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Changing lenses to assess biodiversity: patterns of species richness in sub-Antarctic plants and implications for global conservation

Ricardo Rozzi^{1,2,3*}, Juan J Armesto^{3,4}, Bernard Goffinet⁵, William Buck⁶, Francisca Massardo^{2,3}, John Silander⁵, Mary TK Arroyo³, Shaun Russell⁷, Christopher B Anderson^{2,3}, Lohengrin A Cavieres^{3,8}, and J Baird Callicott¹

Taxonomic groups and ecoregions shape the “lenses” through which biodiversity is assessed and conserved. A historical bias toward vertebrates and vascular plants in the northern hemisphere underpins how global patterns of biodiversity in terrestrial ecosystems are perceived. Here, we focus on the hitherto overlooked non-vascular flora (liverworts and mosses) in the remote sub-Antarctic Magellanic ecoregion of southwestern South America. We report that: (1) this ecoregion hosts outstanding non-vascular floristic richness, with > 5% of the world’s bryophytes on < 0.01 % of the Earth’s land surface; (2) species richness patterns for vascular and non-vascular plants are inverted across 25 degrees of latitude in Chile; and (3) while vascular plants are 20 times more abundant than non-vascular plants globally and in tropical South America, non-vascular plants are dominant in the sub-Antarctic Magellanic ecoregion and Antarctic Peninsula. These findings have been translated into policy and conservation decisions, including the creation of the Cape Horn Biosphere Reserve in 2005 and the introduction there of “tourism with a hand lens” in the diverse “miniature forests” of bryophytes, lichens, and invertebrates. We argue for consideration of ecoregional- or biome-specific indicator groups, rather than a narrow set of global indicator groups, for designing effective conservation strategies.

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Patterns of species richness and endemism used to identify priority areas for biodiversity conservation are strongly biased by our differential knowledge of taxonomic groups, as well as by contrasts in the existence of studies and data among geographical and ecological regions (Isaac *et al.* 2004; Lawler *et al.* 2006). In past decades, influential assessments of global priorities for

conservation have relied on geographic differences in the concentration of diversity and endemism of vertebrates and vascular plants (Myers *et al.* 2000; Rodrigues *et al.* 2004; Lamoreux *et al.* 2006). Taxonomic bias is also illustrated by the fact that more than 80% of the publications on animal conservation during the past 20 years have been devoted to vertebrate species, despite the fact that vertebrates represent less than 5% of the known faunal diversity (Clark and May 2002). Among vertebrates, birds and mammals (endotherms) are favored, being the focus of more than 70% of published articles, despite the fact that ectotherms (fishes, amphibians, and reptiles) comprise more than 70% of species, and include most of the threatened vertebrate taxa (Bonnet *et al.* 2002). Attention has not previously been called to analogous taxonomic biases in plant conservation studies. However, preliminary analyses indicate that the majority of publications on plant conservation focus solely on vascular flora. During the past decade, non-vascular plant conservation articles have remained marginal and diversity patterns of non-vascular flora poorly documented (Rozzi *et al.* in prep).

Regarding biases among geographical and ecological regions in the literature, conservation research has strongly concentrated on the northern hemisphere, with temperate forest biomes of North America and Europe accounting for 30% of publications with a conservation focus (Lawler *et al.* 2006). In contrast, few studies have

In a nutshell:

- At high latitude ecoregions, non-vascular flora should be included in floristic richness assessments
- Reverse latitudinal trends of vascular and non-vascular plant diversity challenge the universality of latitudinal species-richness gradients
- Inconspicuous taxonomic groups such as bryophytes can be important in promoting conservation, when their ecological and aesthetic values are understood by the general public and policy makers
- Metaphors and narratives generated by ecologists can be powerful tools for promoting local conservation and ecotourism

¹Department of Philosophy, University of North Texas, Denton, TX 76201 *(rozzi@unt.edu); ²Omora Ethnobotanical Park, Universidad de Magallanes, Puerto Williams, Antarctic Province, Chile; ³Institute of Ecology and Biodiversity, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile; ⁴Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile (continued on last page)



Figure 1. The sub-Antarctic (or sub-polar) Magellanic ecoregion, showing the full extent of evergreen rainforests (green) and Magellanic moorland (gray) from Cape Horn to Penas Gulf in Chile. Located on Navarino Island, south of Tierra del Fuego, Omora Ethnobotanical Park launched a bryoflora conservation program with international collaboration in 2000. As the research, education, and conservation center for the Cape Horn Biosphere Reserve (WebFigure 1), Omora Park serves as a long-term ecological research site of a nascent Chilean Long Term Ecological Research network, supported by the Chilean Institute of Ecology and Biodiversity (IEB; www.ieb-chile.cl; see Rozzi *et al.* [2006a]).

investigated patterns of species richness in relation to conservation priorities in sub-Antarctic forests, tundra, and adjacent Antarctic ecosystems (Arroyo *et al.* 2005; Lawler *et al.* 2006).

What, then, would happen if we were to move outside of these taxonomic, geographical, and ecoregional boundaries? Would a change in the taxonomic and ecogeographical lenses disclose reservoirs of biodiversity that might have remained invisible to conservation biologists? Here, we describe the consequences of changing “biodiversity conservation lenses”, by focusing on the world’s southernmost forest and tundra ecosystems, in the sub-Antarctic region of western South America (Figure 1). In addition, we address the inconspicuous and largely over-

looked non-vascular flora comprising liverworts and mosses present in this southern geographic region. The analysis of diversity patterns of this frequently overlooked taxonomic group in a remote and striking geographical area of evergreen broadleaf forests and tundra has led us to novel and challenging theoretical and practical questions. In this article, we show how non-vascular and vascular plants display opposite latitudinal species-richness gradients. We argue that conservation should focus on regional patterns of biome-specific biodiversity indicator groups, which are often left out of global assessments.

■ Diversity patterns of the sub-Antarctic non-vascular flora

Bryophyte flora of the archipelago region of southwestern South America

Since 2000, we have been conducting a series of floristic inventories in the region of Cape Horn, which, when combined with previously published data, indicate that more than 5% of the world’s bryophytes are found on less than 0.01% of the Earth’s land surface, at the southern tip of the Americas. Along the narrow southwestern archipelagic margin of Chile, between Cape Horn (56° S) and Penas Gulf (49° S; Figure 1), 818 bryophyte species (He 1998; Villagrán *et al.* 2005) have been recorded from the approximately 15 000 known worldwide (Schofield 2000). Within 125 000 km² of moorland, bogs, forests, glaciers, and alpine ecosystems, this humid and fragmented coast harbors 450 moss and 368 liverwort species (including hornworts; Figure 2; WebTable 1).

Ongoing work suggests that the species richness of this group is likely to grow, as several additions to the bryophyte flora of

Cape Horn Archipelago await formal description, including three new species of *Schistidium* (Grimmiaceae; W Buck in prep). Current phylogeographic studies are shedding new light on the isolation of populations of possibly widespread species, leading to the recognition of additional endemic taxa (MacDaniel and Shaw 2003; Figure 2b). According to recent floristic and taxonomic studies, more than 50% of liverwort and moss species are endemic to the temperate rainforests of southern South America (Engel 1978; He 1998; Buck 2000; Matteri 2000; Villagrán *et al.* 2005; Figure 2d). Moreover, several endemic bryophyte genera are monotypic (Matteri 2000). Thus, we contend that the combination of high bryophyte species diversity, including many geographi-



Figure 2. (a) Mosses and lichens are important pioneer species colonizing bare rocks on glacial moraines, as seen along the Beagle Channel in the Cape Horn Biosphere Reserve (CHBR). Through the weathering of rocks over long time periods, these mosses shape the substrate's physical and chemical properties. (b) One of the pioneer species confined to rock is a moss of the genus *Orthotrichum*, which resembles the globally distributed species *Orthotrichum rupestre*. However, ongoing research shows that some *Orthotrichum* populations in CHBR may warrant species recognition, as is the case with other austral moss populations in other species (Goffinet *in prep*). (c) In the rainforests of the sub-Antarctic Magellanic ecoregion, high annual rainfall (> 4000 mm) favors the development of conspicuous assemblages of liverworts, mosses, and lichens on trees and rocks, which contribute to the flow of nutrients and the overall water balance. (d) *Tayloria mirabilis* (Splachnaceae), an endemic moss of the temperate rainforests of southern South America, stands out due to the bright whitish color of its sporophytes, the spores of which are thought to be dispersed by flies (Caicheo *et al. in prep*). In the northern hemisphere, dispersal by insects is known only for a few moss species belonging to the family Splachnaceae.

cally restricted taxa, makes the sub-Antarctic Magellanic ecoregion a hotspot of global relevance for non-vascular flora. We refer to a bryophyte hotspot in a broad sense, meaning a species-rich area for bryophytes. This meaning is looser than the term “biodiversity hotspot”, as defined by Myers *et al.* (2000), which includes measurements of losses of natural habitat and numbers of endemic vascular plants.

Inverse latitudinal diversity patterns in non-vascular and vascular flora of Chile

The high number of bryophyte species in southernmost South America results from a clear trend toward increased species richness at higher latitudes along the southwestern margin of the continent; the sub-Antarctic Magellanic archipelago contains 67% of 549 liverworts

and 58% of 778 moss species known to Chile (Figure 3a; WebTable 1). Analysis of latitudinal patterns of floristic richness in Chile from 18° to 56° S indicates that more than 50% of bryophyte species (> 500) have a northern distribution limit in the archipelago region, around 41.5° S. Further north (38.5–30.5° S), species richness (estimated for each Chilean Administrative Region) declines to fewer than 100 species of liverworts, and fewer than 250 species of mosses. Finally, in the deserts of northern Chile (19.5–27.5° S), bryophytes are nearly absent and highly restricted (Figure 3a).

Vascular plants, in contrast, fail to exhibit such a dramatic decline in species richness toward the desert region, with nearly 1000 species in each Administrative Region (Figure 3a). The Chilean vascular flora reaches its peak richness in the transition from Mediterranean climate zone to temperate forest zone, between 30.5° and 41.5° S (Figure

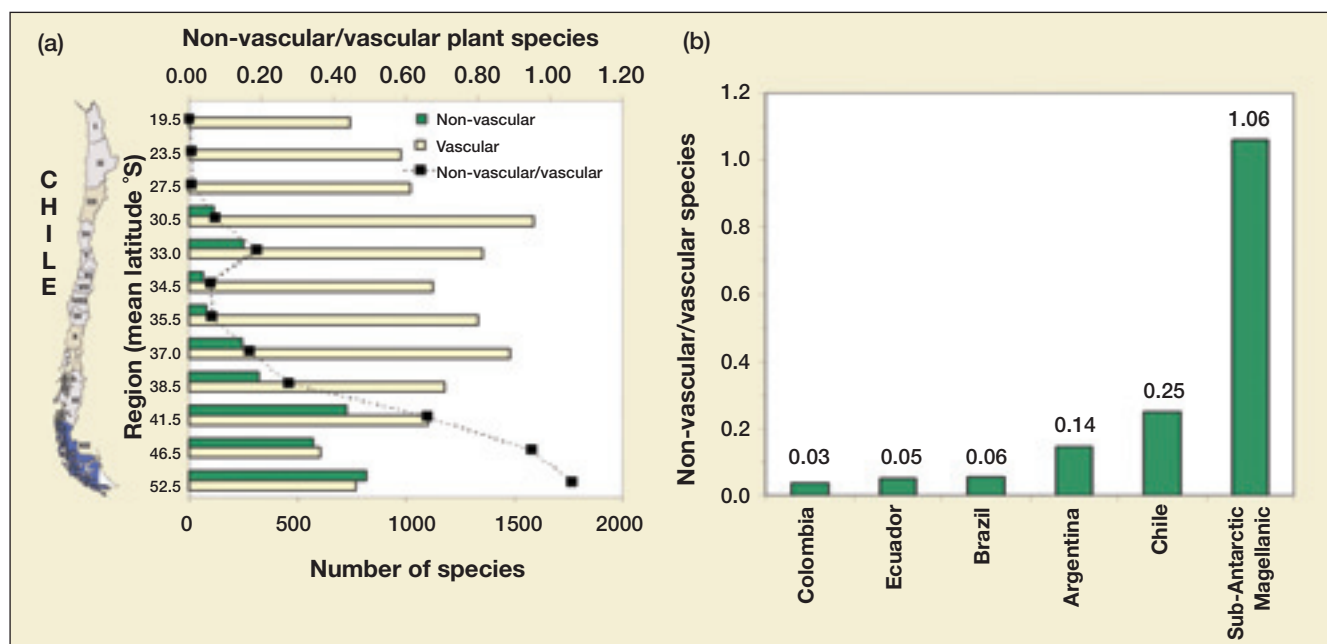


Figure 3. (a) Latitudinal patterns of species richness in non-vascular and vascular plant species in Chile. Values on the vertical axis are for median south latitude for each of the 12 Chilean Administrative Regions (shown on the map at left). The sub-Antarctic Magellanic ecoregion corresponds to the southernmost Region XII, shown in dark blue. The non-vascular to vascular plant species ratio (NV/V; dotted line) is positively correlated with latitude ($r_s = 0.92$, $P \leq 0.001$). (b) Within South America, NV/V increases southward from 0.03 in Colombia to > 1 in the sub-Antarctic Magellanic ecoregion. See WebTables 1 and 2 for species numbers and NV/V ratios.

3a; WebTable 1), with an overall total of 3892 species (Arroyo *et al.* 2004). Among these species, 1605 are endemic (ie $> 0.5\%$ of the global 300 000 plant species). This high vascular plant diversity provided the main argument for including central Chile among the 34 biodiversity hotspots identified worldwide (Arroyo *et al.* 1999, 2004; Myers *et al.* 2000; Mittermeier *et al.* 2004). At higher latitudes in southern Chile, south of 41.5°S , the number of vascular plant species declines with latitude (Figure 3a).

Latitudinal patterns of species richness in southwestern South America differ significantly between vascular and non-vascular flora (two-sample Kolmogorov-Smirnov test; $KS = 0.8333$, $P < 0.001$). While bryophytes reach their maximum species richness near Cape Horn, at the southern tip of the Americas, vascular plant richness is concentrated in central Chile ($30.5\text{--}38.5^\circ\text{S}$).

Non-vascular and vascular plant species ratio in southern South America and Antarctica

To better visualize the contrasting latitudinal patterns of vascular and non-vascular species richness, and to facilitate comparisons with other regions of South America, we define the non-vascular/vascular (NV/V) plant species ratio. As illustrated in Figure 3a, NV/V ratio significantly increases with latitude in Chile (Spearman's rank correlation; $r_s = 0.92$; $P \leq 0.001$), from close to 0 in the northern desert to slightly > 1 at the southern tip of the Americas. The roughly even NV/V ratio at high latitudes in South America contrasts sharply with the much richer vascular floras of tropical South America. In Brazil,

Colombia, and Ecuador, NV/V ratio is ≤ 0.05 (ie the number of vascular plant species exceeds by 20 or more the species richness of non-vascular plants; Figure 3b; WebTable 2). The NV/V ratio increases to 0.14 and 0.25 in more temperate countries such as Argentina and Chile. In the sub-Antarctic region, in turn, this ratio rises to 1.06 (Figure 3b), as the number of bryophyte species slightly surpasses the number of vascular plants.

If we consider the flora of the Antarctic Peninsula ($> 60^\circ\text{S}$), the NV/V ratio increases to 33.5. This high NV/V ratio results from the fact that only two native vascular plant species (*Deschampsia antarctica* and *Colobanthus quitensis*) occur on the islands of the Scotia Ridge and along the western coast of the Antarctic Peninsula (Lewis-Smith 1996). In contrast, 67 native non-vascular plant species have been recorded in the same territory, including 27 liverwort (Bednarek-Ochyra *et al.* 2000) and 40 moss species (Putzke and Batista-Pereira 2001). Consequently, non-vascular flora becomes the dominant plant group at high latitudes in southern South America and Antarctica.

The observed shift in NV/V ratio with increasing latitude in southwestern South America might be associated with historical and ecological factors. Small Pleistocene refugia may have favored survival of non-vascular over vascular plants during repeated glacial cycles (Villagran 2005). This, together with the ability of mosses to tolerate high levels of desiccation and low temperatures (Longton 1982), may have facilitated their survival in micro-refugia within glaciated zones. Following glacial retreats, mosses are often the first plants to colonize the

Panel 1. Linking biodiversity research and conservation: “tourism with a hand lens” in the miniature forests of Cape Horn

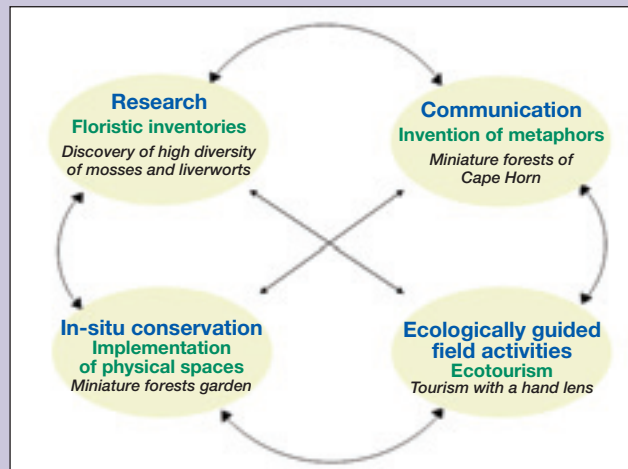
Omora Ethnobotanical Park has developed a four-step cycle linking research and conservation (illustrated in figure at right). Each step (blue, bold) is illustrated according to the method used (green, italics), and the progress made (black) toward conserving non-vascular flora in the sub-Antarctic Magellanic ecoregion. Arrows and lines indicate that interactions among the four steps are multidirectional.

Scientific research based on floristic inventories disclosed globally outstanding richness of bryophytes (mosses and liverworts) at the southern end of the Americas. This discovery presented scientists with the challenge of communicating information about the diversity of these tiny plants, often lacking common names, to decision makers and the general public.

Communication of this scientific discovery to government authorities and the general public was facilitated through the invention and use of metaphors such as the “miniature forests of Cape Horn”, which proved useful in conveying the notion of these highly diverse biotic communities, consisting of mosses and liverworts and their associated lichens, fungi, and invertebrates.

Guided field tours in the Omora Ethnobotanical Park, where scientists and graduate students have been accompanying government authorities, school teachers, members of the local community, journalists, and ecotourism groups to enjoy the miniature forests of Cape Horn, led to the concept of “tourism with a hand lens” (Rozzi *et al.* 2006a). This new type of tourism enhanced appreciation of ecological interactions and the beauty of the austral bryoflora, while at the same time providing a sustainable source of income for local communities in the Cape Horn Biosphere Reserve. The Chilean Government supported this innovative idea by funding training courses and publications on the natural history of bryophytes and lichens (Goffinet *et al.* 2006).

In-situ conservation of the austral bryoflora and development of “tourism with a hand lens” stimulated an interdisciplinary team of scientists and artists to design and begin building a “garden of the miniature forests of Cape Horn” in the Omora Ethnobotanical Park. In this garden, the first of its kind worldwide, Omora is currently demonstrating that “tourism with a hand lens” is both environmentally and economically sustainable. With the help of a hand lens, visitors spend hours observing the little-known and unusual biota, and hence stay longer in one place. This increases the number of nights tourists stay in local hotels and restricts environmental impacts to only a very small area (< 1 ha) of the biosphere reserve.



newly exposed ground and bare rocks (Schofield 2000), as can be seen on glacial moraines today (Figure 2b). Finally, patterns of plant species diversity in sub-Antarctic regions are shaped in part by dominant wind currents that favor long-distance dispersal of bryophyte and lichen spores and asexual reproductive structures (such as fragments of mature individuals or special reproductive bodies like gemmae) over propagules of vascular plants (Muñoz *et al.* 2004).

Similarly, in the northern hemisphere, the non-vascular flora prevails in Arctic Alaska (Longton 1982). Thus, the trend toward NV/V ratios ≥ 1 at higher latitudes seems to be a general phenomenon, which contrasts with an average NV/V ratio of 0.05 at a global scale (based on the figures of 300 000 vascular versus 15 000 non-vascular plant species). If non-vascular plants dominate the high-latitude floras in both hemispheres, then sub-Antarctic and sub-Arctic biodiversity assessments may require a transformation of the prevailing “botanical lens”, as the focus on vascular plants will continue to make the high floristic diversity of these ecosystems “invisible” to both scientists and decision makers.

■ The Cape Horn Biosphere Reserve

Our findings on the sub-Antarctic Magellanic non-vascular flora, combined with the invention of an innovative ecotourism activity to appreciate this flora (“tourism with a hand lens”; Panel 1), provided strong support for the proposal to create the Cape Horn Biosphere Reserve

(WebFigures 1 a,b). This proposal involved 5 years of research and negotiations, led by scientists from Omora Ethnobotanical Park (Panel 1) and a broad array of regional, national, and international institutions, with the common goal of integrating the protection of the southernmost ecosystems in the Americas (Rozzi *et al.* 2004). The designation of the Cape Horn Biosphere Reserve by UNESCO in June 2005 documents how the less conspicuous taxonomic groups can motivate the protection of whole ecosystems. Today, the Chilean government recognizes the new Cape Horn Biosphere Reserve as a model for implementing the three main goals of the Convention of Biological Diversity (conserving biodiversity, equitable sharing of its benefits, and sustainable use of biodiversity), through the integration of research, education, and conservation (Rozzi *et al.* 2006 a,b). In this manner, the tiny mosses and liverworts of Cape Horn helped to establish the largest Chilean biosphere reserve (4.9 million ha), representing long-term and novel institutional arrangement to preserve this valuable ecosystem.

■ Lessons learned

The case study of the sub-Antarctic non-vascular flora in southern South America presented here suggests five points of general applicability. First, we argue for the use of “ecoregional- or biome-specific” indicator groups, rather than a narrow set of global indicator groups, when assessing regional biodiversity patterns. In defining prior-

ity areas for conservation of marine ecosystems, it would make little sense to use vascular plants as an indicator group rather than algae. As a direct corollary, if we are concerned about the biodiversity of high latitude biomes and ecoregions, the non-vascular flora should be given the greatest weight in the floristic assessments. Our findings of high species richness and endemism in the sub-Antarctic Magellanic non-vascular flora (which was overlooked prior to this study), and the considerably different trends seen in vascular and non-vascular land-plant species richness along a broad latitudinal gradient in southwestern South America, highlight the limitations arising from the use of a restricted set of common indicator species to identify conservation priorities across the globe.

Second, the opposite latitudinal trend of vascular and non-vascular land-plant diversity in this area raises questions about the universality of latitudinal species-richness gradients and should stimulate new comparative studies of distribution patterns across different taxonomic groups. The distribution of land-plant diversity in Chile raises further questions regarding the definition of “hotspots” based solely on vascular plant or vertebrate diversity patterns, because such concepts implicitly assume that species richness among different taxonomic groups are positively correlated. While species richness in most groups of terrestrial organisms increases toward the equator, we show here that non-vascular plant species richness exhibits the opposite trend across 40 degrees of latitude in Chile.

Third, inconspicuous taxonomic groups, such as bryophytes, can play important roles in promoting conservation when their ecological and aesthetic values are understood by the general public and policy makers. The high diversity of sub-Antarctic Magellanic non-vascular flora was critical in making the case for the establishment of the Cape Horn Biosphere Reserve in June 2005. Bryophytes, although very small organisms in comparison to charismatic megafauna and large tree species, have the potential for becoming emblematic flora at other sub-polar latitudes.

Fourth, our experience suggests that the interdisciplinary and inter-institutional approach can be successful in translating the scientific discovery of an austral species richness center for bryophytes into conservation action, stimulating new research questions in the process. This feedback between biodiversity research and conservation was organized into a four-step cycle, which integrated (1) generation of new scientific knowledge, (2) its communication, (3) in situ education and ecotourism activities, and (4) the creation of a “garden of the miniature forests of Cape Horn”, displaying and conserving in situ sub-Antarctic non-vascular flora (Panel 1). Scientific technical publications with narratives for the general public and a visit by the then President of Chile were instrumental in creating national and international awareness of the charm of these little-known plants for ecotourism in the remote Cape Horn region. Further, the concept of “tourism with a hand lens” and the metaphor of the

“miniature forests of Cape Horn” illustrate an innovative approach to communicating locally relevant scientific research to promote effective regional conservation.

Finally, in our experience, international partnerships enhance research and education programs. Creating a program focused on non-vascular plant diversity in the sub-Antarctic Magellanic region without international collaboration would have been difficult because of the lack of trained Chilean bryologists and taxonomists (cf Simonetti *et al.* 1995). In turn, collaboration among international and Chilean institutions and scientists with different cultural experiences and fields of expertise was essential for promptly translating novel scientific knowledge into regionally and globally significant conservation actions, leading to the creation of the world’s southernmost biosphere reserve.

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⁵Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269; ⁶Institute of Systematic Botany, New York Botanical Garden, New York, NY 10458; ⁷CAZS Natural Resources, University of Wales, Bangor, Wales, LL57 2UW, UK; ⁸Departamento de Botánica, Universidad de Concepción, Casilla 160C, Concepción, Chile

WebTable 1. Number of non-vascular and vascular plant species for each Chilean Administrative Region (AR) included in Figure 3. Regions are arranged from north to south (I–XII).

Administrative region	# of moss species ^{1,2}	# of liverwort species ^{3,4,5}	Total # of non-vascular plant species	# of vascular plant species ^{6,7}	Non-vascular/vascular plant species ratio	Median latitude of AR (°S)
I	0	0	0	745	0.00	19.5
II	8	0	8	977	0.01	23.5
III	8	0	8	1024	0.01	27.5
IV	66	49	115	1591	0.07	30.5
V	169	85	254	1357	0.19	33.0
VI	53	12	65	1127	0.06	34.5
VII	65	16	81	1334	0.06	35.5
VIII	190	58	248	1481	0.17	37.0
IX	234	91	325	1183	0.27	38.5
X	412	316	728	1105	0.66	41.5
XI	310	266	576	608	0.95	46.5
XII	450	368	818	773	1.06	52.5

Notes: ¹He (1998); ²Buck (2002); ³Villagrán et al. (2005); ⁴Barrera (1995); ⁵Engel (1978); ⁶Martcorena (1990); ⁷Martcorena (2005).

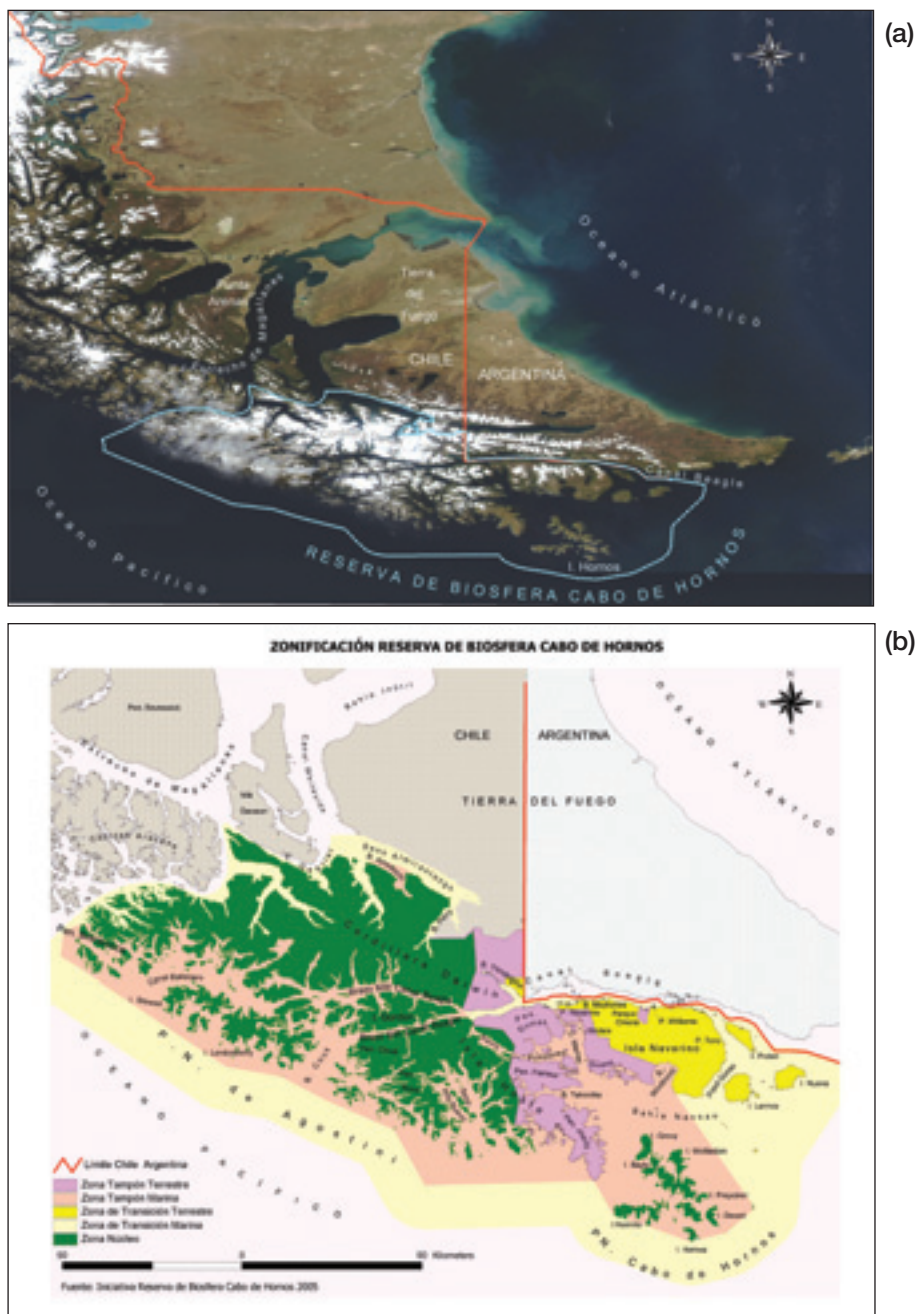
WebTable 2. Richness of non-vascular and vascular plant species for countries and regions included in Figure 4

Country or region	# of moss species	# of liverwort species	Total # of non-vascular plant species	# of vascular plant species	Non-vascular/vascular plant species ratio	Latitudinal range
Colombia	976 ¹	786 ⁶	1762	51 220 ¹¹	0.03	12°N–4°S
Ecuador	854 ¹	148 ³	1002	19 362 ¹¹	0.05	2°N–5°S
Brazil	1964 ²	1160 ²	3124	56 215 ¹¹	0.05	5°N–34°S
Argentina	1002 ³	342 ⁷	1344	9372 ¹¹	0.14	21°S–55°S
Chile	778 ⁴	549 ^{8,9}	1327	5284 ¹¹	0.25	17°S–56°S
Sub-antarctic Magellanic ecoregion	450 ^{4,5}	368 ^{8,10}	818	773 ¹²	1.06	49°S–56°S

Notes: ¹Delgadillo (1994); ²Yano (1996); ³Kuehnemann (1938); ⁴He (1998); ⁵Buck (2002); ⁶Gradstein and Hekking (1979); ⁷Kuehnemann (1949); ⁸Villagrán et al. (2005); ⁹Barrera (1995); ¹⁰Engel (1978); ¹¹WMC (1997); ¹²Henríquez et al. (1995).

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WebFigure 1. (a) Satellite image of the Cape Horn Biosphere Reserve (CHBR), delimited by light blue dotted line. Located south of Tierra del Fuego, this is the southernmost protected area of the world, and with an area of 48 843 km², the largest biosphere reserve in the southern cone of South America (ie Uruguay, Argentina, Chile). (b) Map of CHBR showing its core zone (dark green), dedicated to strict preservation; buffer zones (purple), where sustainable, low-impact activities such as ecotourism are permitted; and transition zones (yellow), where higher impact activities, including construction of infrastructure, are allowed. Maps prepared by the GIS Laboratory, CERE-University of Magallanes and the Omora Foundation.