

ECOGRAPHY

Research

The world's southernmost tree and the climate and windscapes of the southernmost forests

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Ecography

43: 1–11, 2020

doi: 10.1111/ecog.05075

Subject Editor:

Jens-Christian Svenning

Editor-in-Chief: Miguel Araújo

Accepted 14 August 2020



The world's southernmost tree has been documented along with the condition and growth pattern of the world's southernmost forest on Isla Hornos, Chile. The distribution of trees at broad scales is strongly influenced by the abiotic environment and determining the position and condition of tree limits around the world is an important way to monitor global change. This offers an ideal way to test the relationship between the biogeography of individual species and the effects of climate/climate change. The limits of trees, as all ecotones, are also useful communication points – easily understood signposts of ecosystems and their change through time. The southernmost trees in the world exist at soil temperatures that correspond to the low range of global treeline temperatures, with a climate analogous to equatorial treeline despite the high latitude (56° S). However, their fine-scale distribution is strongly influenced by wind exposure rather than simply aspect and/or elevation, as one would expect if temperature were limiting the range. Recent establishment further south was found from core forest areas, however significant dieback along wind-exposed edges of the contiguous forest was also noted. In contrast to the wide extension of land where boreal or subarctic forests grow in the Northern Hemisphere, in the Southern Hemisphere Isla Hornos represents a single point embedded in the ocean under much milder climatic conditions. Documented shifts in wind intensity and direction as result of larger-scale climate change will likely continue to strongly shape the condition of these unique forests.

Keywords: Antarctica, Cape Horn, climate change, plant life, southernmost forest, southernmost tree, Tierra del Fuego, treeline, tree, wind

Introduction

Climate change, particularly warming, should drive the migration of plants to higher latitudes. Plant migration plays a significant role in global climate modelling via changes to albedo, carbon cycling and water balance. Plants are excellent bioindicators of climate change at high latitudes (Smith 1994), with trees particularly useful. The tree growth form, with the growing physiology of the plant decoupled from higher



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ground temperatures (which occur due to soil heating), experiences atmospheric temperature more directly than lower stature plants (Körner 2012).

At broad scales, the limits of tree-form life are assumed to be temperature driven, and idea with strong global evidence (Körner and Paulsen 2004, Paulsen and Körner 2014) and as such anticipated to generally be expanding as climate warms. Approximately half of tree lines are expanding, and very few contracting (Harsch et al. 2009) though only a handful are from the southern hemisphere. However, a variety of confounding effects can also constrain migration (e.g. competition: Schwab et al. 2016, grazing: Wieser et al. 2019; nutrient constraints: Sullivan et al. 2015; drought: Piper et al. 2016). Thus, while general expectations are for expansion, both well described (e.g. competition with shrubs) and less well described (e.g. changes in wind patterns driven by climate change) constraints may limit the expansion of trees around the world.

There is little known about the geographic limits of trees in the Southern Hemisphere compared to the northern hemisphere. Geography constrains potential sites for the world's southernmost tree and forests. The southern hemisphere is ocean dominated, with a smaller temperature range (more maritime climate) than the northern hemisphere (Rozzi et al. 2012, 2014). South of the Antarctic Polar Convergence Zone, which varies from 50 to 60°S and where cold Antarctic water is at the surface, islands are often ice covered unless geothermally heated. Nonetheless, plant life and introductions of various species have occurred (Frenot et al. 2005). However, trees are conspicuously absent on all the major island groups both around and south of this zone (Peat et al. 2007; Supplementary material Appendix 1 Fig. A1); specific surveys include the McDonald Islands (53°S; Jenkin 1997), Macquarie and Heard Islands (55° and 53°S respectively; Hughes 1987, Scott 1990, Bergstrom et al. 2006, Turner et al. 2006), Bouvetøya Island (~54°S; Engelskjøn 1987), the Diego Ramirez Islands (56°S; Pisano 1972, Pisano and Schlatter 1981, Rozzi et al. in press), South Sandwich Islands (with particular focus on geothermally warmed areas; 56–60°S; Longton and Holdgate 1979, Convey et al. 2000), the South Orkney Islands (~60°S; Lewis Smith 1972), the South Shetland Islands (~62°S; Olech 1996) and the Balleny Islands (~66°S; Hatherton et al. 1965). Recent reviews of the Antarctic region south of 60° have only documented a few vascular plants and no tree species (Peat et al. 2007).

The furthest south locality with potential trees identified was Isla Hornos (Fig. 1A; 55.97°S, 67.27°W). The floras of this island had been briefly described by Pisano (1982), which mentions dwarf *Nothofagus* individuals, the most important genus of temperate tree species of the Southern Hemisphere. This island (the southernmost island in the Cape Horn archipelago) has a warmer climate than other islands at similar latitudes due to its position alongside the west side of South America, where the Convergence Zone is deflected southward. It is also closer to a continuous land mass (~100 km southwest from Tierra del Fuego) and presumably has a

higher influx of seeds, though this is relevant only if the climate can support trees. Temperatures are relatively mild year-round, though colder than the hypothesized temperature limit for *Nothofagus* as reported in Wardle (1998) and Körner and Paulsen (2004). Winds are estimated to be $> 72 \text{ km h}^{-1}$ ~7.5% of the time (Sampe and Xie 2007), and storms can exceed 200 km h^{-1} . The goal of this research was to document the world's southernmost tree and the place where trees reach their geographic limit, and examine several questions:

1. Which is the species of the world's southernmost tree? Which tree species dominates the world's southernmost forest? Does it correspond climatically to predictions from other treelines?
2. Are the world's southernmost forests healthy?
3. Are the world's southernmost forests expanding, contracting or static?

Methods

In January and February 2019, an expedition went to Isla Hornos, the southernmost island in the Cape Horn archipelago in southern Chile at the end of the Americas. It is located south of Tierra del Fuego, at the edge of Drake passage. The overarching purpose was to document the world's southernmost individual tree and evaluate the world's southernmost forest. Then, to examine if this latitudinal extreme distribution correspond climatically to patterns identified for high-altitude treelines in other regions, to assess if the tree limits in the south appear to be climatic or some other factor, and assess if climate change is impacting health and distribution of the world's southernmost trees. The extremely low human pressures make these forests a highly useful place to examine ecological/climatic patterns and processes.

To assess tree spatial distribution, species composition and status (expanding/contracting/stasis) given the highly heterogeneous tree sizes and overall landscape, a multiscale sampling scheme was employed covering the interior of the forest, the edge of the forest and the southward individuals that extend beyond the contiguous forest. Trees were defined as single stemmed individuals of one of the three tree-forming species on the island; this definition includes seedlings of those species. An aboveground height definition in this context would be problematic, as single-stemmed individuals often grow horizontally below the wind while still retaining a 'tree form' (Supplementary material Appendix 1 Fig. A2). First, three large plots ($10 \times 10 \text{ m}$) were randomly placed within the interior of the live forest; tree heights above ground were generally around 4–5 m. Second, three sets of paired $5 \times 5 \text{ m}$ plots were randomly placed across the southern edge of the forest, with one inside the live canopy area and the other 5 m away towards true south, outside the continuous live canopy area. Tree height above ground at the edge was generally 2–3 m. Finally, for isolated individuals south of the continuous canopy (which were quite small), three sets of paired $2 \times 2 \text{ m}$

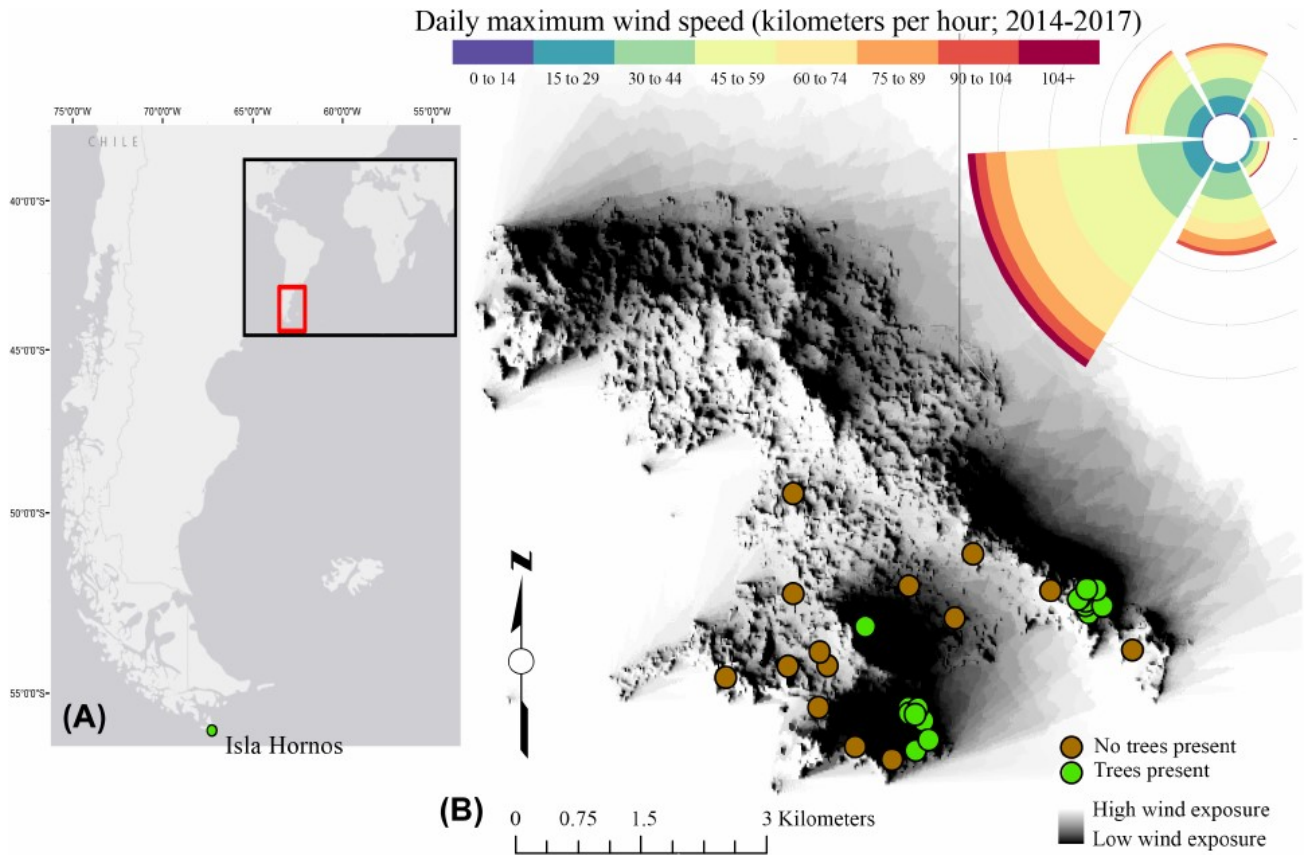


Figure 1. Isla Hornos geography, wind environment and plot locations. (A) Location of Isla Hornos at the far south of the Cape Horn archipelago in southern Chile. (B) Modeled wind exposure for Isla Hornos and plot locations. Wind exposure is a relative scale from high (low protection; white) to low (high protection; black) exposure. The wind rose displays the distribution of maximum daily windspeeds, illustrating the general southeasterly winds and typical max intensity. Plots locations colored by whether trees are present or absent. The distribution is primarily associated with wind exposure, with higher exposed sites less likely to have tree species present.

plots were established using the same protocol as the edge, with one 2×2 encompassing the individual and the second 5 m away. Two of those were placed around randomly chosen individuals; the third was placed on the southernmost individual as determined via an extensive exploration of the island. These are not 'proper' trees, in that their growing stems are not extended well above the warmer thermal environment of the ground (heights generally ~ 1 m, though lengths much longer; see Results). However, this appears to be due to wind, not climatic limitations (see climate data, below). The purpose in their documentation was to assess the age structure of the southernmost individuals of these 'potential' trees.

At each plot, tree height, health (0–100% live canopy) and basal diameter were recorded. Trees were cored as close to ground level as possible, which was often facilitated by their contorted growth (median height = 4.0 cm). While the difficulties in accessing the sites means we cannot at this point assess N availability, we did assess total C and N stocks to provide a baseline datapoint for future expeditions. Four soil samples were collected in each plot, two at 5 cm depth and two at 10 cm depth. Interior and exterior plots were collected separately (total $n = 56$). Soil was retained at field temperatures, dried at 60°C for 48 h, and analyzed for total

C and N on a Costech EA 8020. There was no significant difference between the two depths for both total N (t-test [variance assumption checked], $p > 0.05$, $t = 1.37$) and C:N ratio ($p > 0.05$, $t = 1.45$), so the different depths were pooled for all subsequent analyses. Differences between exterior and interior plots were assessed for both total N and C:N ratio via t-tests (variance equality checked); differences between southern individuals, edges and contiguous canopy plots were assessed via Tukey's HSD tests.

As the landscape is predominantly treeless, 14 sites were also randomly placed on the island and confirmed treeless via high resolution remote sensing and ground control points collected incidentally while exploring the island. Finally, for a related study on canopy epiphyte communities (Diaz et al. unpubl.), tree heights were collected from 16 forested locations in various locations around the island corresponding to climbable trees. We utilized those tree heights and locational data for the two analyses associated with tree presence/absence and height versus wind exposure. Total sample size differs between plot level analyses involving tree presence/absence and height ($n = 45$) and analysis involving tree density ($n = 29$). Heights and densities were modeled as a function of wind exposure using a log-linear regression.

Temperature and climate

Air temperatures from the Chilean Armada weather station on Isla Hornos were obtained, which spanned from 1 March 2014 to 5 January 2018 (Fig. 2). Two types of anomalous readings were observed: recorded median temperatures $> 50^{\circ}\text{C}$ and days where all recorded values were identical, usually zero. Those days were removed from the record. Soil temperatures (10 cm depth) were modeled from air temperatures using equations from a global treeline study (Körner and Paulsen 2004; snow is transient and rare, and so insulating effects on soil temperature were ignored). This was done for comparison purposes to the treeline study. Soil temperature is modeled via the 7-day rolling mean air temperature:

$$\text{Soil temperature } (^{\circ}\text{C}) = 3.2 + 0.5 \times 7 \text{ day mean air temperature}$$

For estimating if climate is limiting tree growth, previously published thresholds were examined. A later study (Paulsen and Körner 2014) identified three primary variables that describe climatic limits to true treelines around the world via a statistical approach: a minimum mean air temperature to constrain the growing season, the length of that growing season and the minimum mean temperature of all the days in that growing season. Globally (at climatically seasonal sites), those parameters are a growing season defined by the sum of days with mean air temperatures above the minimum of

0.9°C , a growing season mean temperature $> 6.4^{\circ}\text{C}$, and a length of growing season at least 94 days long. This definition of a growing season does not work directly in our high latitude, hypermaritime site, as the mean temperature during the growing season as defined with that threshold (days $\geq 0.9^{\circ}\text{C}$) is substantially less than the mean temperature threshold of 6.4°C (results below). Given the lack of seasonality, we then explored variation on these thresholds to identify alternatives which would work with the global treeline dataset. However, we emphasize this analysis is primarily for hypothesis generation given the lack of other data to establish start/end dates of the growing season. (Note that weather station data does not necessarily exactly represent canopy conditions, especially in low-wind conditions; see Discussion.)

A second option for defining seasons (and more direct) is based on the growth of the organism itself. Phenology is often a good approximation, however the southernmost trees found are evergreen *Nothofagus betuloides* and *Drimys winteri* (observed with leaves throughout the year; Rozzi unpubl.), so a phenologically defined season is difficult; the deciduous *Nothofagus antarctica* is present but observations are lacking on leaf on/off dates. Photographs taken for various other purposes in April and May do show *N. antarctica* with yellowing leaves and off-leaf by May, however a quantitative assessment is not possible from these infrequent and non-systematic records. Further work on daily growth increments would be useful in this more direct observation of seasonality.

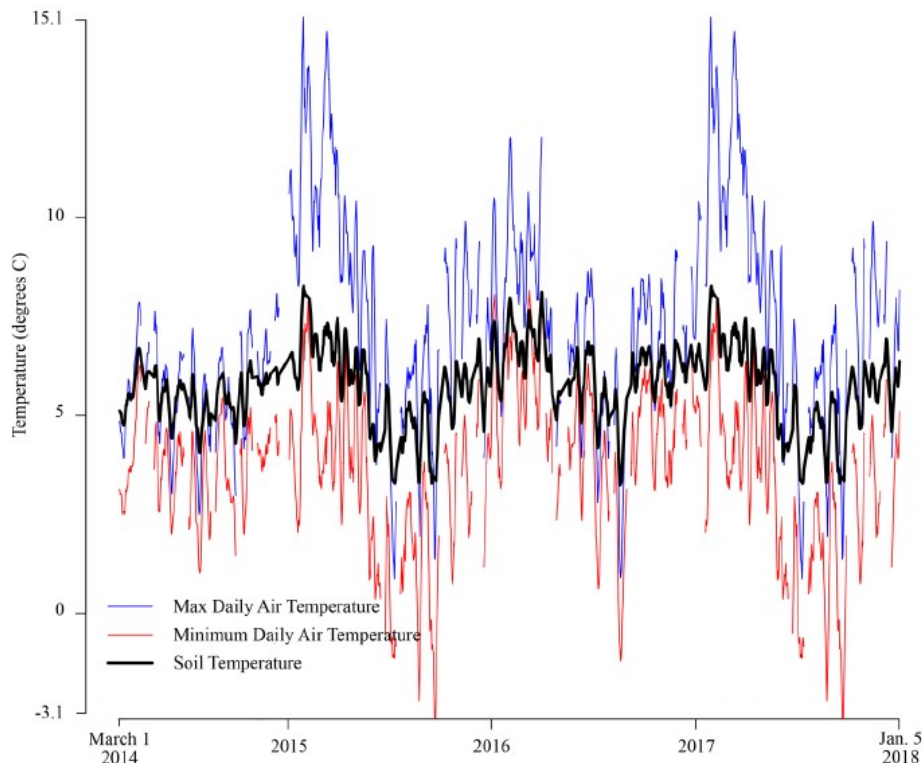


Figure 2. Temperatures on Isla Hornos are mild year-round with only minor variation. The 7-day minimum and maximum air temperatures (rolling average) rarely drop below 0 or above 10°C . Modeled soil temperatures are similarly mild and shown for comparison with a global treeline review (Körner and Paulsen 2004).

Topography and wind exposure

Topographic variables were derived from the NASA ASTER mission (30 m resolution; Supplementary material Appendix 1 Fig. A3). To calculate wind exposure, methods from Buma and Johnson (2015) were used. This methodology has proven effective in similar conditions in the northern hemisphere (Boose et al. 2001, Kramer et al. 2001, Buma and Thompson 2019). Briefly, wind is modeled as a straight-line vector that is deflected over sheltering objects at multiple vertical angles, providing a spectrum of exposure values (1–9). Observed daily maximum wind speeds were used to create a distribution of wind exposures that match both the angle and frequency of observed storm winds. All meteorological data was taken from the Chilean Armada weather station.

All analyses were conducted in R.

Results

The world's southernmost tree species individual is a *Nothofagus betuloides* located on a shallow northeast facing slope at -55.9754 latitude and -67.2658 longitude. Age at coring height (2.5 cm above ground surface) is 42 years old (the tree establishment estimate dates to 1978); individual is approximately 2 m long though bent horizontal at 57 cm above the ground surface due to wind. The next individual, approximately 1 m to the north, is bent horizontal at 103 cm above the ground and is 4 m in length. Numerous smaller seedlings were noted to the north. Two other tree species are present in the world's southernmost forests: *Drimys winteri*, and *N. antarctica*, whose last individual is approximately 17 m north of the southernmost *N. betuloides*. The edge and core

of the forest are similar in age structure, primarily comprised of trees < 100 years old with a few older individuals (> 200 years old) with heights above ground ranging from 2–3 m to 8+ m (Supplementary material Appendix 1 Fig. A2). The southernmost individuals are all substantially younger (average age at coring height = 48 years; Fig. 3).

Tree presence is strongly patterned on the landscape, limited to north to east aspects (~ 320 – 110°) overall. However, many NE-facing slopes, which theoretically correspond to higher solar exposure coupled with warmer afternoon conditions had little no tree cover. Instead, actual tree occurrence is limited to areas of low wind exposure (wind refugia) within those settings (Fig. 4). Tree density is significantly higher (marginally) at lower exposures (log transformed, $p = 0.05$; $F = 4.2_{1,21}$, $r^2 = 0.17$), though the relationship is driven primarily by the clustering of forested plots at low exposure and the high number of non-treed plots at high exposure. The height above ground that trees attain (not ultimate length) is strongly related to wind exposure (Fig. 4; log transformed, $p < 0.001$; $F = 26.0_{1,37}$, $r^2 = 0.41$).

Type and condition

Out of 146 trees on the plots, 145 were *N. betuloides* and one *D. winteri*. *Nothofagus antarctica* was found on ridge-lines and exposed gullies, but not on any of the plots. No other tree forming species were seen. Heights above ground range from < 1 m on the southernmost edge of the island to > 8 m in sheltered locations (Fig. 5). The largest trees are located in the interior plots (mean height = 303 cm, mean basal diameter [BD] = 17.6 cm) compared to the forest edge plots ($h = 215$ cm, $BD = 14$ cm) or the southward

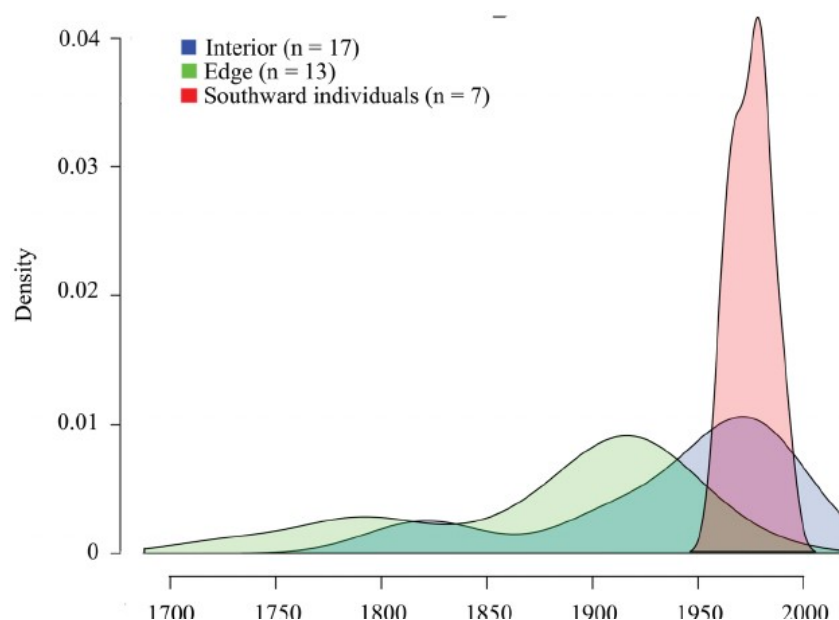


Figure 3. Density plot of establishment dates for all trees sampled on the island. Southward individuals have all established more recently, with a peak in the distribution in the latter 1900s; interior plots show two peaks of establishment in the early 1800s and then latter 1900s. Edge plots were intermediate, with both older individuals and a peak in the early 1900s. Sample size in legend.

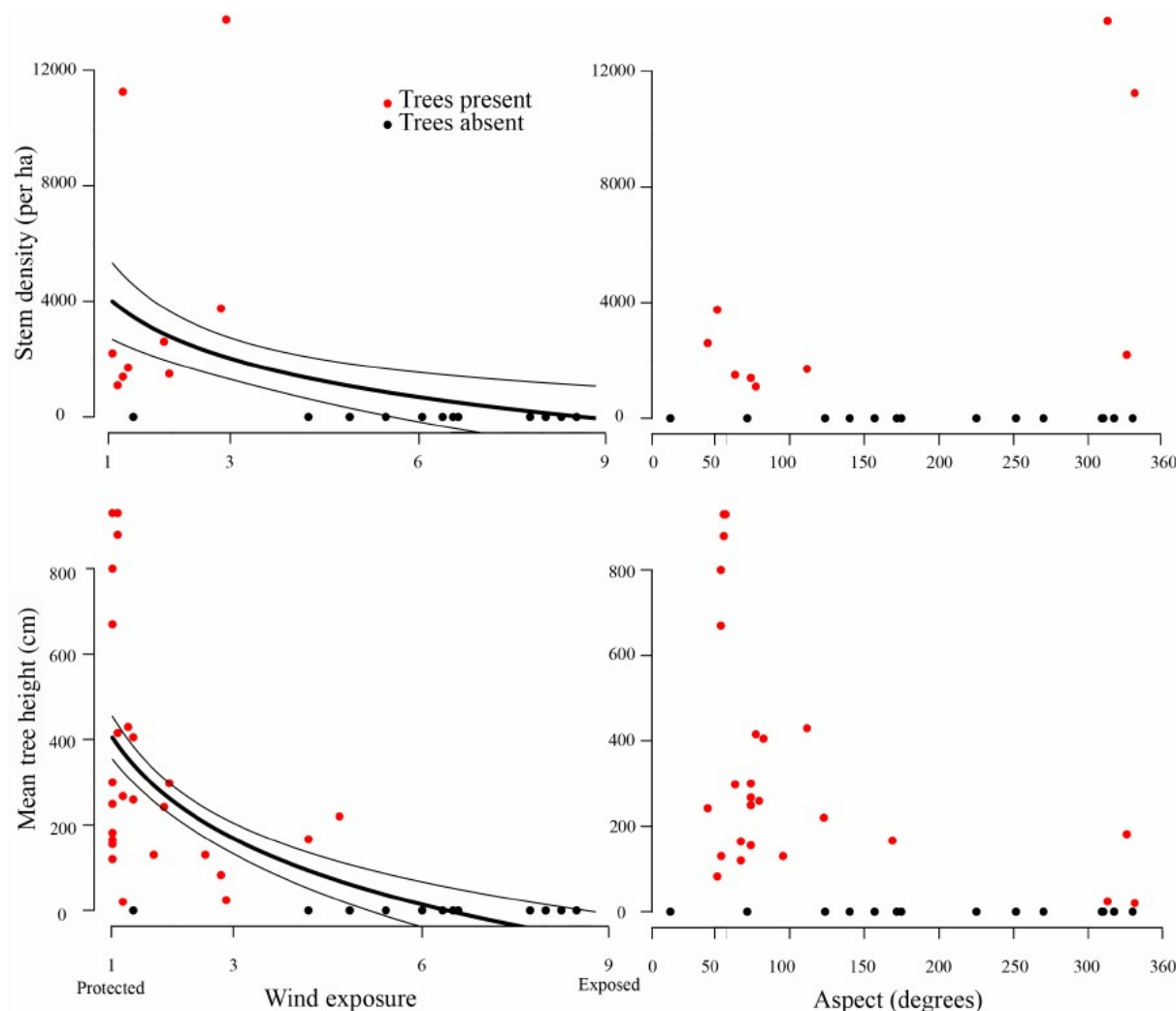


Figure 4. Tree density and size (height) as a function of wind exposure and aspect. Curves (± 1 standard error) are significant between exposure and tree height $p < 0.001$; $F = 26.0_{1,37}$, $r^2 = 0.41$) as well as exposure and density ($p = 0.05$; $F = 4.2_{1,21}$, $r^2 = 0.17$).

individuals ($h = 34$ cm, $BD = 4$ cm); differences in height between all groups was significant (Tukey's HSD, $p < 0.001$ for all comparisons). Basal diameter was not significantly different (Tukey's HSD, $p > 0.05$) between interior (17.6 cm) and edge (13.9 cm) plots, though both were significantly larger ($p < 0.05$) than the southward individuals (3.9 cm). Tree health varied by location. Forest interior plots had a significantly (Tukey's HSD) higher fraction of dead individuals overall (46%) versus edge (16%; $p = 0.003$) or southward individuals (18%; $p = 0.013$); the latter two locations of which were highly similar ($p = 0.988$). There were no significant differences between live individual canopy health across the locations (forest interior = 89.6% healthy, edge = 79%, southern individuals = 86.5%; $p = 0.07$ for interior versus edge, 0.379 for southern versus edge and 0.814 for southern versus interior). However, the edge plots were starkly divided between interior and exterior plots. Trees on the exterior of the edges were predominantly dead and the edge interior plots predominantly live (63 versus 3% mortality)

and with lower canopy health scores (17.5 versus 82.9%; Fig. 5).

Nitrogen stocks varied by location. There is significantly lower N stocks ($p < 0.05$) on the tree-covered portions of the plots (1.2%, standard deviation = 0.37%) than on the exterior paired plots (1.5%, 0.27% SD), and correspondingly a lower C:N ratio (lower by 8.2; $p = 0.0006$) on the outside versus inside of live forest (27.2 versus 35.4 respectively). Within just live treed plots, total N declined from the southern individuals (1.4%, $SD = 0.44$) to the edges (1.24%, $SD = 0.30$) to the interior (1.03%, $SD = 0.23$), though only the extremes (southern individuals versus interior) were significantly different overall ($p = 0.022$, Tukey's HSD test). The C:N ratio followed a similar pattern, from lower in the southern individuals (31.0, $SD = 11.2$), higher on the edge (33.4, $SD = 9.4$) and highest in the interior (41.2, $SD = 11.8$). These distances with the interior appear to be robust (interior versus edge: -11.0 , $p = 0.004$; southern versus interior: -11.9 , $p = 0.003$; southerly versus edge: -0.9 , $p = 0.95$).

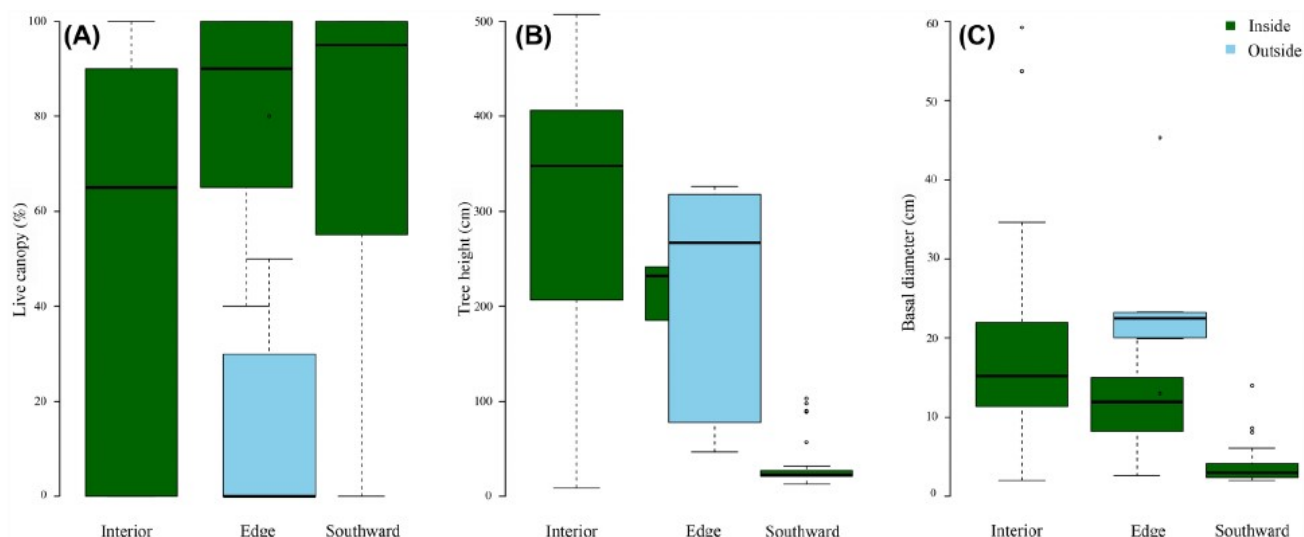


Figure 5. (a) Tree canopy condition (% alive), (b) tree height and (c) tree basal diameter for interior, edge and southernmost individual plots. For the edge plots, trees inside the contiguous live edge and outside the contiguous edge are plotted separately. For the southward individuals there were no individuals outside the interior plots.

Climate at southern treeline

Conditions at the global southern treeline are very moderate, with no clearly climatically defined season. Due to the island's maritime climate, atmospheric temperatures rarely dropped below freezing (Table 1), and diurnal variation is minimal (median 3°C) (Fig. 2). Consequently, both soil and air temperatures were mild year-round (Fig. 2, Table 1). Throughout the available data period (March 2014 to Jan. 2018), the mean minimum daily air temperature was 3.6°C (absolute lowest temperature recorded: -4.5°C) and the mean maximum daily was 7.2°C (absolute max temperature recorded: 19°C). Growing season length with a threshold that matches the global estimate for alpine treeline ($> 0.9^{\circ}\text{C}$ daily air temperature) is long, 328–343 d, but the average daily temperature over those dates is cool, ranging from 5.5 to 5.8°C, below the seasonal mean temperature globally. Average daily temperatures $> 6.4^{\circ}\text{C}$ were met on 100, 111 and 129 d for 2014–2015, 2015–2016 and 2016–2017 respectively. If instead the threshold for a growing season is set at the globally observed seasonal mean temperature (in essence, letting the minimum temperature set the growing season), a minimum temperature for the growing season threshold ranged from 3.2 to 4.0°C (Supplementary material Appendix 1 Fig. A4).

Isla Hornos is windy from the west/southwest, with a daily median wind speed of 31 km h⁻¹ and a mean daily maximum wind speed of 51 km h⁻¹ (Fig. 1B). High winds are common; daily maximum wind speeds are > 80 km h⁻¹ 7.3% of the time, evenly distributed throughout the data period (Supplementary material Appendix 1 Fig. A5).

Discussion

Treeline and the latitudinal limits of trees are expected to be closely linked to warming conditions, given the close relationship between treeline location and growing season temperatures. The geographic limits of trees are also a noticeable datapoint for science communication, as they are easily observable and understood as sensitive ecotones to climate and climate change. As a result, determining their precise location and controls is important for clarity in interpreting and communicating their shifts (or lack thereof). The world's southernmost tree is a special case, representing the single current point where trees cease on the way towards Antarctica. Finding it represents an important global discovery as well as a significant and unique signpost to follow in the future as climate changes.

Table 1. Observed air temperature (°C), modeled soil temperature (°C) and days where the low temperature reached below freezing for the three years of complete climate data. For minimums and maximums see text.

Year (July–June)	Modeled soil temperatures			Observed daily mean air temperatures (percentiles)					Days below freezing (absolute minimum)
	Min	Mean	Max	Min	10%	50%	90%	Max	
2014–2015	3.8	5.9	8.3	-1.4	2.1	5.4	8.5	12.4	13
2015–2016	3.3	5.8	8.1	-3.4	1.5	5.1	8.5	11.6	39
2016–2017	3.2	6.0	8.3	-1.9	2.2	5.8	8.6	12.4	19

The world's current southernmost tree is a *N. betuloides*, located on a northeast slope near sea level on Isla Hornos. The best approximation to growth forms elsewhere would be a krummoltz tree. However individuals do not form 'typical' krummholz form with multiple upright shoots or twisted stems, but rather a typical tree architecture, just one that grows horizontally for several meters rather than vertically (Supplementary material Appendix 1 Fig. A3). In sheltered locations, these individuals do grow to substantial heights (> 5 m frequently) suggesting that temperature is not limiting their height. Rather, it appears to be wind. Wind strongly shapes tree life at the southern end of their distribution and appears to be a more significant constraint than climate on the global southern extent of trees (see McIntire et al. 2016 for high elevation wind influence). We hypothesize the substantial edge-mortality of large trees as primarily being driven damage due to wind and potentially desiccation, given the strong robust nature of the individuals inside the edge (~10 m away), though note that dead trees may remain standing for a considerable amount of time and so estimates of net change must be made with caution and repeat visits are warranted.

The southernmost forest in the world contains three tree species: *N. betuloides*, *N. antarctica* and *D. winteri*. The dominant species is *N. betuloides* in almost all locations, and thus the overall forest is classified as an evergreen forest (Rozzi et al. 2020). Other species are absent, most notably *N. pumilio*, a deciduous species which dominates the region only slightly to the north (Navarino Island and surrounding region) and prefers drier habitat (Rozzi et al. 2007). We also find it interesting that the world's southernmost tree is an evergreen broadleaf species while the world's northernmost tree (found to date) is a deciduous conifer, *Larix gmelinii*, on the Taimyr Peninsula in Russia (Abaimov 2010). We speculate this may be a result of the intersection between biological growth constraints and the extreme seasonality in the north versus the 'extreme lack' of seasonality in the south (resulting from ocean dominated southern hemisphere versus the land dominated northern hemisphere; Rozzi et al. 2012).

The climate at the global southern limit of trees is somewhat difficult to compare to global temperature thresholds for true climatic treelines on continents (Paulsen and Körner 2014) or lower latitude islands (Karger et al. 2019) given the hypermaritime nature of the island. The vast majority of the year, temperatures are above the growing season definition found in those studies (daily mean temperature of 0.9°C), and even the absolute minimum temperature recorded was the relatively mild (for these species) -4.5°C. (Maximum temperatures are well above the threshold [Supplementary material Appendix 1 Fig. A4], but it is impossible to do a direct comparison given that study only reported daily means). Perhaps the best functional analog is, surprisingly, equatorial treelines, with similarly long growing seasons, low seasonal variation and low growing season temperatures (see Fig. 4.7 and 4.9 in Körner 2012). We note that a hard threshold temperature for tissue formation appears to be

approximately 5°C (see Körner 2008 and references therein); the daily means reported here are generally above that threshold and the daily maximum almost always above that threshold. In sum, atmospheric temperature is unlikely to be limiting occurrence. As additional evidence, although some individuals here are < 3 m, such that their thermal environment may be higher than air temperatures (Grace 1988), the occurrence of many individuals > 8 m on the small island, at the same elevation, aspect and exposure, also suggests the short stature is not a result of thermal limitations. This lends credence to the hypothesis that the geographic limit of trees in the extreme south is primarily a function of wind (either physical damage or desiccation), land and potentially dispersal limitations, not genus specific/physiological temperature constraints noted in *Nothofagus* ('treeline depression,' Wardle 1998). In other words, this does not appear to be a climatic treeline proper, but rather a geographic limit due to wind and available land. It is unknown if this spatial constraint imposed by wind is chronic (e.g. annual) or episodic (such as infrequent extreme wind events).

Our tree-ring age data shows recent establishment beyond the older, intact forest edge (Fig. 3). It is unclear however if and to what extent that establishment was favored by climate, either via temperature, precipitation, wind (lack thereof), seed availability or some combination (Case and Buckley et al. 2015). *Nothofagus* species have mast seeding that greatly vary by species and is influenced by interannual climate variability (Monks and Kelly 2006, Smaill et al. 2011). Seed production rates on Isla Hornos remain unknown. There are only a few seed predators on the island which may reduce tree establishment. In addition to a small mouse (likely *Akodon herskovitzi*), two bird species may eat tree seeds: the Patagonian-sierra finch *Phrygilus patagonicus* and the white-brindlet finch *Melanodera melanodera* (Rozzi et al. 2014). Future work should determine how these ecological interactions are developing as climate shifts in this untouched area. An alternative explanation which we cannot discount at this time is that turnover of individuals may be higher in those more exposed locations. If this were the case, we would see ongoing recent establishment (as we did). We did not see the concurrent amounts of dead individuals south of the edge that would correspond to increased turnover, but we did not explicitly quantify live and dead at a scale necessary to distinguish the two possibilities due to time limitations.

We also report N stocks and C:N ratios, primarily as a baseline for future researchers. N availability may constrain some treeline distributions, though it is difficult to disentangle N availability from soil temperatures and other confounding factors (Sullivan et al. 2015). Given the difficulty of reaching the site, our field measurements were limited. Although N percentages and C:N ratios are not direct metrics of N availability, they are often correlated (Qian and Schoenau 2002). The exterior plots with high mortality had higher N percentages and lower C:N ratios. Contiguous forest plots had the lowest N totals despite the largest trees. An open question remains as to the role of penguins (*Spheniscus*

magellanicus and *Aptenodytes patagonicus*) in N-fertilization; they were frequently observed in and moving through forested areas and are a substantial source of N in Antarctic regions (Bokhorst et al. 2019). Our observations were that penguins preferred nesting areas that were not covered by trees, which could drive the higher N stocks at forest edges. Regardless, given the correlation of N with soil organic matter and other factors, further work should investigate N availability directly if possible.

While it appears that temperature is not as limiting as wind in terms of occurrence (e.g. if winds were reduced trees would spread throughout the island), Isla Hornos is somewhat near the climatic limit noted for other trees in terms of growing season upper temperatures. (We did not assess the role of seasonal light limitations on growth, but the latitude is not particularly high compared to the northern hemisphere.) This suggests that tree migration further south may be slow, given both the difficulty of dispersal/establishment due to wind and the strong temperature gradient just to the south of Cape Horn when crossing the Antarctic Convergence zone. Colonization by tree species can be further constrained by competition from other species if those species are densely established prior to seed arrival (Buma et al. 2019). Vascular life further south is dominated by two species, *Deschampsia antarctica* and *Colobanthus quitensis* (Komárková et al. 1990, Peat et al. 2007) which have been present for some time (the earliest plant found in the sub-Antarctic was likely *Deschampsia antarctica*, by Sherratt in 1821; Lewis Smith 1981). Their ability, if any, to limit colonization of other species is unknown. That being said, geothermal heating and localized warm locations, such as on Zavodovski, Candlemas and Bellingshausen Islands could facilitate colonization by more temperate species (part of the South Sandwich Islands; Convey et al. 2000; Supplementary material Appendix 1 Fig. A1) and may provide a natural stepping-stone as those islands are also downwind.

The story of the southernmost tree and forest highlights wind as an understudied aspect of vegetation ecotonal dynamics. Wind speeds of the Antarctic Polar vortex are increasing at approximately 1% per year (Young et al. 2011). The nearby Falkland Islands (to the northeast) have recorded a significant increase in wind speeds and a shift in wind direction favoring more northwesterly winds (Jones et al. 2016), and Cape Horn is in the top 10 windiest places in the world ($> 72 \text{ km h}^{-1}$ approximately 7.5% of the time, Sampe and Xie 2007). The increase in winds is attributed to a poleward movement of the Westerlies converging with the polar vortex, both consequences of large-scale warming and stratospheric ozone depletion (Thompson et al. 2011, Zhang 2014). Due to warming, the increase in winds in the region is expected to continue. Given the strong influence of wind on tree presence and size and their overall slow growth, wind changes could cause additional mortality and forest loss and/or facilitate further new establishment outside the contiguous forest area (as with the southernmost individuals), reshaping these wind-scapes.

Conclusion

The world's southernmost individual tree is ~42 years old and low growing due to the wind, on a northeast facing slope on Isla Hornos, Chile. If a definition of a minimum height of 3 m above ground is applied, the southernmost tree is approximately 200 m north of that. The global southern tree limit does not appear to be strongly constrained by temperatures. Rather the wind appears to control the distribution of the southernmost forest in the world. Winds are intensifying and shifting, which we hypothesize is causing the observed die-backs on the edge of contiguous forest areas. This represents an understudied aspect of climate change and vegetation – the role of wind in shaping distribution, growth and spread. Because of their unique structure, universal familiarity and potential to rapidly create habitat and transform ecosystems, shifting tree distributions in the southern hemisphere should continue to be monitored and explored.

Data availability statement

Data available from the DataBasin platform (<https://data-basin.org/datasets/352c2c76ce9c4aac8466732a38f28152>).

Acknowledgements – The authors would like to thank John Harley for extensive help with everything, Omar Barroso and the extensive field team; Kelli Moses and colleagues at the Omora Ethnobotanical Station; Ezio Firmani and the crew of the Oveja Negra; and the Alcalde de Mar of the Chilean Armada in Isla Hornos, Mr. Andrés Morales and its family. The authors also thank Christian Körner and an anonymous reviewer for their constructive comments.

Funding – The National Geographic Society funded the expedition (NGS 147S-18), with additional funding from the Network for Extreme Environment Research (NEXER), Univ. de Magallanes, and Basal Funding CONICYT AFB170008, Inst. of Ecology and Biodiversity IEB-Chile. AH thanks additional support from NSF (award no. 1832483).

Permits – The Chilean Forestry Service authorized research at Parque Nacional Cabo de Hornos (CONAF-Resolución no. 679/2018).

References

- Abaimov, A. P. 2010. Geographical distribution and genetics of Siberian larch species. – In: Osawa, A. et al. (eds), Permafrost ecosystems. Springer, pp. 41–58.
- Bergstrom, D. M. et al. 2006. Restricted plant species on sub-Antarctic Macquarie and Heard Islands. – *Polar Biol.* 29: 532.
- Bokhorst, S. et al. 2019. Nitrogen inputs by marine vertebrates drive abundance and richness in Antarctic Terrestrial ecosystems. – *Curr. Biol.* 29: 1721–1727.
- Boose, E. R. et al. 2001. Landscape and regional impacts of hurricanes in New England. – *Ecol. Monogr.* 71: 27–48.
- Buma, B. and Johnson, A. C. 2015. The role of windstorm exposure and yellow cedar decline on landslide susceptibility in southeast Alaskan temperate rainforests. – *Geomorphology* 228: 504–511.
- Buma, B. and Thompson, T. 2019. Long-term exposure to more frequent disturbances increases baseline carbon in some

- ecosystems: mapping and quantifying the disturbance frequency-ecosystem C relationship. – *PLoS One* 14: e0212526.
- Buma B et al. 2019. Primary succession observations over a century do not support textbook explanations of facilitation/sequential change. – *Ecology* 100: e02885.
- Case, B. S. and Buckley, H. L. 2015. Local-scale topoclimate effects on treeline elevations: a country-wide investigation of New Zealand's southern beech treelines. – *PeerJ*. doi: 10.7717/peerj.1334
- Convey, P. et al. 2000. The flora of the South Sandwich Islands, with particular reference to the influence of geothermal heating. – *J. Biogeogr.* 27: 1279–1295.
- Engelskjøn, T. 1987. Botany of Bouvetøya, South Atlantic Ocean. II. The terrestrial vegetation of Bouvetøya. – *Polar Res.* 5: 129–163.
- Frenot, Y. et al. 2005. Biological invasions in the Antarctic: extent, impacts and implications. – *Biol. Rev.* 80: 45–72.
- Grace, J. 1988. The functional significance of short stature in montane vegetation. – In: Werger, M. J. A. et al. (eds), *Plant form and vegetation structure*. SPB Academic Publishers, The Hague, pp. 201–209.
- Harsch, M. A. et al. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. – *Ecol. Lett.* 12: 1040–1049.
- Hatherton, T. et al. 1965. Balleny Islands Reconnaissance Expedition, 1964. – *New Zealand J. Geol. Geophys.* 8: 164–179.
- Hughes, J. M. 1987. The distribution and composition of vascular plant communities on Heard Island. – *Polar Biol.* 7: 153–162.
- Jenkin, J. F. 1997. Vegetation of the McDonald Islands, sub-antarctic. – *Polar Biol.* 18: 260–272.
- Jones, P. D. et al. 2016. Long-term trends in gale days and storminess for the Falkland Islands. – *Int. J. Climatol.* 36: 1413–1427.
- Karger, D. N. et al. 2019. Why tree lines are lower on islands – Climatic and biogeographic effects hold the answer. – *Global Ecol. Biogeogr.* 28: 839–850.
- Körner, C. 2008. Winter crop growth at low temperature may hold the answer for alpine treeline formation. – *Plant Ecol. Divers.* 1: 3–11.
- Körner, C. 2012. Alpine treelines: functional ecology of the global high elevation tree limits. – Springer.
- Körner, C. and Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. – *J. Biogeogr.* 31: 713–732.
- Kramer, M. G. et al. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. – *Ecology* 82: 2749–2768.
- Komárková, V. et al. 1990. Additional and revisited localities of vascular plants *Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl. in the Antarctic Peninsula Area. – *Arctic Alpine Res.* 22: 108–113.
- Lewis Smith, R. I. 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. – British Antarctic Survey, Cambridge.
- Lewis Smith, R. I. 1981. The earliest report of a flowering plant in the Antarctic? – *Polar Record* 20: 571–572.
- Longton, R. E. and Holdgate, M. W. 1979. The South Sandwich Islands: IV. Botany. – British Antarctic Survey, Cambridge.
- McIntire, E. J. et al. 2016. Wind exposure and light exposure, more than elevation-related temperature, limit tree line seedling abundance on three continents. – *J. Ecol.* 104: 1379–1390.
- Monks, A. and Kelly, D. 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). – *Austral Ecol.* 31: 366–375.
- Olech, M. 1996. Human impacts on terrestrial ecosystems in West Antarctica. – *Proc. NIPR Symp. Polar Biol.* 9: 299–306.
- Paulsen, J. and Körner, C. 2014. A climate-based model to predict potential treeline position around the globe. – *Alpine Bot.* 124: 1–12.
- Peat, H. J. et al. 2007. Diversity and biogeography of the Antarctic flora. – *J. Biogeogr.* 34: 132–146.
- Piper, F. I. et al. 2016. Mediterranean and temperate treelines are controlled by different environmental drivers. – *J. Ecol.* 104: 691–702.
- Pisano, E. 1972. Observaciones fito-ecológicas en las Islas Diego Ramírez. – *Anal. Inst. Pat.* 3: 161–169.
- Pisano, E. 1982. Comunidades vegetales vasculares de la isla Hornos (Archipiélago del Cabo de Hornos, Chile). – *Anal. Inst. Pat.* 13: 125–143.
- Pisano, E. and Schlatter, R. P. 1981. Vegetación y flora de las islas Diego Ramírez (Chile). II. Comunidades vegetales vasculares. – *Anal. Inst. Pat.* 12: 195–204.
- Qian, P. and Schoenau, J. J. 2002. Availability of nitrogen in solid manure amendments with different C:N ratios. – *Can. J. Soil Sci.* 82: 219–225.
- Rozzi, R. et al. 2007. La Reserva de Biosfera Cabo de Hornos: un desafío para la conservación de la biodiversidad e implementación del desarrollo sustentable en el extremo austral de América. – *Anal. Inst. Pat.* 35: 55–62.
- Rozzi, R. et al. 2012. Integrating ecology and environmental ethics: earth stewardship in the southern end of the Americas. – *BioScience* 62: 226–236.
- Rozzi, R. et al. 2014. The omora park long-term ornithological research program: study sites and methods. – In: Rozzi, R. and Jiménez, J. E. (eds), *Magellanic subantarctic ornithology: first decade of forest bird studies at the Omora Ethnobotanical Park, Cape Horn Biosphere Reserve*. Univ. of North Texas Press – Ediciones Univ. de Magallanes, Denton TX, USA, pp. 3–40.
- Rozzi, R. et al. in press. Extensión de la Red de Estudios Socio-Ecológicos a Largo Plazo (LTSE-CHILE) en la Reserva de la Biosfera Cabo de Hornos y el Nuevo Parque Marino Islas Diego Ramírez-Paso Drake. – *Magallania*.
- Sampe, T. and Xie, S. P. 2007. Mapping high sea winds from space: a global climatology. – *Bull. Am. Meteorol. Soc.* 88: 1965–1978.
- Schwab, N. et al. 2016. Treeline responsiveness to climate warming: insights from a krummholz treeline in Rolwaling Himal, Nepal. – In: Singh, R. B. et al. (eds), *Climate change, glacier response and vegetation dynamics in the Himalaya*. Springer, pp. 307–345.
- Scott, J. J. 1990. Changes in vegetation on Heard Island 1947–1987. – In: *Antarctic ecosystems*. Springer, pp. 61–76.
- Sherratt, R. 1821. Observations on South Shetland. – *Imperial Magazine* (London), Columns, pp. 1214–1218.
- Smaill, S. J. et al. 2011. Climate cues and resources interact to determine seed production by a masting species. – *J. Ecol.* 99: 870–877.

- Smith, R. L. 1994. Vascular plants as bioindicators of regional warming in Antarctica. – *Oecologia* 99: 322–328.
- Sullivan, P. F. et al. 2015. Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in north-west Alaska. – *Ecology* 96: 716–727.
- Thompson, D. W. et al. 2011. Signatures of the Antarctic ozone hole in Southern Hemisphere surface climate change. – *Nat. Geosci.* 4: 741–749.
- Turner, P. A. M. et al. 2006. Probable long distance dispersal of *Leptinella plumosa* Hook. f. to Heard Island: habitat, status and discussion of its arrival. – *Polar Biol.* 29: 160–168.
- Wardle, P. 1998. Comparison of alpine timberlines in New Zealand and the Southern Andes. – *R. Soc. New Zealand Misc. Publications* 48: 69–90.
- Wieser, G. et al. 2019. Effects of climate change at treeline: lessons from space-for-time studies, manipulative experiments and long-term observational records in the Central Austrian Alps. – *Forests* 10: 508.
- Young, I. R. et al. 2011. Global trends in wind speed and wave height. – *Science* 332: 451–455.
- Zhang, J. 2014. Modeling the impact of wind intensification on Antarctic sea ice volume. – *J. Clim.* 27: 202–214.
- Supplementary material (available online as Appendix ecog-05075 at <www.ecography.org/appendix/ecog-05075>). Appendix 1.