

Patterns of bryophyte and lichen diversity in bogs and *Tepualia stipularis* forests of Northern Patagonia (Chile): evidence of a novel ecosystem in southern South America

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Abstract

Bryophytes and lichens are an important component of biodiversity. Nevertheless, these cryptogamic groups are rarely included in floristic and ecological studies in southern South America. We present the first comparison of patterns of alpha and beta diversity of bryophytes and macrolichens in peatlands and *Tepualia stipularis* forests (TF) on Isla Grande de Chiloé, Chile. Two kinds of *Sphagnum* peatlands were studied, which were defined according to their origin and their vegetation, natural peatlands (GP) and anthropogenic peatlands (AP). A total of 86 species were found: 42 liverworts, 29 mosses and 14 lichens. The most species-rich sites were AP with a total of 52 species, followed by TF with 45 species, and GP with 21 species. The total bryo-lichenic diversity reported in this study was considerably higher than that reported in other studies for Patagonian peatlands. The three types of studied habitats showed significant differences in species richness and diversity indices. We found clear distinctions between the three habitat types, with significant differences in the floristic composition of GP, AP, and TP. Moreover, AP presented a species composition that has not been previously documented in TF or GP. They are the result of human action, but do not depend on continued human intervention for their maintenance. Therefore, here we propose to denominate AP as a novel ecosystem.

Keywords: biodiversity patterns, emerging ecosystem, liverworts, macrolichens, mosses, Chile.

Patrones de diversidad de briófitos y líquenes en turberas y bosques de *Tepualia stipularis* en Patagonia norte (Chile): evidencia de un ecosistema emergente en el sur de Sudamérica

Resumen

Los briófitos y líquenes son un componente importante de la biodiversidad. Sin embargo, estos grupos criptogámicos son escasamente incluidos en estudios ecológicos y florísticos en el Sur de Sudamérica. En este estudio se presenta la primera comparación de patrones de diversidad alfa y beta de briófitos y macrolíquenes en turberas y bosques de *Tepualia stipularis* (TF) de la Isla Grande de Chiloé, Chile. Se estudiaron dos tipos de turberas esfagnosas, las cuales fueron definidas de acuerdo a su origen y vegetación, turberas naturales (GP) y turberas antropogénicas (AP). En este estudio se reporta un total de 86 especies, de las cuales 42 fueron hepáticas, 29 musgos y 14 líquenes. Los sitios con mayor riqueza de especies fueron los AP (52 especies), seguidos por TF con 45 especies y GP con 21 especies. La diversidad brio-líquénica reportada en este estudio es considerablemente más alta en relación a lo reportado en otros estudios para las turberas patagónicas. Los tres tipos de hábitats analizados mostraron diferencias significativas en riqueza de especies e índices de diversidad. Además, se encontraron claras diferencias en la composición florística de GP, AP, y TP. AP presentó una composición de especies que no había sido previamente documentada en TF o GP. Esta nueva conformación es el resultado de la acción antrópica sobre estos lugares, pero no dependen de la intervención humana para su mantenimiento. En consecuencia, proponemos denominar a AP como ecosistemas noveles.

Palabras clave: ecosistemas emergentes, hepáticas, macrolíquenes, musgos, patrones de biodiversidad, Chile.

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Bryophytes and lichens are an important component of biodiversity (Rozzi *et al.* 2008) and play a key role in ecosystems such as peatlands (Minayeva 2008). Some of them, specifically *Sphagnum* spp., have been considered ecosystem engineers. These organisms directly or indirectly modulate the availability of resources to other species and, additionally, they modify, maintain and/or create habitats (Jones *et al.* 1994). Moreover, the ground layer in peatlands is dominated by a 90-100 % cover of bryophytes (Vitt & Belland 1995) and the functions of the peatland ecosystem is highly dependent on this layer. For instance, nutrient sequestration, water-holding abilities, decomposition, and acidification are all influenced by this layer (Vitt 2000). Nevertheless, these cryptogamic groups are rarely included in floristic and ecological studies (Pharo *et al.* 1999, Lang *et al.* 2009). Southern South America is no exception.

Vast expanses of peatland can be found in Chilean Patagonia. A significant number of peatlands were formed by peat accumulation in open water after glacial retreat (Heusser 1984, Villagrán 1988, Villagrán 1991), referred to here as glaciogenic peatlands (GP). However, in northern Patagonia, the use of fire and clearcutting since the middle of the 19th century in places with low drainage have created areas of wetlands dominated by species of the genus *Sphagnum* L. (Zegers *et al.* 2006, Díaz *et al.* 2008). When *Tepualia* forests (TF), characterized by poor drainage, are burned or cleared, waterlogged conditions hinder forest recolonization and stimulate *Sphagnum* colonization (Díaz *et al.* 2007, Díaz & Silva 2012). These habitats are called anthropogenic peatlands (AP).

Besides, TF are swamp habitats, closely related to peatlands. This type of forest is dominated by *Tepualia stipularis* (Hook. & Arn.) Griseb. (Myrtaceae), and can be associated with *Podocarpus nubigenus* Lindl. (Podocarpaceae), *Pilgerodendron uviferum* Florin. (Cupressaceae) and/or *Drimys winteri* J. R. Forst. & G. Forst. (Winteraceae). It grows in waterlogged areas (García & Ormazabal 2008) and accumulates organic matter (Veblen & Schlegel 1982). Several studies show that peatlands and TF have been linked by their floras demonstrating that the vascular and bryophytic floras of these habitats are highly similar (Villagrán & Barrera 2002, Villagrán *et al.* 2002, Villagrán *et al.* 2003, Villagrán *et al.* 2005). Díaz *et al.* (2008) reported differences in floristic composition that allow to distinguish between GP (natural) and AP. However, there are no comprehensive studies that quantify and compare the floristic composition of AP, GP, and TF. Another connection is that these ecosystems are seriously threatened. Peatlands are threatened and degraded because peat extraction and *Sphagnum* harvesting, mainly to use as a substrate in horticulture (Díaz & Silva 2012). In Chile, *Sphagnum* exports increased by over 400 % between 2002 and 2011 (ODEPA 2016). TF are also threatened because their firewood is one of the main energy sources on the island (Neira & Bertin 2010).

We are studying AP as an ecosystem that has been shaped by human activity. Its transformation of landscape has caused changes to biological communities, posing new challenges for traditional thinking in conservation and resource management (Lindenmayer *et al.* 2008). Taking into account this changes in ecosystem-human relation, Milton (2003) presented a novel concept of emerging ecosystems. This concept defines an ecosystem whose species composition and relative abundance have not previously occurred within a given biome. The key characteristics of these ecosystems are: new species combinations, with the potential for changes in ecosystem functioning, and they are the result of deliberate or inadvertent human action, but do not depend on continued human intervention for their maintenance (Hobbs *et al.* 2006). Under this concept we wonder, if AP is a novel or an emerging ecosystem?

In this research, we study alpha and beta diversity of mosses, liverworts, and lichens in AP, GP, and TF of Isla Grande de Chiloé (Chile). In particular, we address the following questions: i) Are there significant variations in species composition between the studied habitat types? ii) Are AP more floristically related to TF? iii) Do GP (natural habitats) have a higher bryo-lichenic diversity than AP? iv) Is there evidence to recognize AP as a novel ecosystem?

Methods

Study Site. The study area was located in the Isla Grande de Chiloé, Los Lagos Region, Chile (42°-43° S and 73°-75° W). The prevailing climate is wet temperate with a strong oceanic influence (di Castri & Hajek 1976). The total annual rainfall is about 2,300 mm (CONAF 2009),

Figure 1. Location of studied site in Chiloé. Glaciogenic peatlands (GP) (black circles): PL, Púlpito; CA, Caulles; and RN, Río Negro. Anthropogenic peatlands (AP) (gray circles): SD, Senda Darwin; CH, Chepu; PM, Pumanzano; LC, Lecam and TG, Tegel. *Tepualia* forests (TF) (white circles): CU, Chiloé National Park and SDB, Senda Darwin forest.



reaching 5,000-6,000 mm in some areas, with a mean summer temperature of 10.2 °C and a mean winter temperature of 6.2 °C (Pérez *et al.* 2003).

We selected ten sites located in the northern and central parts of the island (Figure 1). Two kinds of *Sphagnum* peatlands were studied, which were defined according to their origin and their characteristic vegetation (Díaz *et al.* 2008). Three study sites represented the glaciogenic peatland type (GP): Río Negro (GP-RN), Los Caulles (GP-CA) and Púlpito (GP-PL); five study sites represented the anthropogenic peatland type (AP): Senda Darwin (AP-SD), Lecam (AP-LC), Pumanzano (AP-PM), Río Chepu (AP-CH) and Tegel (AP-TG). In addition, two sites represented the *Tepualia* forest type (TF): Chiloé National Park (TF-CU) and another area of Senda Darwin (TF-SDB) (Figure 1).

Species composition. On each site we established three lineal transects of 50 m. In each transect, three equidistant sample plots were placed. We extracted a block from the surface layer measuring 20 × 20 × 10 cm from each sample plot. These blocks were used to evaluate species richness and biomass, following Bullock's harvest method (1997). Dry biomass was used to estimate species abundance for each sample plot. Specimens were carefully determined according to

morphological characters, and their characteristics were compared with the literature (Engel 1978, Schuster 2000, Schuster 2002, Larrain 2007, Buck & Goffinet 2010), type specimens or other herbarium specimens deposited in PC, S, MACB and CONC herbaria. For lichens, chemical characters were also used. Lichen substances were identified using thin layer chromatography (TLC), following the protocol of White & James (1985). Specimens were deposited in MACB and CONC herbaria.

Although *Drosera uniflora* Willd. is a vascular plant, its presence was registered due to its great significance as an indicator of GP species. Due to their tiny size, the liverworts *Calypogeia sphagnicola*, *Cephalozia skottsbergii* and *Hyalolepidozia bicuspadata* were considered as a functional group. Likewise, the lichens *Cladonia pycnoclada*, *C. mitis* and *C. arbuscula* subsp. *squarrosa* were considered as the subgenus *Cladina* following Ruoss and Ahti (1989), because chemical tests are required for correct determination. Appendix 1 includes a list with the collected species.

Data analysis. Alpha diversity was evaluated in two scales following Gray's (2000) concepts: point species richness (SR_p), the species richness of a single sampling unit (quadrant); and sample species richness (SR_s), the species richness of a number of sampling units from a site of a defined area (site). In addition, we calculated the Shannon diversity index (H') and evenness (J') to combine the effects of species richness and abundance (Magurran 2004). To assess changes in species composition among habitat types, we calculated beta diversity using the Bray-Curtis dissimilarity index (Bray & Curtis 1957). Moreover, cluster analysis was performed using the unweighted pair group metric with averaging method (UPGMA) and Bray-Curtis presence/absence distance to evaluate the resemblance among sites. Non-metric multidimensional scaling (NMDS) was used to compare plant communities from AP, GP, and TF. Relative abundance and Bray-Curtis distance was used as a general measure of ecological similarity for NMDS ordination (Beilman 2001). Analysis of similarities (ANOSIM) was used to test for differences in species composition for the three habitat types. R values of ANOSIM were generated using 9,999 random permutations. We used the Non-Parametric Kruskal-Wallis H ANOVA to test significant differences in the richness and diversity measures among habitats and sites.

We employed PAST (Hammer *et al.* 2001) for indices, cluster analysis, NMDS and ANOSIM. STATISTICA 7.0 (StatSoft 2004) for the Kruskal-Wallis H test.

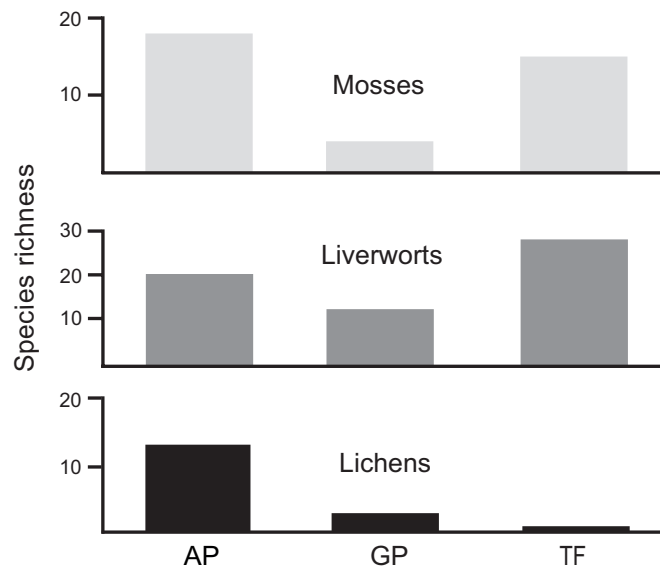
Results

Alpha Diversity. A total of 86 species was found: 42 liverworts, 29 mosses, 14 lichens and one insectivorous flowering plant. Fifty three-point five percent (53.5 %) of the species were found at only one site and are here considered potentially rare within the studied peatlands: 16 mosses, 21 liverworts and 9 lichens. AP had a total of 52 species (18 mosses, 21 liverworts and 13 lichens), TF had 45 species (15 mosses, 29 liverworts and 1 lichen), and GP had 21 species (4 mosses, 13 liverworts and 3 lichens) (Figure 2). Of the 86 species, 29 were only found in TF, 27 were exclusive of the AP and five occurred only in GP. Nevertheless, we found shared species between habitat types, nine species between AP and GP, nine species between AP and TF, six species between TF and GP, and seven species that were shared among the three habitats.

Table 1. Species richness and diversity index by habitat type. SR_p , point species richness; SR_s , sample species richness; \bar{x}_p : mean per cuadrant, s_p : richness or index per type of habitat. (*) significant differences ($p < 0.001$, Kruskal-Wallis test) among habitat types. Anthropogenic peatlands (AP), glaciogenic peatlands (GP), and *Tepualia* forests (TF).

| | AP | GP | TF |
|-----------------------------|------|------|------|
| $SR_{p\text{total}}$ * | 5 | 4.6 | 10.6 |
| $SR_{s\text{total}}$ | 52 | 21 | 45 |
| Shannon index \bar{x}_p * | 0.62 | 0.49 | 1.28 |
| Shannon index s_p | 1.64 | 0.89 | 2.86 |
| Evenness \bar{x}_p * | 0.39 | 0.32 | 0.57 |
| Evenness s_p | 0.41 | 0.29 | 0.75 |

Figure 2. Species richness of mosses, liverworts, and lichens, in the three habitat types. Anthropogenic peatlands (AP), glaciogenic peatlands (GP) and *Tepualia* forests (TF).



SR_p , SR_s and diversity indices were significantly different among the three habitat types. TF showed the highest SR_p and diversity index, while AP presented the highest SR_s (Table 1). Species richness and abundance were significantly different between study sites (Figure 2 y 3). SR_s ranged between 7 and 34 species where AP-SD and TF-CU were the highest, and AP-LC and GP-RN the lowest. SR_p ranged between 2 and 14 species per quadrant. Diversity indices followed the same trends in species richness where AP-SD, TF-SDB and TF-CU had the highest values. Nevertheless, AP-PM and AP-PL presented the lowest diversity indices.

When analyzing the SR_s per botanical groups, it was seen that AP-SD and TF-SDB had the highest number of mosses, TF-CU the most liverworts and AP-TG and AP-SD the most lichens.

Beta Diversity. Dendrogram of floristic composition based on Bray-Curtis similarity clearly shows two groups of habitats with a similarity of over 30 % (Figure 4). The first group included three locations, TF-SDB and TF-CU (both TF, which had a similarity of 48 %, and AP-SD,

Figure 3. Relative species abundance of mosses, liverworts, and lichens in the three habitat types. Anthropogenic peatlands (AP), glaciogenic peatlands (GP) and *Tepualia* forests (TF).

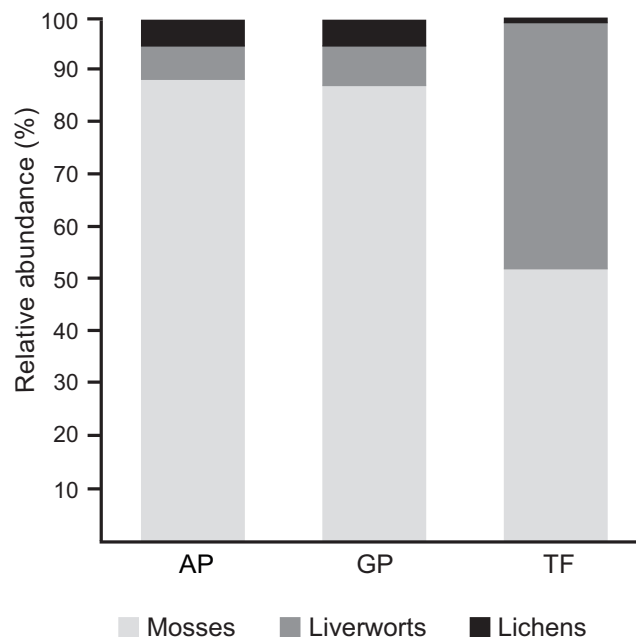
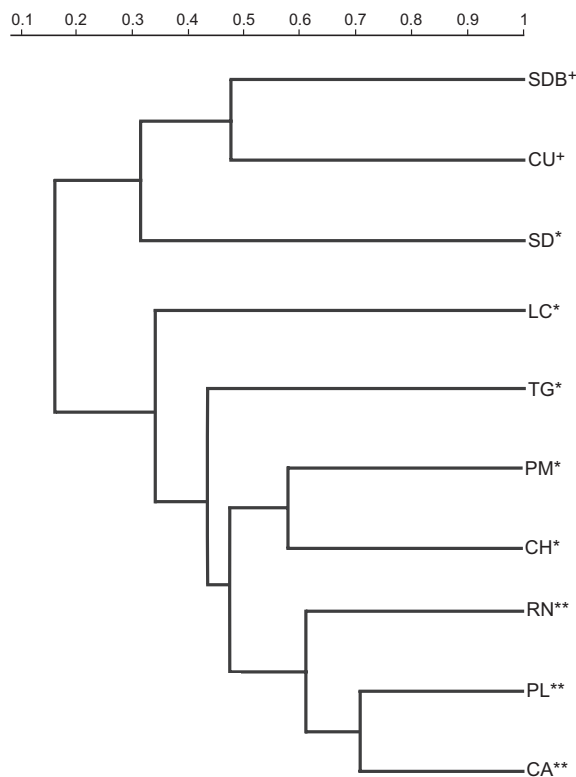


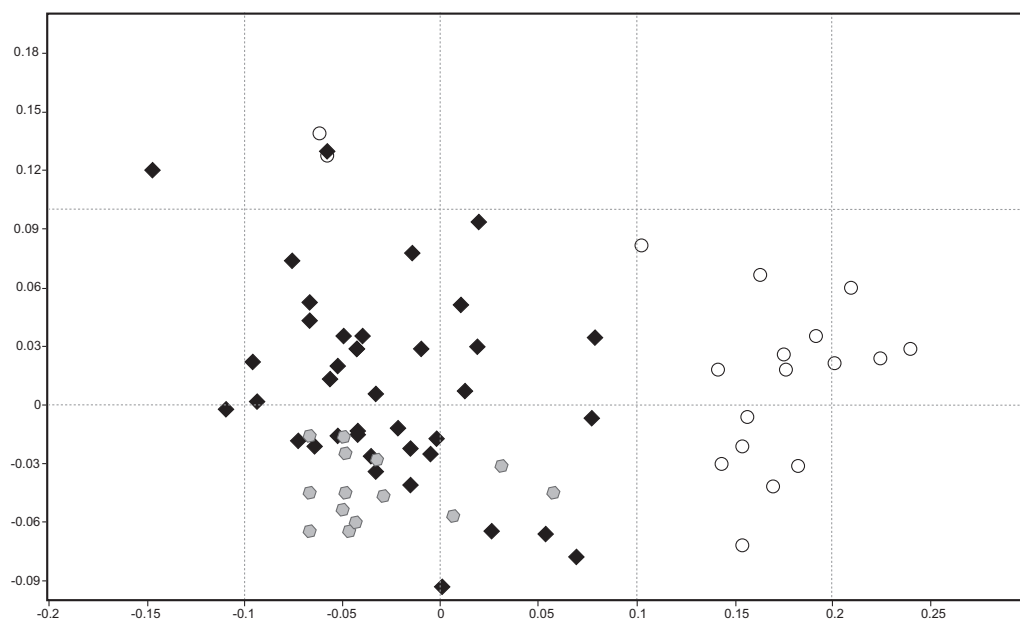
Figure 4. Bray-Curtis similarity dendrogram of floristic composition among studied habitats. *Tepualia* forests (+): TF-CU, Chiloé National Park and TF-SDB, Senda Darwin forest. Anthropogenic peatlands (*): AP-CH, Chepu; AP-LC, Lecam AP-PM, Pumanzano; AP-SD, Senda Darwin; and AP-TG, Tegel. Glaciogenic peatlands (**): GP-CA, Caulles; GP-PL, Púlpito; and GP-RN, Rio Negro.



which is a sister site of the clade formed by these sites. The second group included the seven remaining locations. In this group, AP-LC and AP-TG were individually separated and sub-grouped with a similarity of 45 %. Within this sub-group, two subclusters were formed: GP-RN, GP-PL and GP-CA, which have a similarity of 60%, and AP-PM and AP-CH with a similarity of 58 %.

Based on non-metric multidimensional scaling (NMDS), the structure in species composition revealed differences in the habitat type (Figure 5). In this plot we can see a clear separation of TF

Figure 5. Non-parametric multidimensional scaling ordination representing similarity in bryophyte and lichen species composition between habitat types. Black diamonds represent anthropogenic peatlands (AP), grey hexagons glaciogenic peatlands (GP), and white circles *Tepualia* forests (TF) (n = 90).



samples (white circles), while AP (black diamonds) are arranged in a dispersed form in the plot and not distantly separated from GP (grey hexagons). AP and GP samples are closer than TF.

The statistical significance of differences in abundance and species composition among habitats was confirmed by the ANOSIM tests ($R_{\text{ANOSIM global}} = 0.412$, $p = 0.0001$). When ANOSIM pair-wise comparisons were performed, we detected that TF vs. AP ($p = 0.0001$; $R_{\text{ANOSIM}} = 0.770$) and GP vs. TF ($p = 0.0001$; $R_{\text{ANOSIM}} = 0.930$) were significantly different in species composition; however, AP vs. GP ($p = 0.3453$; $R_{\text{ANOSIM}} = 0.012$) were more closely related.

Discussion

Cryptogamic diversity. Bryophyte and lichen diversity have repeatedly been underestimated due to limited knowledge of these groups, especially in southern South America. Indeed, our research demonstrates the importance of these groups as our results show that the total bryophyte and lichen diversity were considerably higher than that previously reported from Patagonian peatlands. Díaz *et al.* (2008) reported 27 species of bryophytes and lichens in peatlands of Chiloé, Villagra *et al.* (2009) recorded five species of terricolous lichens in *Sphagnum* peatlands of Aisén, and Kleinebecker *et al.* (2010) found 54 bryo-lichenic species in the peatlands of Magallanes. In our study, 56 species of bryophytes and lichens were reported for peatlands of Chiloé (AP and GP). Under these circumstances, in a diversity context, the peatlands of Los Lagos Region are as rich as the peatlands of Magallanes, which have been considered significantly important due to their location. The Magallanes Region reports the highest diversity of bryophytes and lichens in the country (Goffinet *et al.* 2006). On the other hand, if the number of species recorded in this study is compared with species found in bogs of the Northern Hemisphere, for instance, Canada with 36 species (Vitt & Belland 1995) or Britain with 39 species (Wheeler 1993), the diversity observed in our study shows great relevance. This is especially remarkable because the peatlands of the Southern Hemisphere are under-represented compared to the vast percentage of land they occupy in the Northern Hemisphere (Joosten & Clarke 2002).

Differences between habitats. Our results also showed differences in species richness, composition and diversity indices among study sites and among types of studied habitats (Table 1). This trend is more evident in the AP group, as seen in the cluster analysis (Figure 4). This analysis

Table 2. Species richness and diversity index by sites. SR_p , point species richness; SR_s , sample species richness; \bar{p} , mean per cuadrant; s , richness or index per type of habitat. *Tepualia* forests: TF-CU, Chiloé National Park and TF-SDB, Senda Darwin forest. Anthropogenic peatlands: AP-CH, Chepu; AP-LC, Lecam AP-PM, Pumanzano; AP-SD, Senda Darwin; and AP-TG, Teguel. Glaciogenic peatlands: GP-CA, Caulles; GP-PL, Púlpito; and GP-RN, Rio Negro. (*) significant differences ($p < 0.001$, Kruskal-Wallis test) among sites.

| | AP | | | | | GP | | | TF | |
|-------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|
| | AP-CH | AP-LC | AP-PM | AP-SD | AP-TG | GP-CA | GP-PL | GP-RN | TF-CU | TF-SDB |
| $SR_{\bar{p}} \text{ total}^*$ | 4.7 | 2.1 | 4.3 | 7.3 | 6.4 | 5.6 | 4.6 | 3.7 | 13.8 | 7.4 |
| $SR_s \text{ total}$ | 14 | 7 | 10 | 34 | 22 | 15 | 16 | 9 | 32 | 27 |
| $SR_{\bar{p}} \text{ mosses}^*$ | 2.7 | 1.8 | 1.6 | 3.9 | 2.2 | 1.8 | 1.3 | 1.4 | 3.2 | 3.7 |
| $SR_s \text{ mosses}$ | 6 | 4 | 2 | 13 | 7 | 4 | 2 | 3 | 7 | 14 |
| $SR_{\bar{p}} \text{ liverworts}^*$ | 1.7 | 0.3 | 2.2 | 2.2 | 1.8 | 2.4 | 2.2 | 1.8 | 10.1 | 3.8 |
| $SR_s \text{ liverworts}$ | 5 | 3 | 5 | 14 | 6 | 8 | 11 | 4 | 24 | 13 |
| $SR_{\bar{p}} \text{ lichens}^*$ | 0.3 | 0 | 0.6 | 1.2 | 2.4 | 1.3 | 1 | 0.4 | 0.4 | 0 |
| $SR_s \text{ lichens}$ | 3 | 0 | 3 | 7 | 9 | 2 | 2 | 1 | 1 | 0 |
| $SR_s \text{ insectivorous}$ | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 |
| Shannon index \bar{p}^* | 0.61 | 0.35 | 0.30 | 1.07 | 0.78 | 0.63 | 0.37 | 0.47 | 1.50 | 1.07 |
| Shannon index s | 1.26 | 0.74 | 0.42 | 2.00 | 1.61 | 1.03 | 0.59 | 0.82 | 2.43 | 2.45 |
| Evenness \bar{p}^* | 0.37 | 0.42 | 0.20 | 0.55 | 0.41 | 0.37 | 0.22 | 0.36 | 0.57 | 0.57 |
| Evenness s | 0.48 | 0.38 | 0.18 | 0.57 | 0.52 | 0.38 | 0.21 | 0.37 | 0.7 | 0.74 |

shows that GP and TF form delimited groups and have less within-group variability, while AP are more heterogeneous. These differences could be related to processes carried out in the cryptogamic community establishment, and the chemical and topographic characteristics of the sites. For instance, AP-SD has greater similarity to TF and this similarity could be attributed to its early stage of formation. In this locality, the peat layer was the smallest of the sampled sites and is located very close to the forest. Moreover, it could be labeled as an ecotonal zone between the forest and peatland. Another highlighted example is AP-LC, which is part of the AP and GP cluster; however, it is the first to diverge from the group. This site has particular hydrological characteristics (León *et al.* In review) because the water level is very high and not significantly lower in summer; something that does not happen in any of the other study sites. Furthermore, the highest richness, diversity index and number of exclusive species were observed in AP. In contrast, GP showed the lowest values of these community parameters. TF showed a high richness, independent of the scale (point or sample), and this habitat type presented a large number of exclusive species. These results can be understood by their phylogeographic location. TF form part of the temperate forest of Chile, an ecosystem that has been classified as a biodiversity hotspot for conservation of global significance by its uniqueness and high threats (Myers *et al.* 2000). Moreover, in NMDS (Figure 5) and ANOSIM analyses, we could also see clear differences among the three habitat types. There were significant differences in the floristic composition of GP, AP, and TF, where GP and AP were more closely related to each other because they share a large number of species and environmental characteristics. On the contrary, TF were distantly related to the other two groups. The significant differences between AP and GP in floristic composition concurred with Díaz *et al.* (2008) who described differences in floristic composition between GP (natural) and AP. Nonetheless, the clear differences between the flora of peatlands and TF reported in this research differs from previously published studies (Villagrán & Barrera 2002; Villagrán *et al.* 2002; Villagrán *et al.* 2003; Villagrán *et al.* 2005) that suggest that the flora of peatlands and TF are similar.

Novel ecosystems, ecosystem services and implication for management. According to our results, AP have very distinct and singular characteristics. They are characterized by high values of diversity (Table 1), with a large number of endemic species of southern South America (León *et al.* 2014). Moreover, new records for the bryophyte flora of the island and Chile have been found (León *et al.* 2013). In addition, even when all species growing in AP belong to the Valdivian ecoregion and it is not possible to attribute them to other biomes, these ecosystems show a singular composition of species that did not previously occur when they were TF (before clearcutting). These new species combinations have the potential to change ecosystem functions, as discussed below. They are the result of human action, but do not depend on continued human intervention for their maintenance. According to Hobbs *et al.* (2006), these are all characteristics that define a novel ecosystem. Therefore, applying the concepts of Hobbs *et al.* (2006) and Milton (2003), we can denominate AP as a novel ecosystem. In these novel ecosystems, the new species compositions have deeply changed the landscape of the island and ecosystem services. Díaz & Armesto (2007) showed that *Sphagnum* cushions could act as a nursery species, facilitating the establishment of *Embothrium coccineum*. Nevertheless, these cushions could inhibit the establishment of pioneer species such as *Drimys winteri* and *Baccharis patagonica* in successional scrubs of Chiloé, which is a limiting factor for forest regeneration. On the other hand, the colonization and the establishment of large populations of *Sphagnum* in sites where the forest was removed have also changed ecosystem functioning. León & Oliván (2014) found that AP are accumulating peat and therefore are also acting as carbon sinks and reservoirs of freshwater; ecosystem services relevant to the island. It is important to highlight that the peatlands of Chiloé are threatened and degraded by *Sphagnum* harvesting, especially AP. Unfortunately, Chile has no legal regulation for the extraction of *Sphagnum* moss. These sites have been excessively exploited without sustainable protocols, and as a consequence, they show evident signs of overexploitation. This imposes the need to promote conservation and restoration of these ecosystems. However, three important questions arise and require a deeper analysis: What would be the direction of the restoration in AP? Would it be to recover the temperate rainforest (historical setting)? Or would it be to recover telmatic wetlands formed after a

disturbance? These are significant points of discussion about the conservation and management of these emerging ecosystems, because in many parts of the world, primary motivations for ecosystem management are associated with human survival rather than considerations of historic fidelity (Hobbs *et al.* 2009). In this case, considering their high social and economic value, a focus on ecosystem functions rather than recomposition of species (historical) or the cosmetics of landscape surfaces would be useful according to Choi (2007). A reasonable way would be to promote the growth of *Sphagnum* and to restore the ability to store water and peat. This would have a significant impact on local communities because Chiloé peatlands are very important for fresh water supply on the island. This island has no freshwater input from snowmelt as found on mainland Chile; the freshwater input is mainly from precipitation (Zegers *et al.* 2006). Thus, according to the climate change scenario, low rainfall rates in recent years means that freshwater on the island is at risk and the conservation of peatlands is of even more importance to the population.

Finally, we do not know about the dynamics of species composition under new abiotic conditions, especially *Sphagnum* species, which are ecosystem engineers. Therefore, it is necessary to increase efforts to understand their functioning and the main environmental factors driving these ecosystems. Moreover, these studies could provide insights into the effects that global change factors can have on these novel ecosystems, and could provide important information for management and ecological restoration.

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Appendix 1. Occurrence (X) of species in anthropogenic peatlands (AP), glaciogenic peatlands (GP) and Tepualia forests (TF) of North Patagonia.

| Species | Anthropogenic peatlands | Glaciogenic peatlands | Tepualia forests |
|---|-------------------------|-----------------------|------------------|
| Mosses | | | |
| <i>Acrocladium auriculatum</i> (Mont.) Mitt. | | | X |
| <i>Breutelia subplicata</i> Broth. | | | X |
| <i>Campylopus acuminatus</i> Mitt. | | X | |
| <i>Campylopus introflexus</i> (Hedw.) Brid. | X | | |
| <i>Campylopus pyriformis</i> (Schultz) Brid. | X | | |
| <i>Dicranella circinata</i> Herzog | X | | |
| <i>Dicranoloma billarderii</i> (Brid.) Paris | X | X | X |
| <i>Dicranoloma imponens</i> (Mont.) Renauld | X | X | |
| <i>Dicranoloma robustum</i> (Hook. f. & Wilson) Paris | X | | |
| <i>Distichophyllum dicksonii</i> (Hook. & Grev.) Mitt. | | | X |
| <i>Dendrohypopterygium arbuscula</i> (Brid.) Kruijer | | | X |
| <i>Eucamptodon perichaetialis</i> (Mont.) Mont. | X | | |
| <i>Hymenodontopsis mnioides</i> (Hook.) N. E. Bell, A. E. Newton & D. Quandt | | | X |
| <i>Hypopterygium didictyon</i> Müll. Hal. | | | X |
| <i>Hypnum chrysogaster</i> Müll. Hal. | X | | |
| <i>Hypnum cupressiforme</i> var. <i>mossmanianum</i> (Müll. Hal.) Ando | | | X |
| <i>Pohlia nutans</i> (Hedw.) Lindb. | X | | |
| <i>Polytrichastrum longisetum</i> (Sw. ex Brid.) G. L. Sm. | X | | |
| <i>Ptychomniella ptychocarpa</i> (Schwägr.) W. R. Buck et al. | | | X |
| <i>Ptychomnion cygnisetum</i> (Müll. Hal.) Kindb. | X | | X |
| <i>Rhaphidorrhynchium callidum</i> (Mont.) Broth. | X | | X |
| <i>Rigodium brachypodium</i> (Müll. Hal.) Paris | | | X |
| <i>Rigodium pseudothuidium</i> Dusén | | | X |
| <i>Sphagnum capillifolium</i> (Ehrh.) Hedw. | X | | |
| <i>Sphagnum falcatulum</i> Besch. | X | | X |
| <i>Sphagnum fimbriatum</i> Wilson | X | | X |
| <i>Sphagnum magellanicum</i> Brid. | X | X | |
| <i>Sphagnum</i> cf. <i>subsecundum</i> Nees | X | | |
| Liverworts | | | |
| <i>Anastrophyllum schismoides</i> (Mont.) Stephani | | X | |
| <i>Balantiopsis asymmetrica</i> (Herzog) J. J. Engel | | | X |
| <i>Balantiopsis cancellata</i> (Nees) Stephani | X | | |
| <i>Bazzania peruviana</i> (Nees) Trevis. | X | X | X |
| <i>Calypogeia sphagnicola</i> (Arnell & J. Perss.) Warnst. & Loeske | X | X | |
| <i>Cephalozia skottsbergii</i> Steph. | X | X | |
| <i>Cheilolejeunea</i> cf. <i>obtruncata</i> (Mont.) Solari | X | | X |
| <i>Chiloscyphus attenuatus</i> (Stephani) J. J. Engel & R. M. Schust. | | | X |
| <i>Chiloscyphus breutelii</i> (Gottsche) J. J. Engel & R. M. Schust. | | | X |
| <i>Chiloscyphus horizontalis</i> (Hook.) Nees | | | X |
| <i>Chiloscyphus magellanicus</i> Steph. | | | X |
| <i>Chiloscyphus striatellus</i> C. Massal. | | | X |
| <i>Cryptochila grandiflora</i> (Lindenb. & Gottsche) Grolle | | X | |

Appendix 1. Continuation.

| Species | Anthropogenic peatlands | Glaciogenic peatlands | Tepualia forests |
|--|-------------------------|-----------------------|------------------|
| <i>Frullania</i> cf. <i>boveana</i> C. Massal. | X | X | X |
| <i>Herbertus runcinatus</i> (Taylor) Kuhnem. | | X | |
| <i>Hyalolepidozia bicuspidata</i> (C. Massal.) S.W. Arnell ex Grolle | X | | |
| <i>Jamesoniella colorata</i> (Lehm.) Spruce ex Schiffn. | X | X | X |
| <i>Kurzia setiformis</i> (De Not.) J. J. Engel & R.M. Schust. | X | X | |
| <i>Lepicolea ochroleuca</i> (Spreng.) Spruce | X | X | X |
| <i>Lepidogyna menziesii</i> (Hook.) R. M. Schust. | | | X |
| <i>Lepidozia chordulifera</i> Taylor | | | X |
| <i>Lepidozia fuegiensis</i> Steph. | | | X |
| <i>Leptoscyphus huidobroanus</i> (Mont.) Gottsche | X | | X |
| <i>Plagiochila chonotica</i> Taylor | | | X |
| <i>Plagiochila hookeriana</i> Lindenb. | | | X |
| <i>Plagiochila lechleri</i> Gottsche | X | | |
| <i>Plagiochila lophocoleoides</i> Mont. | | | X |
| <i>Plagiochila rubescens</i> (Lehm. & Lindenb.) Lindenb. | | | X |
| <i>Plagiochila subpectinata</i> Besch. & C. Massal. | X | | X |
| <i>Porella subsquarrosa</i> (Nees & Mont.) Trevis. | X | | |
| <i>Radula decora</i> Gottsche ex Steph. | | | X |
| <i>Riccardia amnicola</i> Hässel | X | | |
| <i>Riccardia alcicornis</i> (Hook. f. & Taylor) Trevis. | | | X |
| <i>Riccardia floribunda</i> (Stephani) A. Evans | X | X | X |
| <i>Riccardia hyalitricha</i> Hässel | | | X |
| <i>Riccardia prehensilis</i> (Hook. & Taylor) C. Massal. | X | X | X |
| <i>Riccardia rivularis</i> Hässel | X | X | |
| <i>Riccardia spinulifera</i> C. Massal. | | | X |
| <i>Saccogynidium australe</i> (Mitt.) Grolle | X | | |
| <i>Schistochila lamellata</i> (Hook.) Dumort. | | | X |
| <i>Telaranea blepharostoma</i> (Stephani) Fulford | X | | X |
| <i>Telaranea plumulosa</i> (Lehm. & Lindenb.) Fulford | X | | X |
| Lichens | | | |
| <i>Cladia terebrata</i> (Laurer) S. Parnmen & Lumbsch | X | | |
| <i>Cladonia arbuscula</i> (Wallr.) Flot. | X | | |
| <i>Cladonia bellidiflora</i> (Ach.) Schaer. | X | | |
| <i>Cladonia gracilis</i> subsp. <i>elongata</i> (Wulfen) Vain. | X | X | |
| <i>Cladonia lepidophora</i> Ahti & Kashiw. | X | | |
| <i>Cladonia scabriuscula</i> (Delise) Leight. | X | | |
| <i>Cladonia squamosa</i> (Scop.) Hoffm. | X | X | |
| <i>Cladonia</i> P. Browne subgen. <i>Cladina</i> | X | X | |
| <i>Cladonia subsubulata</i> Nyl. | X | | |
| <i>Hypogymnia subphysodes</i> (Kremp.) Filson | X | | |
| <i>Usnea</i> sp. | X | | |
| <i>Peltigera polydactylon</i> (Neck.) Hoffm. | X | | |
| <i>Parmotrema reticulatum</i> (Taylor) M. Choisy | X | | |
| <i>Pseudocyphellaria faveolata</i> (Delise) Malme | | | X |
| Insectivorous plants | | | |
| <i>Drosera uniflora</i> Willd. | | X | |