# Potential impacts of UV exposure on lichen communities: a pilot study of *Nothofagus dombeyi* trunks in southernmost Chile

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**Abstract.** High-latitude terrestrial ecosystems face the triple threats of climate warming, increased exposure to UV arising from polar ozone depletion, and deforestation. Lichen communities of southernmost Chile are recognized for their high diversity, which includes nitrogen-fixing cyanolichens. Such lichens are common on forest trees, contribute nitrogen to forests, and are sensitive to exposure following deforestation (widespread in this region). In a pilot study of exposure effects on tree lichens, using nondestructive imaging methods, we compared lichen communities on trunks of isolated vs. forest tree trunks of southern Chilean beech (*Nothofagus dombeyi,* Nothofagaceae). We chose trees of similar diameter and trunk lean angle in conserved forest and nearby logged meadow on Navarino Island, XII Region Magallanes and Chilean Antarctica, Chile, within the annual southern ozone hole. Ninety-five percent of cyanolichen records, including *Nephroma antarcticum,* and 66% of records for other foliose lichens were from the forest, whereas pendulous usneoid lichens dominated *N. dombeyi* bark at the meadow site. Limitation of cyanolichen growth on isolated trees could affect ecosystem function in this poorly studied habitat. Possible factors contributing to strong community differences were increased light intensity, UV radiation, and wind stress, plus limited ability of lichens to colonize isolated trees in the logged meadow. UV radiation was likely an important stressor for some lichen species but not others. We recommend more extensive monitoring to pinpoint causes of differing lichen communities, and we encourage better protection of bark-dwelling lichens in southern hemisphere regions facing multiple threats.

**Key words:** bark lichens; Chile; cyanolichens; deforestation; forest fragmentation; lichen diversity; Nothofagus dombeyi; southern ozone hole; UV radiation.

## Introduction

Lichens and bryophytes (mosses, etc.; together called cryptogams), when common, play significant roles in Earth's carbon and nitrogen (N) cycles (Elbert et al. 2012); in particular cyanolichens (those with a cyano-bacterium photosynthetic partner) typically fix atmospheric N into a chemical form usable by other organisms (Nash 2008). Lichens and bryophytes are notably diverse and abundant in southernmost South America (Rozzi et al. 2008), a region threatened by global climate change, as indicated by increases in land-surface air temperature (Osborn and Jones 2014). This region is also threatened by land-use changes, such as logging, that thin and fragment forests, as well as by increased ultraviolet radiation (UV) arising from stratospheric ozone depletion (Madronich et al. 1998) during an extensive annual spring southern ozone hole (Armesto et al. 1998, Ballaré et al. 2001, Bianciotto et al. 2003, Pancotto et al. 2003, Robson et al. 2005, Rozema et al. 2005, Manrique et al. 2012). Climate and land-use changes affect forests worldwide, but potential impacts from ozone depletion are geographically restricted.

Spring ozone depletion in polar air masses has been linked to interactions with chlorofluorocarbon pollutants, and more-recently-detected ozone-depleting substances of unknown source are a matter of concern (Laube et al. 2014). Even with declining rates of ozone depletion, recovery is estimated to require one to five decades (Salby et al. 2011). Models suggest that UV levels will persist longer at higher latitudes (McKenzie et al. 2011), with potential effects on high-latitude organisms. Effects of increased UV radiation have been documented on bryophytes of Tierra del Fuego, Argentina (Searles et al. 1999, Robson et al. 2003), but little or nothing is known regarding possible impacts on the lichen floras of southernmost Chile, which are also impacted by deforestation and climate change. The three impacts may interact to exacerbate negative effects of exposure on forest lichens.

Studies have indicated that lichens generally respond to UV exposure by increasing the production and accumulation of secondary chemicals that reduce UV penetration, and that lichen species may vary in their responses to UV (Björn 2006). For example, UV-treated populations of the lichen *Cladonia arbuscula* ssp. *mitis* accumulated more UV-absorbing phenolics; fiber-optic measurements showed reduced UV penetration (Hall et al. 2002). Sun-tolerant *Xanthoria parietina* and shade-adapted *Lobaria pulmonaria* accumulated more sun-screening pigments after irradiation with UVB (Solhaug et al. 2003), compared with controls.

Lichens differ in their UV-protectant metabolites; such variation arises from differences in chemicals from the fungus as well as variation in production by the photosynthetic partner (Nguyen et al. 2013). For example, some cyanolichens have photosynthetic partners that produce polyaromatic scytonemin (Soule et al. 2007) and mycosporines, which provide UVA, but not UVB protection. These observed differences in lichens lead to variation in their ability to resist UV damage, suggesting that UV exposure influences lichen diversity and community structure. Differences might be greater in regions affected by polar ozone depletion.

In addition to UV-induced responses, studies by Hilmo et al. (2011) in the north temperate zone (outside the northern winter ozone hole) documented that bark-living lichens on trees isolated by logging and other management regimes respond to several changes in environmental conditions. These changes include more exposure to light (and UV radiation) and accompanying heat and cold stress, more drying and greater mechanical stress from wind exposure, and limits on colonization including dispersal and reduced establishment due to unsuitable microhabitat. Sillett et al. (2000) showed that greater distance from propagule sources for dispersal to arrive at a site was the factor that most limited occurrence of cyanolichens outside the United States Pacific Northwest forests they studied.

In a January 2014 pilot study, we compared the diversity and community composition of lichens occurring on the bark of southern Chilean beech (*Nothofagus dombeyi*) at two sites of similar elevation but contrasting exposure (intact forest vs. isolated trees) on Navarino Island, XII Region Magallanes and Chilean Antarctica, Chile. Southern beech forests on the island have abundant and species-rich epiphytic lichen communities (Caldiz et al. 2007, Quilhot et al. 2012). We hypothesized that species diversity and relative cover of common species would differ significantly on comparable trees at the two sites, reflecting variation in response of lichen species to contrasting exposure regimes linked to shade and solar radiation (including UV), stress linked to wind, and other factors correlated with high vs. low forest cover. Reduction in forest canopy on Navarino Island, and elsewhere under southernmost Chile's ozone hole (Fig. 1A), exposes lichens to substantial UVB, in addition to other stressors mentioned in the preceding paragraph.

Our working hypothesis was that the bark lichen communities of intact forest would differ from those of the closest areas with the same tree species remaining after deforestation. We subsampled tree trunks to test the additional hypotheses that different sides of each tree and/or different heights above the ground influence lichen community composition. We were particularly interested in the response of cyanolichens that are often important sources of usable N in ecosystems. For example, the bark-living cyanolichen *Lobaria oregana* provided significant input of new usable N (as much as 16.5 kg $N_2 \cdot ha^{-1} \cdot yr^{-1}$ converted) to old-growth Douglas fir forests of the Pacific Northwest (USA; Antoine 2004) and thus improved nutrition for other forest organisms. Cyanolichens can be sensitive to UVB radiation (Solhaug et al. 2003), as well as to effects of tree isolation and general exposure (Sillett et al. 2000, Marini et al. 2011).

## Materials and Methods

In South America, Navarino Island (Isla Navarino, 2473-km$^2$ area) is the landmass closest to the Antarctic continent, located in XII Region Magallanes and Chilean Antarctica, Chile. Navarino Island is south of and separated from Isla Grande Tierra del Fuego by the Beagle Channel. Visits are limited by one commercial air flight up to six days per week (depending on weather conditions) or a two-day boat trip. This island is located within the UNESCO Cabo de Hornos Biosphere Reserve (Goffinet et al. 2012), which harbors a high diversity of bryophytes and lichens (Rozzi et al. 2008). Two study sites were located along the northern coastal strip near the capital, Puerto Williams (Fig. 1, Table 1). Omora Ethnobotanical Park is characterized by primary and secondary deciduous Magellanic forest, mostly species of southern beech (*Nothofagus*). The secondary forest site has abundant large trees, suggesting >60 yr of regrowth (exact dates not known). The second site, an anthropo-
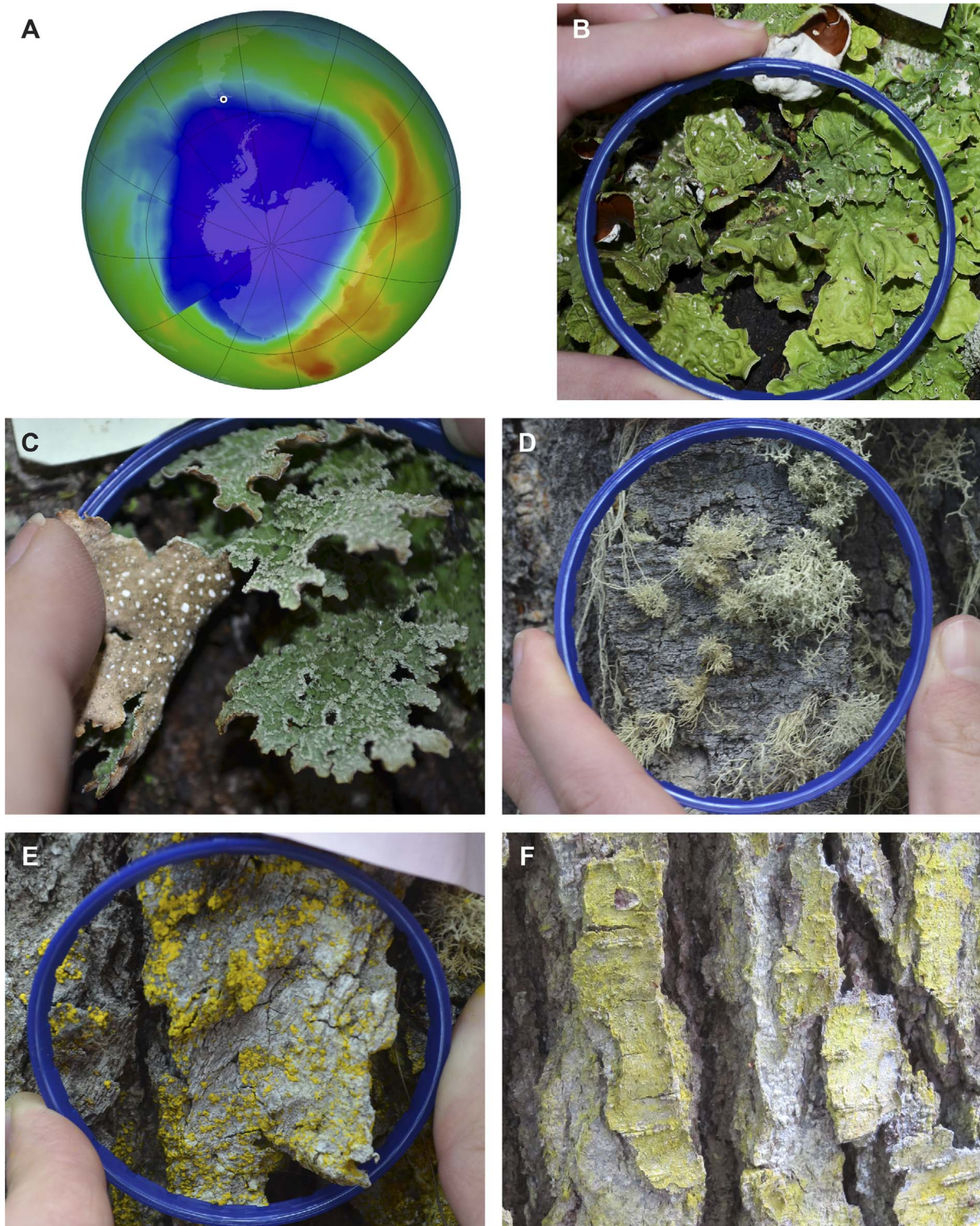
**Fig. 1.** (A) The southern ozone hole as of 16 September 2013 (from NASA; http://ozonewatch.gsfc.nasa.gov/Scripts/big_image.php?date=2013-09-16&hem=S), with the location of the Isla Navarino, Chile sampling sites shown by white circle. The deepest blue corresponds to an atmospheric ozone level of about 200 Dobson units; turquoise color corresponds to an atmospheric ozone level of about 250 Dobson units. Dominant bark-living lichens at sampling sites included (B) *Nephroma antarcticum*, (C) *Pseudocyphellaria granulata*, (D) usneoid lichens in the meadow, (E) brightly pigmented *Chrysothrix candelaris* in the meadow site, and (F) less-brightly pigmented *Chrysothrix candelaris* in the Omora Ethnobotanical Park forest site. (B)–(E) Photos by Marie T. Trest; (F) photo by Linda Graham.

**Table 1.** Tree location and data.

| Tree | Geographic coordinates | Diameter (cm) | Tree lean angle (°) | Aspect of trunk upper surface |
|------|------------------------|---------------|---------------------|-------------------------------|
| 1 | 54°56.590′ S 67°39.400′ W | 60.5 | 32.7 | North |
| 2 | 54°56.635′ S 67°39.455′ W | 48.9 | 38.2 | Northwest |
| 3 | 54°56.610′ S 67°39.470′ W | 45.7 | 22.4 | East |
| 4 | 54°55.978′ S 67°38.953′ W | 56.6 | 22.4 | Southwest |
| 5 | 54°55.983′ S 67°38.956′ W | 40.7 | 24.4 | Southwest |
| 6 | 54°55.951′ S 67°38.979′ W | 46.5 | 24.4 | Southwest |

*Note:* Tree 1 was in the secondary forest at Omora Ethnobotanical Park, Chile, trees 2 and 3 were in the primary forest at Omora Park, and trees 4–6 were in the nearby anthropogenic meadow (currently a pasture used by livestock).

genic meadow that is currently a livestock pasture, was open in a 1969 aerial photo (Google Earth 2014*a*) and remains open to the present. Both primary and secondary forest sites had closed canopy in the 1969 aerial photo. Annual precipitation averages 467 mm and is distributed fairly evenly throughout the year (some as snow). The average temperature is 6°C. Navarino Island has undergone an increase in air temperature over time, according to CRUTEM4 records disseminated via Google Earth (Osborn and Jones 2014) for nearby station 879 380 UshuaiaA1. Sustained strong winds (~40–60 km/h) blew from the southwest during field work, and all meadow trees leaned northeast; official summaries for prevailing winds in this area were not found. Omora Park is southwest and thus perhaps upwind of the meadow much of the time. The island lies within the southern ozone hole that occurs during the Southern Hemisphere spring; NASA data for in this general area indicate an ozone level of 250–300 Dobson units on 16 September 2013 (Fig. 1A), four months before our study. Data compiled from several sources indicate that the southern ozone hole was smaller in 2013 than it had been for the past decade (Welch 2014), suggesting that Navarino Island lichens have been exposed to increased springtime UV for at least a decade.

We sampled southern Chilean beech (*Nothofagus dombeyi*) trees; we sampled only the largest-diameter trunks to enhance the likelihood of finding cyanolichens. At least some cyanolichens occur most abundantly on old trees (Hilmo et al. 2011). Also, if species accumulated over time, large-diameter trunks should harbor the greatest lichen diversity. We selected trunks of similar lean angle (22.4°–38.2°), so that we could sample bark surfaces with the same species at differing abundance levels, rather than entirely different composition, as we observed on nearly horizontal trunk surfaces. We allocated equal sampling effort to forest and meadow.

Three large-diameter trunks per area within the designated range of lean angle represented a maximum sampling level attainable with available resources; aspect (compass direction it faces) of trunk upper surface could not be matched within the forest or with meadow trees (Table 1). The logged meadow site had few remaining large-diameter trunks of designated lean angle range. The three meadow sample trees were 10–65 m from each other and were 0.35–0.6 km from the nearest edge of intact forest (Google Earth 2014*b*). In addition, we observed lichens of many nearby tree trunks of varying trunk diameter and lean angle to detect species we might have missed in sampling.

We sampled north and south sides on the trunk of each selected tree (the north side has more sun exposure in the Southern Hemisphere). Each plot was a plastic ring 6.8 cm in diameter (Fig. 1) placed on north and south sides of each tree at 0.25, 0.75, 1.25, and 1.75 m from the base, for a total of eight plots per tree, 48 plots total (Table 2). This design allowed comparisons at three spatial scales: whole trees, parts of trunks, and single plots. Destructive sampling was not allowed in the protected forest, so we took digital images (Nikon D5100; Nikon, Tokyo, Japan) of lichen plots on trunks of all sample trees. We later determined presence of all lichen taxa and estimated cover for one large, prominent species. Additional images were taken to indicate context or focus on particular lichens at higher magnification. Detailed field notes on presence of lichens in each plot facilitated later identifications of lichens.

Habitat structure indicators of exposure intensity (to sunlight, wind, etc.) plus measured UV radiation (described in the following paragraph) were our environmental variables. The variable "openness" was assigned for the entire tree, with all eight plots per tree given the same score based on a visual estimate of canopy cover (shade) as seen from the trunk: 1 for >80% cover, 2 for 50–80% cover, and 3 for 20–50% cover (the maximum recorded) and the greatest assumed exposure. Plot height (higher was assumed to mean greater exposure), compass direction the plot faced (plot aspect), and side relative to lean of the trunk each represented a different sub-tree estimate of exposure. A plot on the north side of a trunk was coded 2 for greater exposure than a plot on the south side coded 1 for less exposure. Each plot was additionally scored based on upper vs. lower surface of leaning trunk: 1 for lower surface, 2 for lateral, and 3 for the presumed most-exposed upper surface. Since trees leaned different directions (Table 1), this variable represented degree of plot exposure differently from plot aspect.

We measured UVA + UVB directly at each of the 48 plots; this also indirectly represented photosynthetically active radiation (PAR; mostly visible). We used a digital UVAB (UV513AB) meter (General Tools and Instruments, New York, New York, USA; Cardona-Correa et al. 2015) with a 290–370 nm spectral range, which was

**Table 2.** Plot data.

| Plot location | UVA + UVB (mW/cm$^2$) |
|---|---|
| 1 | |
| North, 0.25 m | 0.05 |
| North, 0.75 m | 0.05 |
| North, 1.25 m | 0.06 |
| North, 1.75 m | 0.04 |
| South, 0.25 m | 0.04 |
| South, 0.75 m | 0.01 |
| South, 1.25 m | 0.01 |
| South, 1.75 m | 0.03 |
| 2 | |
| North, 0.25 m | 0.42 |
| North, 0.75 m | 1.1 |
| North, 1.25 m | 0.4 |
| North, 1.75 m | 0.5 |
| South, 0.25 m | 0.08 |
| South, 0.75 m | 0.13 |
| South, 1.25 m | 0.11 |
| South, 1.75 m | 0.09 |
| 3 | |
| North, 0.25 m | 0.13 |
| North, 0.75 m | 0.08 |
| North, 1.25 m | 0.09 |
| North, 1.75 m | 0.12 |
| South, 0.25 m | 0.1 |
| South, 0.75 m | 0.06 |
| South, 1.25 m | 0.09 |
| South, 1.75 m | 0.09 |
| 4 | |
| North, 0.25 m | 2.14 |
| North, 0.75 m | 1.97 |
| North, 1.25 m | 1.93 |
| North, 1.75 m | 1.44 |
| South, 0.25 m | 0.72 |
| South, 0.75 m | 1.27 |
| South, 1.25 m | 4.0 |
| South, 1.75 m | 1.6 |
| 5 | |
| North, 0.25 m | 0.57 |
| North, 0.75 m | 1.25 |
| North, 1.25 m | 1.3 |
| North, 1.75 m | 1.13 |
| South, 0.25 m | 0.52 |
| South, 0.75 m | 2.0 |
| South, 1.25 m | 1.55 |
| South, 1.75 m | 1.58 |
| 6 | |
| North, 0.25 m | 0.98 |
| North, 0.75 m | 1.16 |
| North, 1.25 m | 0.94 |
| North, 1.75 m | 0.92 |
| South, 0.25 m | 1.71 |
| South, 0.75 m | 2.47 |
| South, 1.25 m | 2.34 |
| South, 1.75 m | 2.83 |

*Notes:* Plot locations are side of trunk and height by tree number. Each plot was a plastic ring 6.8 cm in diameter (Fig. 1) placed on the north and south sides of each tree at 0.25, 0.75, 1.25, and 1.75 m from the base, for a total of eight plots per tree, 48 plots total.

not responsive to wavelengths greater than 375 nm, thus not to PAR and visible light at 400–700 nm. The instrument does not distinguish UVA from UVB, so readings are reported as UVA + UVB, and UV from here

on refers to both. Instrument responsiveness to UVB as well as UVA was confirmed by comparing readings from reference lamps with different known UVB output.

Lichen species composition of each field plot image was determined independently in the lab on a large-screen computer by three teams of three to four persons each, then reviewed by an expert in lichen identification (M. T. Trest). Lichen identifications followed Goffinet et al. (2012), which provides high-quality color images and detailed taxonomic information for the most common lichens occurring in and near Omora Park. Some taxa (one taxon: one group of individuals presumed to be genetically related and/or with similar appearance; less precisely defined than genus or species) were identifiable only to genus or to form group based on appearance. Form taxa, such as usneoid lichens, could include multiple species (*Usnea* and *Protousnea* in the case of usneoid). Any discrepancies among team decisions were resolved by rechecking the original image, examining close-up images, and reviewing detailed field notes. This conservative procedure gave a clean data set with minimum species estimates that avoided false inflation of differences between the most and least diverse plots. The cyanolichen *Nephroma antarcticum* was large and easily identified in images, so we estimated cover of this species using the ImageJ image analysis software (U.S. National Institute of Health, Bethesda, Maryland, USA) and Photoshop (Adobe, San Jose, California, USA). The percent cover of *N. antarcticum* was calculated for eight of 24 forest plots whose images showed identifiable individuals of this lichen species.

Investigation of data used multivariate analyses in PC-ORD v5.33 (McCune and Mefford 2006) and direct pairwise correlations (SPSS, version 21; IBM, Armonk, New York, USA). General patterns of lichen community composition and relationship to environmental variables were investigated with nonmetric multidimensional scaling ordination (NMS of primary matrix of untransformed presence on plots of lichen taxa, using Sørenson/Bray-Curtis distance measure and autopilot slow and thorough option, correlations between second matrix environmental variables and solution axes). Composite environmental variables were developed from original data using principal components analysis (PCA of data standardized to mean ± unit variance, with cross-products variance–covariance matrix centered by factors). NMS ordination can efficiently display major gradients of variation in samples by species-presence data sets with many zero occurrences of species; PCA can derive independent composite variables from a suite of measured variables that covary and have primarily monotonic relationships with one another (McCune and Grace 2002, Legendre and Legendre 2012). Direct Pearson correlations between lichen taxon presence or cover and environmental variables also supported interpretations of results. To account for multiple
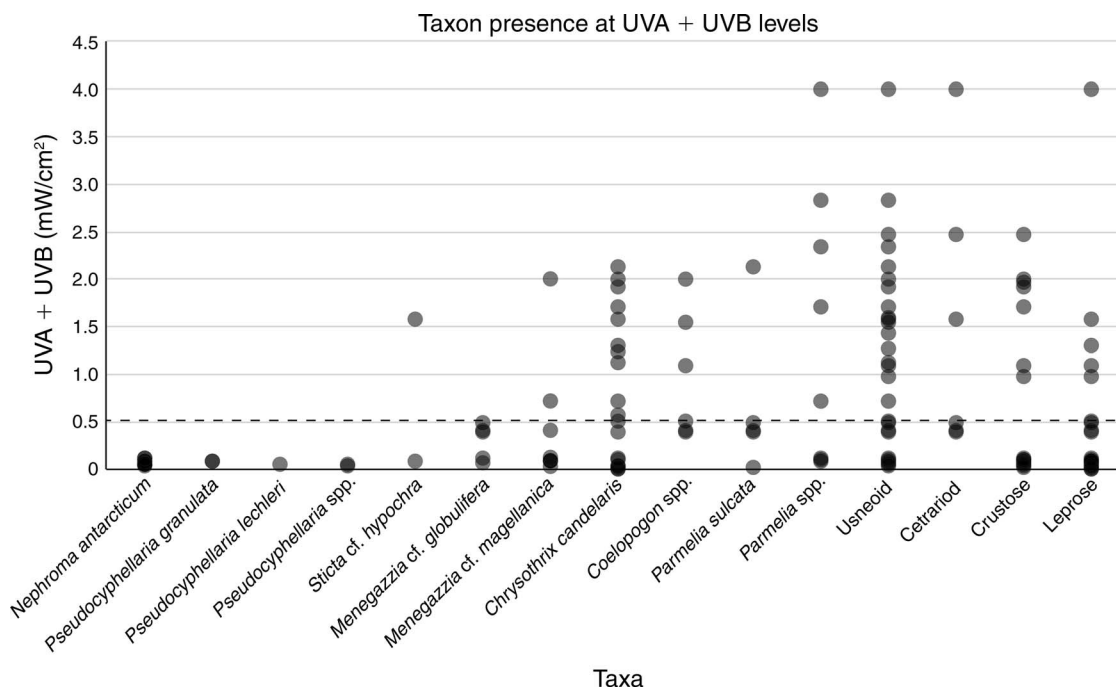
**Fig. 2.** Distribution of major lichen taxa along a gradient of measured UVA + UVB radiation. Horizontal dashed line indicates the maximum UVA + UVB value measured in the Omora Park plots. Darker shading is from overlapping points. Usenoid, cetrariod, crustose, and leptose are all functional groups (see *Materials and methods*).

## Results

Trunks of the southern beech *Nothofagus dombeyi* supported several common lichen taxa; *Nephroma antarcticum*, *Pseudocyphellaria granulata*, *Menegazzia magellanica*, *Parmelia sulcata*, *Chrysothrix candelaris*, and the form taxon usneoid lichens (Figs. 1B–F, 2). We found a total of 27 lichen taxa on 45 of the 48 plots surveyed (no lichens present on three lower side plots, height 0.75–1.75 m, on meadow tree 6). No additional lichen taxa were observed in areas adjacent to the plots or on the trunks of nearby *N. dombeyi*, though *Pseudocyphellaria crocata* was seen on fallen logs in the study area. Taxa characteristic of Omora Park plots included the conspicuous cyanolichen *N. antarcticum* that is symbiotic with a green alga, as well as the cyanobacterium *Nostoc*. *M. magellanica*, *P. sulcata*, and the unidentified gray-green leprose (with granular masses rather than a defined structure) taxon that were also characteristic of Omora Park; all three of these taxa are symbiotic with green algae. These taxa were not abundant at the meadow site, which was instead dominated by the fruticose usneoid form taxon and the yellow leprose species *C. candelaris*. There were substantial differences in occurrence of lichen taxa across the range of summer UV radiation levels that we measured; the latter indicated general

trunk exposure at the plot scale (Fig. 2).

Our lichen diversity analysis (NMS ordination, Fig. 3) indicated that the most important variation among bark lichen communities was a gradient (not distinct communities) between trees in primary or secondary forests of Omora Park (to left on axis 1) and those in the nearby deforested meadow (to right on axis 1). The ordination (best three-dimensional solution of 200 runs, nonrandom with $P = 0.004$, final stress 13.980, final instability 0.00000, 83.9% of original information) was of 45 plots based on presence of lichen taxa divided into nine groups, each with similar ecological response (many taxa had sparse occurrences). Mutually exclusive groups (Gp) and their taxa are Gp cyanolichens (*N. antarcticum*, *N*. cf. *parile*, *Pseudocyphellaria lechleri*, *Pseudocyphellaria* spp., *Sticta* cf. *hypochra*, *Sticta* spp.), Gp *C. candelaris* (only group member), Gp crustose (only group member), Gp foliose forest (*Menegazzia* cf. *globulifera*, *M*. cf. *magellanica*, *P. granulata*, brown foliose), Gp foliose meadow (cetrarioid form, *Hypotrachyna* sp., *Xanthoria* sp.), Gp fruticose (*Coelopogon* sp., *Ramalina* sp.), Gp leprose (only group member), Gp *Parmelia* all (*P. sulcata*, *Parmelia* spp.), and Gp usneoid (only group member).

Arrows in Fig. 3 illustrate that the environmental variables UV (measured UVA + UVB; + with axis 1, $r^2 = 0.472$) at plot scale and openness (+ with axis 1, $r^2 = 0.406$) at tree scale were both strongly correlated with major community variation. No composite environmental variable from PCA was stronger than either of these two single variables, suggesting that each affected
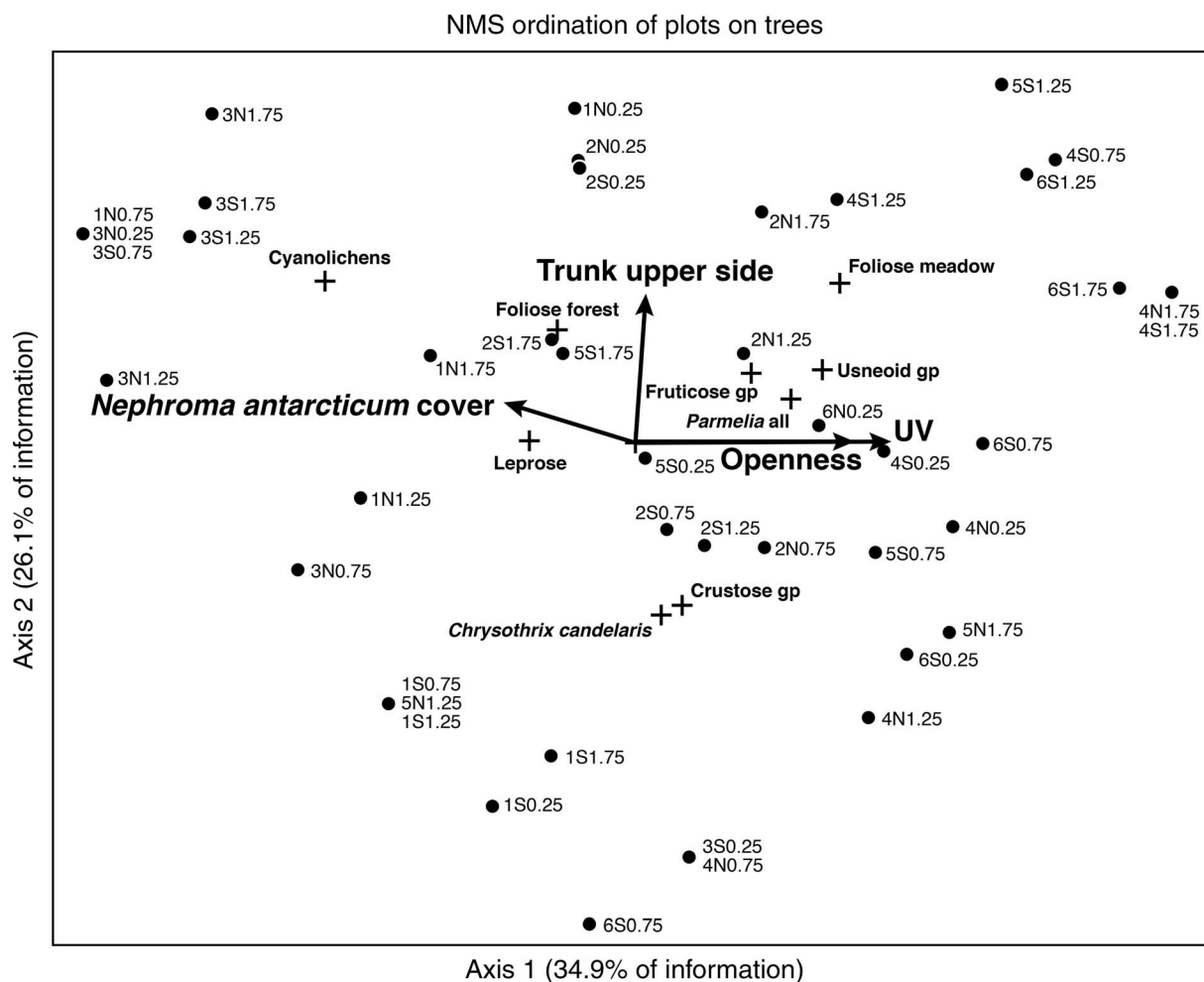
**Fig. 3.** Ordination of plots on trees based on occurrence of nine lichen groups (see *Materials and methods*, and Fig. 3 for axis labels). Points represent plots; for example, plot 3N1.75 refers to tree 3, north side, height 1.75 m aboveground. Trees 1–3 are in forest, trees 4–6 are in deforested meadow (see Table 1). Multiple plot codes near a single point indicate overlapping plots. Crosses represent the center of distribution for each named lichen group. Direction and length of arrows represent the direction and degree of correlation ($r^2 > 0.2$) between named environmental variables (*N. antarcticum* cover, upper side of trunk, openness, and UV) and ordination axes.

lichens somewhat independently even though they were directly correlated (Pearson $r^2 = 0.534$, $P < 0.0001$, $n = 48$). Cover of *N. antarcticum* (– with axis 1, $r^2 = 0.236$, $P < 0.001$, $n = 45$) was less strongly correlated with the same lichen community gradient in the opposite direction. Important additional variation among lichen communities illustrated on ordination axis 2 (Fig. 3) was linked to side of leaning trunks: those high on axis 2 were found more on upper sides ($r^2 = 0.298$).

Lichen groups segregated among plots and trees (Fig. 4) in three general patterns on the ordination: (1) cyanolichens, foliose forest, and leprose groups trended toward upper left; (2) foliose meadow, usneoid taxa (+ fruticose gp), and *Parmelia* groups all trended toward upper right; and (3) the common crustose and *C. candelaris* groups trended toward lower center. Differences between patterns (1) and (2) are consistent with responses of individual taxa to UV (Fig. 2) and of some

taxa or groups to openness or UV overall (Table 3). Differences of pattern (3) from patterns (1) and (2) are also supported; some of the taxa or groups were found more often on the upper, and some more often on the lower side of trunks (Table 3). The sub-tree-scale variables plot aspect and height, and the plot-scale variable number of lichen taxa per plot were not correlated with lichen community patterns across both sites. Trunk side variables were associated differently in forests vs. the meadow. In the meadow plots on trees that all leaned northeast (Table 1), aspect and position on upper side of leaning trunk were completely correlated ($r = -1.0$) with each other while neither was significantly correlated with UV. Plots on the south aspect and upper side of a meadow tree often received more sun radiation than their height-matched plot on the north aspect (UV measurements, Table 2). Responses of some lichens to these were strong in the meadow
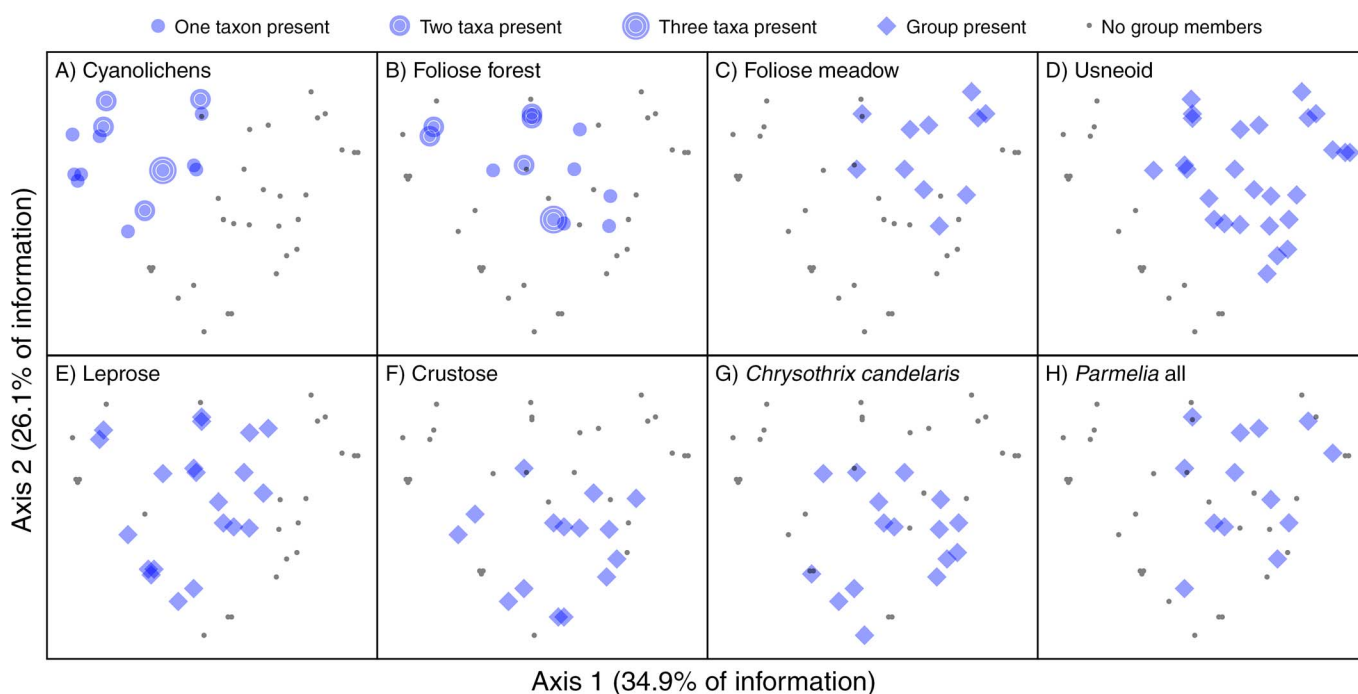
**Fig. 4.** Overlay of selected lichen groups on the nonmetric multidimensional scaling ordination (see *Materials and methods*): (A) cyanolichens (similar pattern for *N. antarcticum* cover); (B) foliose forest, (C) foliose meadow, (D) usneoid (similar pattern for fruticose gp.), (E) leprose, (F) crustose, (G) *C. candelaris*, and (H) *Parmelia* all. The *x*- and *y*-axes of each graph are identical to those of Fig. 3, as is the relative placement of all dots.

(Table 3; other individual taxa, $P = 0.028–0.001$). However in the forest, plot aspect and side relative to lean were uncorrelated with each other, and each was weakly correlated with UV. Responses of lichens to upper vs. lower surface of leaning trunks were mostly stronger than to plot aspect in forests (Table 3; other individual taxa, $P = 0.04–0.006$). Height on trunk by itself appeared to be unimportant to lichen composition both overall and within each site.

Direct comparisons and correlations between lichen taxa or groups and habitat variables provided more detailed information about relationships in some cases. The five records of mature *P. sulcata* (four in forest; mature refers to having asexual reproductive structures) were in plots with low to intermediate light intensity exposure (Fig. 2) and with many lichen species ($r = 0.350$, $P = 0.015$). In contrast, *Parmelia* spp., with only small specimens (all possibly immature *P. sulcata)*, were significantly positively correlated with higher UV levels overall and in the meadow (Table 3). Their overall negative correlation with north-facing (expected to be more exposed) trunks (Fig. 3, Table 3) appears to reflect primarily their strong negative correlation with north-facing lower trunk sides (apparently often less exposed) of meadow trees. *Parmelia* spp. distribution relative to tree lean contrasted between sites, found more on lower surfaces of trunks in Omora forest but more on upper surfaces in the meadow. Seventy-seven percent of records for the leprose taxon (17 of 22) were in forest,

as were 66% of all foliose lichens (including *Parmelia*) with green algal symbionts (29 of 44 records).

More detailed analyses of cyanolichen taxa supported the general patterns from multivariate analysis. *N. antarcticum* was absent from the meadow site and negatively correlated with openness and UV overall, while in the forest it was associated with upper surfaces (Table 3). Correlations of cyanolichens as a group showed patterns similar to those for *N. antarcticum* (19 forest plots; one meadow plot). Cyanolichens in the genus *Pseudocyphellaria* were also more common in the less open forest plots with lower UV: *Pseudocyphellaria* spp. $r = -0.373$, $P = 0.009$, with openness; *P. lechleri* was recorded only at one low-UV plot (Fig. 2). The uncommon *P. granulata* (Fig. 1C), which has only a green algal partner, shared the pattern for the genus; it occurred only in two lower-UV forest plots (Fig. 2).

Two lichen taxa showed no limitation due to high exposure. The usneoid taxon, the most common in our study (27 records: 10 forest, 17 meadow), was positively correlated with higher exposure in at least one analysis of each environmental factor (Table 3). *C. candelaris*, also widespread across sample trees (19 records: eight forest, 11 meadow), was correlated with environmental factors only in Omora forest (Table 3). Its yellow color appeared brighter in the meadow (Fig. 1E) than within the forest (Fig. 1F), suggesting higher amounts of secondary chemicals in the meadow individuals. Its lack of correlations with environmental variables overall or in

**Table 3.** Representative Pearson correlation *r* (probability), between lichen variables and habitat variables representing exposure.

| Lichen groups | Overall (*n* = 48) | Omora Park (*n* = 24) | Anthropogenic meadow (*n* = 24) |
|---|---|---|---|
| Number of species/plot (0–8) | | | |
| Openness | −0.343 (0.017) | NS | NS |
| Upper surface | 0.302 (0.037) | NS | 0.602 (0.002) |
| North facing | NS | NS | −0.602 (0.002) |
| Cyanolichen species count ( ≥1 in 14 plots) | | | |
| Openness | −0.522 (0.000) | NS | NS |
| Upper surface | NS | 0.472 (0.020) | NS |
| North facing | NS | 0.434 (0.034) | NS |
| UVA + UVB | −0.442 (0.002) | NS | NS |
| *Nephroma antarcticum* presence (in nine plots) | | | |
| Openness | −0.501 (0.000) | NS | . . . |
| Upper surface | NS | 0.422 (0.040) | . . . |
| UVA + UVB | −0.420 (0.003) | NS | . . . |
| *N. antarcticum* rank of cover (cm$^2$) | | | |
| Openness | −0.486 (0.000) | NS | . . . |
| Upper surface | 0.403 (0.004) | 0.528 (0.008) | . . . |
| UVA + UVB | −0.417 (0.003) | NS | . . . |
| *Chrysothrix candelaris* presence (in 19 plots) | | | |
| Openness | NS | −0.438 (0.033) | NS |
| Upper surface | NS | −0.433 (0.035) | NS |
| *Parmelia* spp. presence (in eight plots) | | | |
| Upper surface | NS | −0.463 (0.023) | 0.513 (0.010) |
| North facing | −0.447 (0.001) | NS | −0.513 (0.010) |
| UVA + UVB | 0.299 (0.039) | NS | 0.480 (0.018) |
| Usneoid species presence (in 27 plots) | | | |
| Openness | 0.338 (0.019) | NS | NS |
| Upper surface | 0.414 (0.003) | NS | 0.642 (0.001) |
| North facing | NS | NS | −0.642 (0.001) |
| UVA + UVB | 0.430 (0.002) | 0.473 (0.020) | NS |

*Note:* Cyanolichen includes *N. antarcticum* in counts of species/plot; *n* is sample size, NS means not significant, and an ellipsis means the correlation was not applicable.

the meadow suggest that its pattern on ordination axis 2 (Figs. 3 and 4) was driven entirely by its forest occurrences. Its contrasting association with less-open trees and lower trunk surfaces in Omora Park (Table 3) suggested competition with foliose lichens in general, which were more frequent on upper trunk surfaces and the more exposed trees there, rather than direct response to habitat factors.

## Discussion and Conclusions

Our observations of lichen taxa on southern beech *Nothofagus dombeyi* were consistent with previous reports for Navarino Island (Caldiz et al. 2007, Quilhot et al. 2012) of *Nephroma antarcticum*, *Pseudocyphellaria granulata*, *Menegazzia magellanica*, *Parmelia sulcata* (broad concept; Molina et al. 2011), *Chrysothrix candelaris*, and the form taxon usneoid lichens. Our pilot study supported the general hypothesis that composition and diversity of lichens differ among sites with contrasting exposure regimes, including visible solar radiation (forest cover and trunk exposure), UV, and wind, which together contribute to increased desiccation stress (Bartak et al. 2006). The general lichen diversity patterns led us to hypothesize further that environmental

conditions at the meadow site are less conducive to colonization and/or long survival of foliose lichens. Correlations of lichens with our habitat variables measured at different spatial scales are interpreted to help evaluate the importance of the different possible environmental drivers of the contrasts. Lichens that were correlated with openness, evaluated at the tree scale, may have responded to radiation (visible light plus UV) exposure, damage and desiccation from wind exposure, limits on colonization (arrival plus establishment), or all three. With an average temperature of 6°C on Navarino Island, day–night temperature variation is not expected to be limiting in this habitat (Nash 2008). Lichens correlated with the sub-tree variables (upper vs. lower trunk surface, plot aspect, or plot height) were probably responding to the intensity of light exposure and/or damage and desiccation from wind exposure, not to limits on arrival at the tree. UV was the only plot-scale habitat variable that we quantified, and it was only weakly correlated with the sub-tree variables height, aspect, and trunk side. Lichens correlated with UV, (1) when evaluated across all 48 plots may have responded more to radiation exposure, but also to wind stress and/or limits on both parts of colonization, but (2) when evaluated only in Omora forest or only in the meadow

were probably responding primarily to intensity of radiation exposure.

The broad occurrence of *Parmelia* spp. contrasting with limited occurrence of *P. sulcata* in plots suggests limitation primarily by intensity of exposure to radiation. Arrival and establishment of *Parmelia* spp. small individuals were not hindered in the meadow. Restriction of mature *P. sulcata* to low-UV plots mostly in the forest thus points to other causes. The remaining explanations are that growth to reproductive size was limited by factors associated with higher radiation or with mechanical and desiccation stress from wind in the meadow. The association of *Parmelia* spp. with trunk lower surfaces in the forest suggests lower light and likely less moisture there (less rain, faster runoff) may have limited growth (keeping individuals small), while some individuals on the forest trunk upper surfaces grew large and mature enough to be identifiable as *P. sulcata*. This species is cosmopolitan (Brodo et al. 2001, Galloway 2007), widespread, and common in fully exposed and windy sites in temperate and subpolar ecosystems in both hemispheres outside the ozone holes. Based on these reports, the absence of mature individuals from plots with high exposure to sunlight and wind in our study suggests that damage from increased UVB within the southern ozone hole was a more likely cause than wind and desiccation stress.

Hypothesizing causes of patterns for cyanolichens is more difficult from our results. For instance, the greater frequency and higher cover of *N. antarcticum* on upper surfaces of forest trees suggests it needed at least intermediate light levels to thrive. Absence of any identifiable small individuals of this species from meadow trees means that all three kinds of stress (radiation, wind stress, and limits on both parts of colonization) might have been possible causes. Monaci et al. (2012) found abundant mature *N. antarcticum* (>10 cm diameter) with *Usnea* sp. on trunks of isolated trees in similar anthropogenic meadows in Chilean Patagonia about 150 km north of our study and just outside the 2013 southern ozone hole. This suggests that inability to colonize meadow trees might have been less important in our results. Opportunities for wind to assist dispersal to meadow trees by lichens from Omora Park to the southwest and upwind existed at least sometimes, though much shorter distances from the nearest source limited arrival by cyanolichens and others in northern temperate forests (Sillett et al. 2000, Hilmo et al. 2011). *N. antarcticum* is typically bark-living as we observed, although it sometimes occurs on the ground or mossy rocks, and was characterized as "tolerant of a wide range of light levels" in Tierra del Fuego of Chile and Argentina, both within and outside the southern ozone hole (White and James 1988). Comparison of our results with the presence of healthy mature *N. antarcticum* individuals in high light environments from these other two studies suggests that levels of UVB, rather than general radiation intensity, might have limited the species to partly shaded forest plots in our study. However, wind and desiccation stress cannot be ruled out since the Monaci et al. (2012) study area and most of the relevant White and James (1988) survey area presumably had much less wind stress. The similar patterns for cyanolichens other than *N. antarcticum* also suggested greater sensitivity to exposure intensity (radiation and/or wind stress) than colonization limitation.

Patterns for the common usneoid taxon and *C. candelaris* clearly suggest they are not limited by environmental factors linked to exposure. While this is indirect evidence that neither species is sensitive to UVB radiation, the brighter yellow color of meadow *C. candelaris* more directly suggests a protective response to solar radiation, perhaps enhanced under desiccation stress. Observations that UV-absorbing compounds were higher in Antarctic populations of *Umbilicaria aprina* exposed to higher levels of UV (Singh et al. 2012) suggest that similar assessments should be done for *C. candelaris* and other Navarino Island lichens.

Our pilot study of lichen composition did not clearly differentiate effects of radiation exposure intensity from the mechanical and desiccation stress of wind, and sometimes these were confounded with distance from colonizer sources. But comparisons with other studies suggest strong influences of UV exposure on several species. Greater UV exposure related to southern ozone hole development each spring could influence both the occurrence of cyanolichens and the ability of *P. sulcata* to mature, as well as the development of pigmentation in *C. candelaris*.

We recommend more extensive and more targeted studies in this region very soon to quantify effects of increased UVB radiation and to identify management strategies to mitigate damage to these vulnerable ecosystems. Field transplant studies of *N. antarcticum* to exposed sites in the area coupled with UVB filtering could distinguish between UV and wind as causes for their absence from meadow trees. Future laboratory studies could assess fluorescence quenching to estimate the degree to which photosystems of several at-risk lichens might be protected during desiccation, as has been accomplished for *P. sulcata* (Veerman et al. 2007). Future measurements should separate solar irradiance as PAR, UVA, and UVB during the peak of the southern ozone hole, and PAR/UV ratios should be calculated for each site. Analyses of the impact of winter snow reflectivity on bark lichen distribution might also be fruitful, not as a benefit for photosynthesis, but to assess possible harm from UVB damage.

Limited occurrence of cyanolichens in the meadow, whatever the causes, suggests that the cutting of *Nothofagus dombeyi* forests has reduced the input of nitrogen fixed by lichens into the system. Future work should include studies of fixed-N contributed by

cyanolichens to forested areas of Isla Navarino. More extensive comparative studies of forested vs. logged sites are needed to assess impacts of increased exposure on the distribution, abundance, or morphology of bark lichen taxa, particularly cyanolichens.

In conclusion, bark lichen community composition in the forested and open meadow sites differed greatly in ways that potentially impact ecosystem functioning through changes in nitrogen availability, as well as affecting lichen diversity in general. Because Isla Navarino is influenced by the southern ozone hole, particularly at its greatest extent in the Southern Hemisphere winter and spring, we predict that logging elevates levels of UVB radiation, as well as those of PAR plus mechanical and desiccation stress from wind, to affect sensitive lichens. Our pilot results themselves warrant modification of current logging practices in advance of more extensive studies. For instance, loggers should leave trees in clumps rather than isolated; this might facilitate retention of nitrogen-fixing cyanolichens. Omora Park still harbors high biodiversity, but it faces the triple threats of climate and surrounding deforestation plus increased UVB exposure. Further studies are warranted to determine the drivers of variation in lichen species distributions and community composition in Southern Hemisphere reserves, to facilitate better maintenance of ecosystem function as well as conservation of biodiversity in these vulnerable regions.

## Acknowledgments

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