.org/10.1080/0028825X.2017.1364273)

To link to this article: <http://dx.doi.org/10.1080/0028825X.2017.1364273>



Published online: 23 Aug 2017.



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SHORT COMMUNICATION



## Vertical patterns of epiphytic bryophyte diversity in a montane *Nothofagus* forest in the Chilean Andes

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Epiphytic bryophytes are an important component of many forest ecosystems. Several studies have reported vertical distribution patterns for this species, finding many taxa growing along the entire vertical profile of host trees, some in the most exposed upper areas of the canopies. Many studies in Chilean forests have focused on epiphytes, but most of them were located in lowland and coastal forests. This study is the first scientific exploration of the epiphytic communities that occupy the entire vertical profile of large *Nothofagus dombeyi* (Mirb.) Oerst. trees in a montane *Nothofagus* forest in the Chilean Andes (39°25'S). Our goals were (i) to describe the richness of the epiphytic species inhabiting large *N. dombeyi* trees, (ii) to evaluate differences in composition related to the height, azimuth and diameter of each host tree, and (iii) to explore the distribution of epiphytic species within the vertical profile of trees. We climbed 10 large *N. dombeyi* trees located between 940 and 1190 m in altitude. All epiphytes were sampled every meter, from the base up to the highest climbable branch. The epiphytic community was dominated by non-vascular epiphytes, with 17 taxa, all of which were bryophytes. *Frullania rostrata*, *Gackstroemia* aff. *magellanica*, *Hypnum skottsbergii* and *Zygodon penstachius* were the most frequently observed taxa. Species composition varied with height on the tree, but no differences between trees were observed. The vertical distribution showed that three taxa were restricted to the crown, five were abundant throughout the whole vertical profile and four were restricted to the trunk close to the ground. The information here could be relevant due to the pressure to manage these *Nothofagus* forests, where the associated biodiversity is not even recorded in forestry inventories.

### ARTICLE HISTORY

Received 20 March 2017  
Accepted 2 August 2017

### KEYWORDS

Epiphytes; forest canopies; liverworts; mosses; Southern South American temperate rainforests

### ASSOCIATE EDITOR

Professor Lohengrin Cavieres

## Introduction

Epiphytic bryophytes are an important component of most forest canopies, from boreal forests in the Northern Hemisphere to temperate forests in the Southern Hemisphere, including tropical forests (Esseen et al. 1997; Friedel et al. 2006; Mežaka et al. 2008; Díaz et al. 2010). For instance, in a lowland tropical forest in Guiana, one single tree can hold up to 67 epiphytic bryophyte species (Gradstein et al. 1990); meanwhile in a temperate forest in western Oregon, up to 32 species of epiphytic bryophytes have been reported to be found on 20 individuals of a single tree species (Pike et al. 1975). Bryophytes conduct important functions within the canopy, such as the storage of water from rain and fog, which maintains the canopy's humidity during dry periods (Rhoades 1995). Also, bryophytes can provide the substrate necessary for the establishment of other epiphytes, contributing to an increase in canopy biodiversity (Nadkarni 1984; Sporn et al. 2010).

Vertical distribution patterns of epiphytic bryophytes have been described in tropical (Cornelissen and Ter Steege 1989; Cornelissen and Gradstein 1990; Sporn et al. 2010) and temperate (McCune 1993; McCune et al. 1997; Lyons et al. 2000) forests. For instance, Cornelissen and Ter Steege (1989) found a clear relationship between epiphytic species, their life-forms and the vertical zones they occupied in their host trees. Sporn et al. (2010) reported that 45% of the epiphytic bryophytes found in their study were restricted to the crowns of emergent trees. Finally, Lyons et al. (2000) described that bryophytes were more abundant in the lower and middle zones of the *Tsuga heterophylla* trees studied. Vertical distribution patterns can be explained by the wide microhabitat heterogeneity present throughout the vertical profile of host trees (Hietz and Briones 1998; Freiberg 2001; Woods et al. 2015) and the ability of epiphytes to colonise each microhabitat, according to their physiological requirements and adaptations (Hietz-Seifert et al. 1996; Nieder et al. 1999; Sporn et al. 2010).

Southern South American Temperate Rainforests (SATR) are recognised as a biodiversity hotspot with a high percentage of endemic species under strong human pressure (Olson and Dinerstein 1998; Myers et al. 2000). There are many relevant studies on SATR epiphytes (Muñoz et al. 2003; Woda et al. 2006; San Martín et al. 2008; Parra et al. 2009; Saldaña et al. 2014; Parra et al. 2015); nevertheless, these studies had a ground-based perspective. Few studies have considered the entire vertical profile of SATR (Clement et al. 2001; Díaz et al. 2010), and those that have showed a high diversity and abundance of both vascular and non-vascular epiphytes along the whole vertical profile. Most of the studies mentioned above also correspond to lowland or coastal SATR, which are widely dominated by vascular epiphytes (Smith-Ramírez 2004). Although lowland and coastal SATR are significant, an important fraction of forested areas of the SATR are located in the Andes, where the climate and forest species composition are both very different from those along the Coastal Range. Andean montane forests are widely dominated by *Nothofagus* species (Gajardo 1994) and the climatic conditions are harsher, with colder snowy winters and hot sunny summers. Most Andean forests between 37°S and 45°S are dominated by *Nothofagus dombeyi* (Mirb.) Oerst trees (Donoso 1996; Donoso et al. 2004). This evergreen species is frequently one of the largest individuals in the forest, reaching 50 m in height and over 2 m in diameter (Veblen 1985; Donoso et al. 2006). This species resides from sea level up to 1200 m in altitude, but becomes dominant above 600 m in altitude (Donoso et al. 2006).

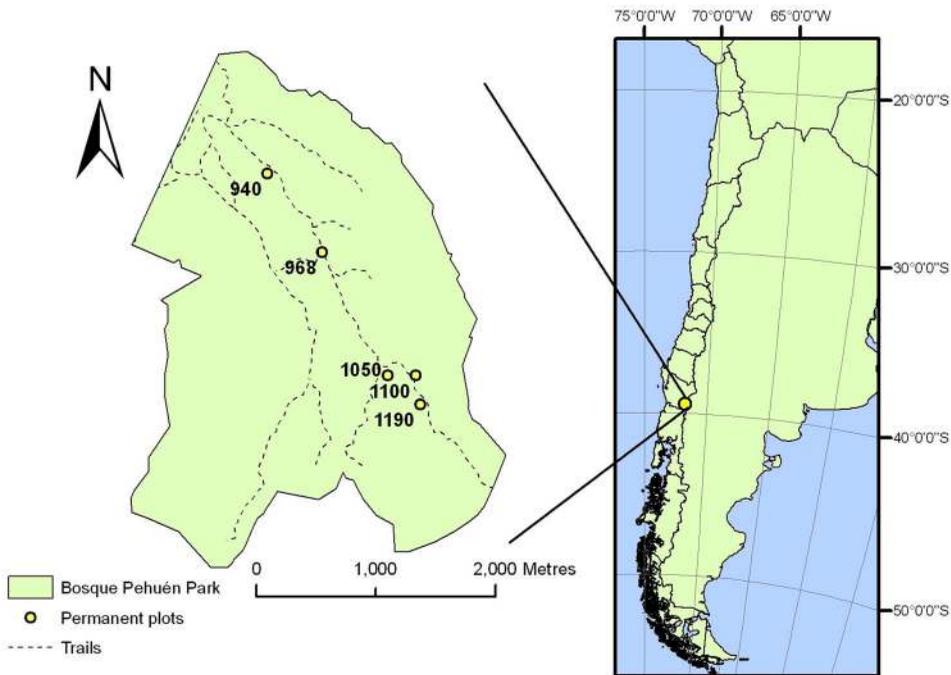
In this study, we characterise the richness and composition of epiphytes in large *N. dombeyi* trees in an Andean montane forest and explore the occurrence of species along the entire vertical profile of their hosts. We addressed the following questions: Do the epiphytic species in *N. dombeyi* trees occupy the entire vertical profile? Do these epiphytic species demonstrate vertical distribution patterns?

Consequently, our main goals were: (i) to describe the richness of the epiphytic species inhabiting large *N. dombeyi* trees, (ii) to evaluate differences in composition related to the height, azimuth and diameter of each host tree, and (iii) to explore the distribution of epiphytic species within the vertical profile of trees. This is the first scientific exploration of canopy epiphytic diversity along the entire vertical profile of trees in an Andean *Nothofagus* forest. The information reported here could be useful to improve forest management plans and biodiversity inventories in SATR located in the Andean range.

## Materials and methods

### Study site

Our study was conducted in the Bosque Pehuén park, a private reserve owned by the Fundación Mar Adentro, a Chilean non-profit government organisation. This forest is located in the southern Andes, at 39°25'S and 71°45'W covering 882 ha along an altitudinal gradient from 860 to 1400 m (Figure 1). The climate is cold temperate, with frequent snow cover in the winter. The annual mean temperature and annual precipitation at the nearest weather station in the city of Pucón [200 m above sea level (asl)] are 10°C and



**Figure 1.** Location of the Bosque Pehuén park in the Andes of southern Chile.

2300 mm, respectively (Agromet-INIA 2013–2014). However, the climate in the Bosque Pehuén park is most likely colder and drier, due to the high altitude and the rain shadow effect of the Villarrica Volcano. Preliminary data showed that Bosque Pehuén had 68 days with temperatures below 0°C throughout 2015, with a minimum of –5.2°C on 20 July in the Austral winter, whereas the summer of 2014–2015 had 18 days over 25°C and a maximum of 30°C on 10 December 2015 (Díaz et al. unpublished data).

The lower elevations of Bosque Pehuén are densely covered by second-growth forests of *Nothofagus alpina* (Poepp. & Endl.) Oerst., *N. dombeyi* and *Nothofagus obliqua* (Mirb.) Oerst. with scattered individuals of *Saxegothaea conspicua* Lindl. (Podocarpaceae). Throughout the mid-altitudes (from 1050 to 1200 m) vegetation corresponds to old-growth forests dominated by large *N. dombeyi* trees, with few human disturbances. At higher altitudes (above 1250 m) forests become a mix of second and old-growth forests dominated by *N. dombeyi*, *Nothofagus pumilio* (Mirb.) Oerst. and *Araucaria araucana* (Molina) K. Koch. (Araucariaceae) trees. Because of the land history of the park (Díaz et al. unpublished data) large *N. dombeyi* trees are biological legacies important for the forest structure and diversity, but it is also the most abundant species in the study site.

### Study design

We accessed the canopy of 10 large *N. dombeyi* trees with diameters at breast height (DBH) between 68 and 204 cm, and heights between 15 and 29 m (Table 1). We used a single rope-climbing technique to reach the crown of each tree (Perry 1978). In each selected tree, we traced a transect along the entire vertical profile, from the base up to the highest climbable branch. At every meter we established circular sub-plots 50 cm in diameter along the main trunk, and collected all of the epiphytes present within these sub-plots for further determination. We also recorded the height and azimuth of each circular plot because of their potential influence on the presence of epiphytic species. Only non-vascular species were found. Lichens were present, but were excluded from this study; due to the complexity of their identification they should be reserved for analyses in future studies. Species determination followed taxonomic keys based on Gradstein et al. (2001), Larraín (2007), Hässel de Menéndez and Rubies (2009) and León and Oliván (2014). Voucher specimens were deposited at the Herbarium of Museo Nacional de Historia Natural (SGO), Chile.

The sampled trees correspond to the two largest individuals found within each of five pre-established 50 × 20 m plots. Each plot was located at a different elevation (from 940 to

**Table 1.** Sampled trees. *Nothofagus dombeyi* individuals, their heights, and locations (meters above sea level). Code numbers are the individual identification codes given to each tree.

Tree (code number)	Diameter at breast height (cm)	Height (m)	Number of epiphytic taxa per tree	Altitude (m)
73	100	26	11	940
104	140	20	9	940
196	81	20	9	968
200	68	20	8	968
29	100	15	9	1050
59	118	21	8	1050
39	179	29	11	1100
5	103	24	9	1100
67	204	28	3	1190
87	102	20	5	1190

1190 m asl). The plots correspond to a long-term monitoring project carried out by Fundación Mar Adentro and the Universidad Austral de Chile. The forest structure of each plot has been previously characterised by Díaz et al. (unpublished data), for details see Table 2.

### Data analyses

We compared epiphytic species richness per tree using sample-based rarefaction curves with 95% confidence intervals, based on the Chao 2 index (Hsieh et al. 2016). Sample-based rarefaction allows for the comparison of species richness among groups of samples with different sizes using a Monte Carlo randomisation procedure for the occurrence data (Gotelli and Colwell 2001). We used permanova and non-metric multidimensional scaling to evaluate the differences in epiphytic composition related to height, azimuth and DBH. The input matrix was constructed by using the species occurrence (presence–absence) within the circular sub-plots in each tree based on Jaccard's distance (Oksanen et al. 2016). Permutation in permanova were restricted per tree and the interaction between height and DBH was added to the model to control their joint effect. However, it must be noted that our study was not intended to perform a full evaluation of the DBH variable, because only the largest trees at each plot were sampled. To compare the relative position of each epiphytic species on the vertical profile of trees of different heights, we standardised the total height of each tree to 100% and plotted the raw occurrence of each epiphyte against the vertical profile of their host trees. In this way, the location of an epiphytic species in the treetop of a tree 15 m tall was equivalent to a similar epiphyte located in the treetop of a 25-m tall tree. In both cases, the location was in the treetop, at 100% of the height. According to this standardisation, the crown represented around 60% of the total height of trees. Analyses were performed in R 3.2.3 (R Core Team 2015) with the packages iNEXT 2.0.12 (Hsieh et al. 2016), vegan 2.4-0 (Oksanen et al. 2016) and analogue 0.17-0 (Simpson and Oksanen 2016).

## Results

### Species richness

We found a total of 17 epiphytic taxa, all of them bryophytes with 11 liverworts and six moss species. Two taxa found are endemic to southern South America, but the rest present a wide distribution range (Table 3). *Frullania rostrata*, *Gackstroemia* aff. *magellanica*, *Hypnum skottsbergii* and *Zygodon penstachus* were the most frequent species (Table 3). The highest richness was found in two trees with eleven taxa each (Table 1).

**Table 2.** Structural characterisation of each plot by Díaz et al. unpublished data.

Altitude (m)	Basal area (m <sup>2</sup> /ha)	Ranging DBH (cm)	Forest type
940	74	23–41	Secondary
960	54	28–81	Secondary
1050	49	37–118	Degraded Old growth
1100	83	51–179	Old growth
1190	137	33–204	Old growth

Note: DBH, diameter at breast height.

**Table 3.** Taxa list, vertical distributions and occurrences.

Family	Taxa	Vertical distribution		Occurrence (%)
		(%)	(m)	
<b>Liverworts</b>				
Lophocoloaceae	aff. <i>Chiloscyphus</i>	0–10	0	0.4
	<i>Chiloscyphus rigens</i> (Hook.F. & Taylor) Hassel de Menéndez	0–10	0–1	0.9
Geocalyceae	<i>Clasmatocolea</i> aff. <i>puccioana</i> (De Not.) Grolle	7–10	2–13	2.2
	<i>Clasmatocolea rigens</i> (Hook. F. & Taylor) J.J. Engel	5–100	1–22	10.1
Jubulaceae	<i>Frullania rostrata</i> (Hook. F. & Taylor) Gottsche, Lindeb. & Nees	0–100	1–29	34.4
Lepidonalaceae	<i>Gackstroemia</i> aff. <i>magellanica</i> (Lam.) Trevis	0–100	1–28	22.9
Lepicoleaceae	<i>Lepicolea scolopendra</i> (Hook.) Dumort. ex.Trevis	20–55	4–11	1.8
Lepidoziaceae	<i>Lepidozia chordulifera</i> Taylor	0–10	0–1	2.2
Metzgeriaceae	<i>Metzgeria divaricata</i> A. Evans	65–100	17–29	1.8
Plagiochilaceae	<i>Plagiochila heterodonta</i> (Hook.f. & Taylor) Gottsche et al.	75	15	2.2
	<i>Plagiochila subpectinata</i> Besch. & C. Massal.	0–10	0	0.9
<b>Mosses</b>				
Lembophyllaceae	<i>Acrocladium auriculatum</i> (Mont.) Mitt.+	0–93	0–21	11.0
Dicranaceae	<i>Dicranoloma robustum</i> (Hook. F. & Wilson) Paris	0–90	0–26	6.2
Hypnaceae	<i>Hypnum skottsbergii</i> Ando +	0–100	0–28	31.7
Lepyrodontaceae	<i>Lepyrodon tomentosus</i> (Hook.) Mitt.	0–100	0–22	5.3
Orthotrichaceae	<i>Ulota</i> sp.	50–100	13–29	2.2
	<i>Zygodon pentastichus</i> (Mont.) Müll. Hal	0–100	2–27	18.9

Despite this, rarefaction curves showed no great differences in richness between the sampled trees. Only two individuals at 1190 m of altitude, stood out with the lowest expected richness (Figure 2).

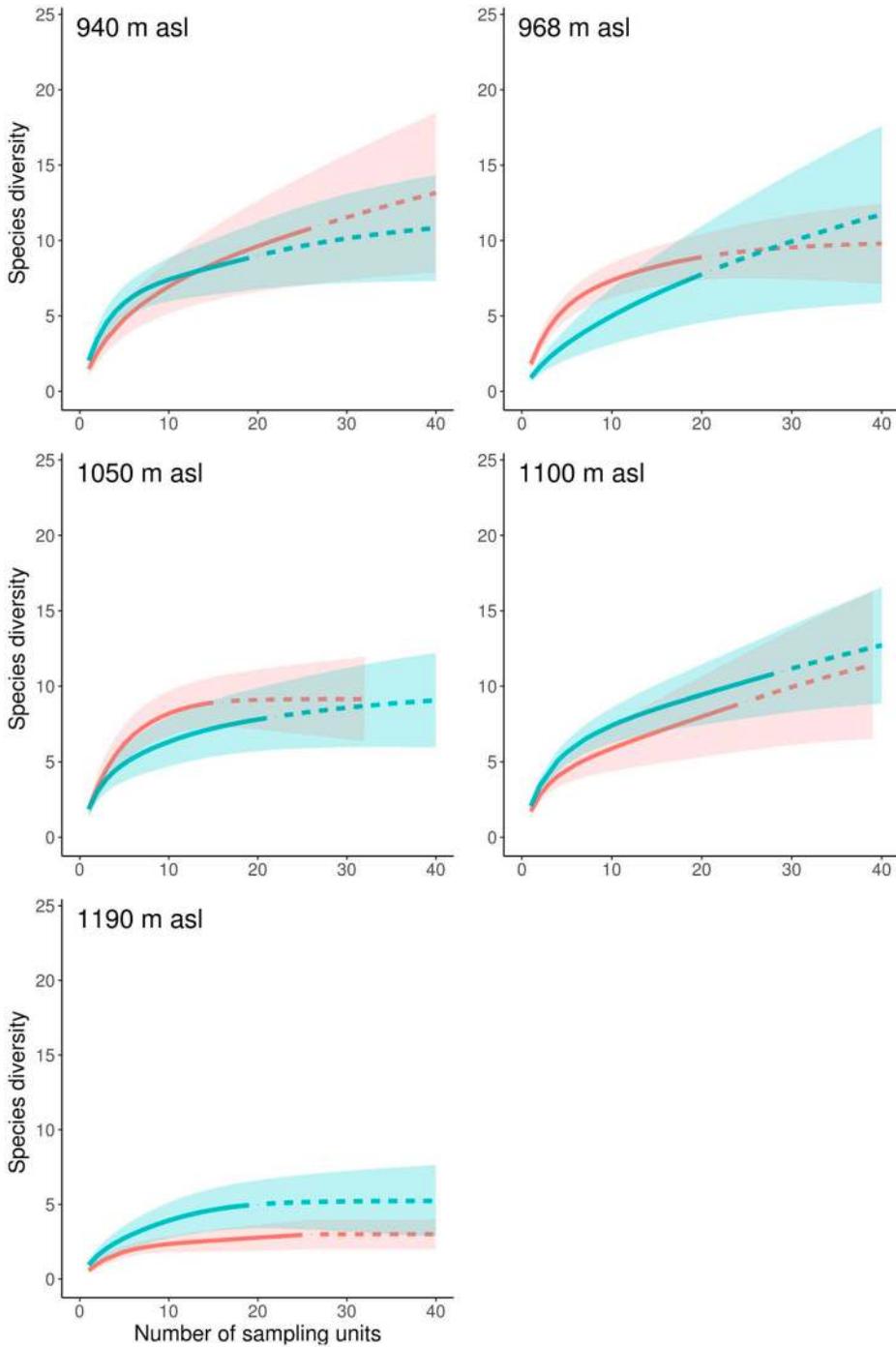
The liverworts *Plagiochila heterodonta* (Hook. f. & Taylor) Gottsche et. al. and *Plagiochila subpectinata* Besch. & C. Massal. have not been previously documented in this region. *Plagiochila heterodonta* was registered at 15 m on the trunk of a *N. dombeyi* tree, at 940 m of altitude, whereas *P. subpectinata* was registered on the lower sections of two trunks of *N. dombeyi* at 968 m and 1100 m asl. In southern Chile, *P. heterodonta* inhabit from 40°S to 44°S, but *P. subpectinata* has been reported from 40°S to 54°S (Hässel de Menéndez and Rubies 2009).

### Vertical distribution of epiphytes

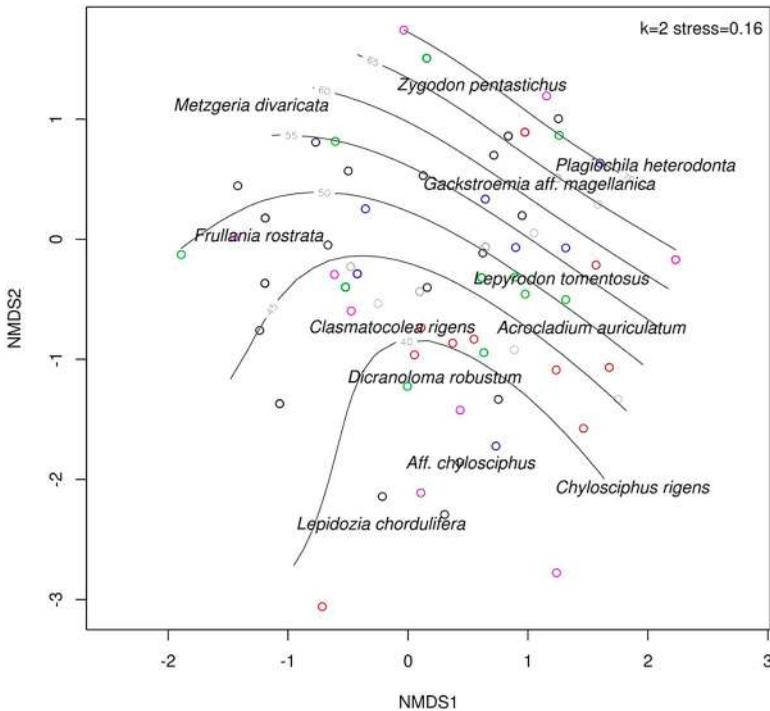
Most trees presented similar epiphyte composition but species tend to differ along the vertical profile of each host tree (Figures 3 and 4). The permanova indicated that height explained c.3% of the variation observed in the composition, but no effects related to azimuth, DBH or the interaction between DBH and height were detected (Table 4). *Frullania rostrata*, *H. skottsbergii*, *G. aff. magellanica*, *Z. pentastichus* and *Lepyrodon tomentosus* were found to be very frequent throughout all of the vertical profiles. Other taxa, such as aff. *Chiloscyphus*, *Chiloscyphus rigens*, *Lepidozia chordulifera* and *P. subpectinata* were found mainly close to the ground, while *P. heterodonta*, *Metzgeria divaricata* and *Ulota* sp. were recorded only in the crowns (Figure 4) at 29 m.

### Discussion

Our results indicated three main characteristics of epiphytic plants in *N. dombeyi* trees at the Bosque Pehuén Park: (i) the dominant species consisted of non-vascular epiphytes,



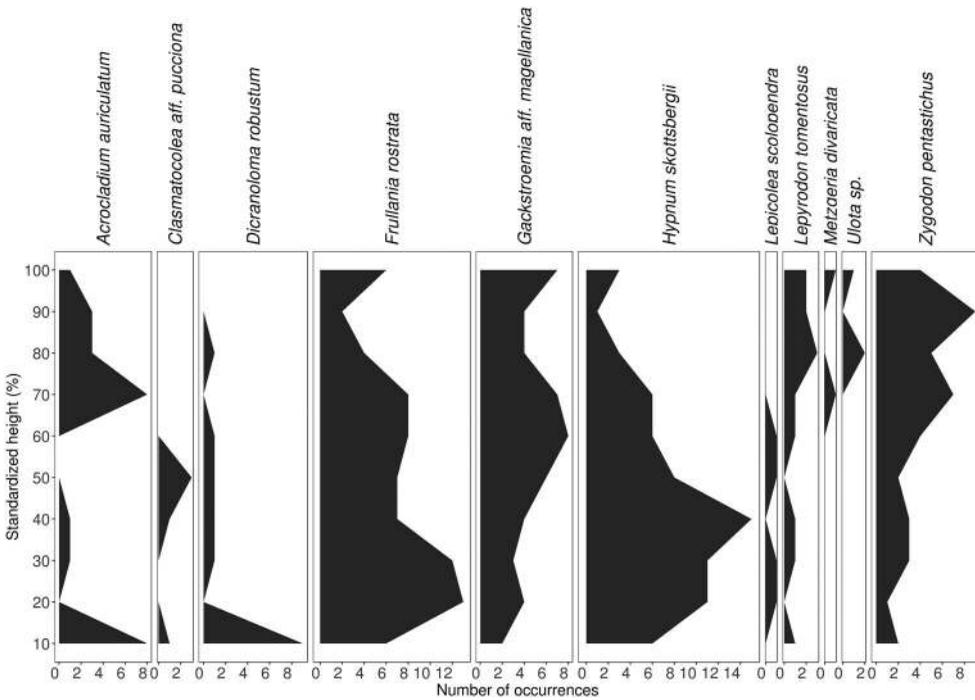
**Figure 2.** Rarefaction curves based on Chao 2 index, with 95% confidence intervals. Trees were grouped by permanent plots. Solid lines represent species diversity from observation and interpolation, and dotted lines represent predicted species diversity based on extrapolation. Coloured areas around curves represent 95% confidence intervals.



**Figure 3.** Non-parametric multidimensional scaling ordination representing the similarity of the species composition among trees. Grey lines indicate standardised heights.

(ii) height within the tree trunk is important to explain epiphytic composition, and (iii) 47% of the total species found occupied the whole vertical profile of sampled trees (Table 3; Figure 4).

In lowlands (20–300 m), large *N. dombeyi* trees can present vascular and non-vascular epiphytes, including filmy ferns, gesneriads and the bromeliad *Fascicularia bicolor* (Cárdenas 2013; Parra et al. 2015). We have also reported the presence of *Hymenophyllum ferrugineum* and other filmy fern species at this study site, but we found that they only associated with rivers, mostly growing as saxicolous (Mellado-Mansilla et al. 2015), and no individuals have yet been found in vertical profiles. Therefore, the absence of vascular epiphytes in the vertical profiles of studied trees and the dominance of non-vascular species could be related to the harsh environmental conditions in the Andes Mountains. In general, the abundance of vascular epiphytes tends to be lower at high elevations than in lowland areas due to freezing temperatures and snow cover (Krömer et al. 2005). Bryophytes, on the other hand, have particular adaptations to survive in environments that are too harsh for vascular species (Barkman 1958; Glime 2007; Méndez et al. 2013). Indeed, most bryophyte species are desiccation-tolerant and can survive dry and freezing conditions by suspending their metabolism (Minami et al. 2005; Proctor et al. 2007). Hence, when conditions improve, the recovery rates for most bryophyte species are extremely rapid, reaching full recovery within a few hours (Oliver et al. 2005), unlike most vascular plants.



**Figure 4.** Number of incidences of epiphytic mosses and liverworts along the vertical profile in Bosque Pehuén park. Tree heights were standardised to a percentage of height (see Materials and methods). Data from all trees were pooled.

Species composition was found to be homogeneous among the sampled trees (Figure 3). This suggests that, despite the differences in forest types and the potential changes in microclimatic conditions along the altitudinal range, large *N. dombeyi* trees are inhabited by almost the same epiphytic taxa. Regarding species richness, only the two trees at the highest altitude (1190 m) tended to show a lower number of species (Figure 2), probably due to the more extreme microclimatic conditions to which they were exposed, including strong winds and lower temperatures. It should also be noted that the slope of the rarefaction curves for some trees tended to be steep (Figure 2), suggesting that richness for those trees could be higher than recorded.

**Table 4.** Permanova analysis of species composition.

Parameters	Df	SS	MS	F	R2	Probability
Azimuth category	3	1.87	0.62	1.87	0.03	0.45
Height	1	1.88	1.88	5.65	0.03	***
DBH	1	0.52	0.52	1.56	>0.01	0.91
Height: DBH	1	0.58	0.58	1.73	>0.01	0.10
Residuals	166	55.20	0.33		0.92	
Total	172	50.05			1.00	

Notes: The azimuth, height, diameter at breast height (DBH) and interaction between height and DBH were added sequentially to the test. A:B indicates interaction between the variables A and B. Df, Degrees of freedom; SS, sums of squares; MS, mean squares; F, F statistic.

\*\*\* $P < 0.001$ .

## Vertical distribution

Of the 17 epiphytic bryophyte species found in this study, almost half of these species occupied almost the entire vertical profile. Also, three species were found only in the crown, high above the soil level (Table 3). Our results suggest that height is a main driver of epiphytic composition within host trees. Height could be important due to its relationship with microclimatic gradients within the vertical profile. For example, from the upper canopy to the forest floor, temperature, wind, vapour pressure deficit and light decrease, while air humidity increases (Parker 1995). Azimuth was not an influential variable in our study; however, this variable could become important at a small-scale level, contributing to explain the variations of epiphytic composition around the trunk at each height (Taylor and Burns 2016). Previous authors have suggested that the habitat preferences of epiphytes along the vertical profile depend on their physiological adaptations and the canopies' environmental conditions (McCune 1993; Costa 1999; Acebey et al. 2003). For instance, epiphytes living in the higher strata of trees can be associated with more exposed microhabitats and are therefore referred to as 'sun epiphytes', but epiphytes located close to the forest floor are considered 'shade epiphytes'. Epiphytes that use both shady and sunny sites are considered 'generalists' (Richards 1984). These ecological classifications are partially reflected in our results, with liverwort generalists such as *Frullania rostrata* and *Gackstroemia* aff. *magellanica*, and moss generalists such as *Lepyrodon tomentosus*, *Zygodon pentastichus* and *Hypnum skottsbergii*. In the case of the aforementioned liverwort species, their ability to use the whole profile, especially the upper zones, may be related to their red-brown pigmentation, which could allow them to resist direct sun radiation (Cornelissen and ter Steege 1989; Proctor 2000; Hooijmaijers and Gould 2007). *Frullania* and *Gackstroemia* also have particular structures called 'water sacs,' where they can store water, allowing them to resist drier conditions (Gradstein and Pócs 1989; Parolly and Kürschner 2004). Another species frequently found throughout almost the entire vertical profile was *Clasmatocolea rigens*, a liverwort with a wide distribution in Chile (Ellis et al. 2013). *Clasmatocolea rigens* was usually found growing in *Z. pentastichus* cushions and *H. skottsbergii* mats, which could help its capacity to thrive throughout the vertical profile. Further studies in ecophysiology and species interactions are required to further clarify why some bryophyte species are more frequent in different sections of trees.

*Zygodon pentastichus* presents papillae in its leaves, which may also help to prevent desiccation, allowing it to colonise drier sites throughout tree crowns (Calabresse 2006; Larrain 2007; Ariyanti et al. 2008). However, *Z. pentastichus* was found to be associated with the accumulation of organic soil in the canopy and was more frequent in the upper parts of the vertical profile. The presence of canopy soils is frequent in many forest ecosystems (Enloe et al. 2006). This soil may retain its humidity for a long period of time, which has been found to occur in other Chilean forests (Vergara 2013). Consequently, we hypothesise that the presence of arboreal soil allows this species to survive in the upper crowns.

The life forms found in this study correspond mostly to mats, turfs and cushions. We found no pendant bryophytes, which are generally related to more humid environments (Kürschner and Parolly 2005). Species such as *H. skottsbergii*, *Lepyrodon tomentosus* and *Acrocladium auriculatum* formed dense mats covering trunks, which can retain water for a

long time, during dry periods (Mägdefrau 1982; Kürschner et al. 1999; Zotz et al. 2000; Gradstein and Sporn 2010; Sporn et al. 2010). Finally, *Uloa* sp. formed cushions and was found mostly in crowns, even at the highest point of the tallest sampled tree. Another advantage of cushion-forming species is that due to their water storage capacity they can remain hydrated, gaining carbon for longer periods (Stanton & Reeb 2016). These adaptations allow some species to occupy more exposed habitats, such as that of the upper canopy (Kürschner and Parolly 2005).

### Bryophyte diversity in forest canopies

The genera and families found in this study have been commonly registered in other epiphytic studies along vertical profiles. The Orthotrichaceae family is commonly found in crowns, even in twigs (Cornelissen and ter Steege 1989; Cornelissen and Gradstein 1990; Holz et al. 2002), here we found both *Z. pentastichus* and *Uloa* sp. growing in the upper parts of the trees. *Frullania* is a common epiphytic genus described in many studies and classified as a vertical generalist (Díaz et al. 2010), upper canopy user (Sporn et al. 2010) and even as a xerophytic twig epiphyte (Parolly and Kürschner 2004).

The species richness found in this study area is very low compared to other forests. For instance, *Nothofagus* forests of Tasmania and New Zealand show a greater number of bryophyte species, particularly in forests at lower altitudes (Scott 1970; Dalton 1998; Hofstede et al. 2001). Oak (*Quercus* spp.) forests in Europe also have higher diversity in low-elevation forests (Mazimpaka and Lara 1995) (Table 5). Cryptogamic epiphytes are

**Table 5.** Comparison of epiphytic species richness among different temperate rainforests in the Southern Hemisphere and a *Quercus* spp. forest in Europe.

Study site	Host tree species	Altitude (m)	Ms	Ls	VP	Source
Temperate rainforest, Coastal range, southern Chile (42°38'S)	<i>Aextoxicon punctatum</i> Ruiz & Pav.	80	16	0	15	Díaz et al. (2010) (cb)
Temperate rainforest, Coastal range, southern Chile (41°47'S)	<i>Eucryphia cordifolia</i> Cav.	190	7	7	16	Díaz et al. (2010) (cb)
Temperate rainforest, Andean range, southern Chile (41°35'S)	<i>Fitzroya cupressoides</i> (Molina) I.M. Johnst.	165	6	12	18	Clement et al. (2001) (cb)
Valdivian rainforest, Valdivia, Chile (39°83'S)	<i>Nothofagus obliqua</i> (Mirb.) Oerst.	16–50	20*	11		Mellado-Mansilla (2013) (cb)
Lowland temperate forest, Southwestland, New Zealand (45°43'S)	<i>Nothofagus menziesii</i> (Hook.f.) Oerst.	>4	23	17	41	Hofstede et al. (2001) (cb)
Rainforest, Western and Northwestern Tasmania, Australia (42°18'S)	<i>Nothofagus cunninghamii</i> (Hook.) Oerst.	5–960	19	36	ns	Dalton (1998) (gb)
Subalpine forest, Astelia Stream, Fiordland, New Zealand (45°42'S)	<i>Nothofagus menziesii</i>	0–300	15	34	ns	Scott (1970) (gb)
Gredos Mountains, Spanish Central Range, Spain (40°29'N)	<i>Quercus pyrenaica</i> Willd.	>400	18	2	ns	Mazimpaka and Lara (1995) (cb)
Temperate rainforest, Andean range, southern Chile (39°26'S)	<i>Nothofagus dombeyi</i>	>900	6	11	0	This study (cb)

Notes: (ns), not studied; (ni), presence or absence not indicated; (cb), the study was developed from a canopy-based perspective; (gb), the study was developed from a ground-based perspective.

\*Bryophytes were not classified, only separated as different morpho-species. Ms, mosses; Ls, liverworts; VP, vascular plants. The vertical distribution was represented in meters and percentages (see Materials and methods). Occurrences were calculated as the number of incidences of each taxa per the total sub-plots sampled ( $n = 227$ ) and were expressed as percentages. + indicates endemic species (southern South America).

conspicuous in old-growth forests in the Pacific Northwest (North America) (Lyons et al. 2000; Sillett and Rambo 2000). For example, Pike et al. (1975) found 32 species of epiphytic bryophytes (25 mosses and 7 liverworts species) growing in an old-growth Douglas Fir forest in western Oregon. The different climatic conditions and host tree species types (angiosperms versus gymnosperms) resulting from the natural histories of the forests mentioned above could be mostly responsible for the differences in epiphytic species richness and composition. An epiphytic bryophyte species richness similar to that reported here was registered by Clement et al. (2001), Díaz et al. (2010) and Mellado-Mansilla (2013) along the vertical profiles of SATR (Table 5), but they also found vascular epiphytes.

## Conclusions

The dominant epiphytes of this Andean *Nothofagus* forest are non-vascular species. Many of the species found occupy the whole vertical profile of trees, even the highest twigs. The information here could be relevant due to the pressure to manage these *Nothofagus* forests, where the associated biodiversity is not recorded in forestry inventories. Despite the high bryophyte richness described in Chile (c.1500 species), there is a serious lack of information about their conservation status: not a single taxon found in this study has registered conservation status information. In addition, forest management in Chile does not consider epiphytes, and is based only on tree species. Considering all of the above, a new policy is urgently needed for the continued protection of epiphytic bryophyte species in SATR.

## Acknowledgements

This study was supported by Fundación Mar Adentro. We are grateful for the support provided in the field by Segundo Mendez, Antonio Lobos, Claudia Pranao, Harriet Sidler and Camila Tejo. We would like to give thanks for the assistance provided by Juan Larraín in identifying difficult species. Finally, we acknowledge Christine Harrower for her valuable comments on the manuscript.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was supported by Fundación Mar Adentro: [Grant Number Proyecto Biodiversidad Bosque Pehuén # 42203908].

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