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# Positive interactions between the lichen *Usnea antarctica* (Parmeliaceae) and the native flora in Maritime Antarctica

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## Abstract

**Questions:** Is the macrolichen *Usnea antarctica* a 'nurse' species to Antarctic flora? Are positive plant–plant interactions more frequent than negative interactions in Antarctic ecosystems? Are microclimatic modifications by cushions of *U. antarctica* responsible for the nurse effect?

**Location:** Two sites in Antarctica: King George Island, South Shetland (62°11′ S, 58°56′ W; 62°11′ S, 58°59′ W).

**Methods:** We evaluated the association of plant species with *U. antarctica* cushions by recording species growing – in equivalent areas – within and outside *U. antarctica* cushions. Additionally, we performed transplant experiments with *Deschampsia antarctica* individuals to assess if *U. antarctica* cushions enhance plant survival. In both study sites we monitored temperature, moisture and nutrient status of soil outside and within the cushions to provide insights into potential mechanisms underlying possible interactions between *U. antarctica* and other plant species.

**Results:** Eight out of 13 species were positively associated with cushions of the widespread lichen *U. antarctica*, while only one species (*U. aurantiaco-atra*) showed a negative association with *U. antarctica*. Survival of *Deschampsia* was enhanced when growing associated with *U. antarctica* cushions. Our results indicate that cushions ameliorated the extreme conditions of Antarctic islands through increased temperature and soil moisture, decreased radiation and evaporative water loss and increased nutrient availability.

**Conclusions:** The nurse effect of *U. antarctica* is verified. Cushions of this macrolichen may be a key component in structuring the Antarctic landscape and maintaining local species richness, and their presence might influence range expansion of other species.

## Introduction

The importance of positive interactions between plants in the structuring of plant communities is now clear (Callaway 1995; Callaway & Walker 1997; Bruno et al. 2003; Brooker et al. 2008). Positive interactions typically occur when the presence of a 'nurse' plant species enhances the fitness of another plant species, and thereby facilitates the establishment of the 'protégée'. Amelioration of extreme temperatures, increased soil moisture, protection against herbivores and higher availability of nutrients are among the most documented positive effects of nurse plants (Molina-Montenegro et al. 2005; Gómez-Aparicio et al. 2008; González-Teuber & Gianoli 2008; Yang et al. 2010). It has been proposed that positive interactions should be particularly important in stressful environments

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(Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998; Bruno et al. 2003).

The Antarctic ecosystems are among the most stressful environments on Earth for plant life. The establishment and survival of Antarctic plants occurs under severe abiotic conditions, including cold temperatures, repeated events of freezing and thawing, desiccation due to wind, low availability of water and nutrients and high irradiance (Robinson et al. 2003; Wasley et al. 2006; Molina-Montenegro et al. 2012). Most of the Antarctic continent's land mass is covered by permanent ice and snow, with only 2% of its area available for colonization by plants and animals (Convey et al. 2008). Antarctic vegetation is composed of ca. 135 cryptogams (mosses, liverworts and lichens) and only two vascular plants, *Colobanthus quitensis* (Caryophyllaceae; hereafter *Colobanthus*) and *Deschampsia antarctica* (Poaceae; hereafter *Deschampsia*) (Kappen 1999; Smith 2003). Both flowering plant species inhabit the Maritime Antarctic islands, down to approximately 68° S, but they are absent from continental Antarctica (Greene & Holtom 1971; Robinson et al. 2003). Lichens, in contrast, can live under more extreme conditions, being distributed down to 86° S (Smith 1984; Schroeter et al. 2000). The macrolichen *Usnea antarctica* (Parmeliaceae) constitutes the dominant vegetation in the South Shetland Islands (Ott 2004) and is widespread in continental Antarctica (Øvstedal & Smith 2001). In fact, it shows the widest ecological breadth of any Antarctic lichen, being abundant in both sheltered and exposed habitats, as well as in moist and dry sites (Øvstedal & Smith 2001).

With regard to positive interactions, Haussmann et al. (2009) showed that cushion plants of *Azorella selago* inhabiting the sub-Antarctic Marion Island play a pivotal role for slope stabilization and enhance the abundance of other plant species by improving moisture and temperature conditions within their canopy, as compared to the surrounding environments. Likewise, cushions of *A. selago* have been suggested to facilitate the establishment of other plants growing on them, including a perennial grass, by enhancing nutrient availability and acting as wind shelters (Haussmann et al. 2010). In the same island, LeRoux & McGeoch (2008) reported that plants benefit from the presence of neighbours when they provide shelter and substrate stability, and that the relative intensity of this positive interaction is greatest at higher altitudes. Conversely, Krna et al. (2009) documented negative effects on *Deschampsia* when growing associated with other vascular plants or mosses on Anvers Island, Antarctic Peninsula. They showed that the presence of *Colobanthus*, mosses or conspecific individuals, albeit increasing air and soil temperature around *Deschampsia*, actually decreased biomass accumulation of the target *Deschampsia* compared to individuals growing alone (Krna et al. 2009). The lichen *U. antarctica* is often found associated with other plant species in Antarctica (Øvstedal & Smith 2001), but no study has tested the occurrence of positive (or negative) interactions between them or between any lichen or moss and their companion plants in the Antarctic continent.

Recent warming has led to a retreat or almost complete loss of a number of ice shelves in the Antarctic Peninsula (Alley et al. 2005; Vaughan 2006), thus increasing the ice-free area suitable for plant colonization. The ice- and snow-free lands are mainly found along the Antarctic Peninsula, the associated islands and along the coastal shores (Convey et al. 2008). The importance of positive interactions in primary succession of recently deglaciated habitats has been shown mainly for Arctic ecosystems (e.g. Crocker & Major 1955; Chapin et al. 1995; Klanderud & Totland 2004), with only one case in the Antarctic continent (Krna et al. 2009). In the likely scenario of continued warming in Antarctic ecosystems, it is possible that the vascular plant species, *Deschampsia* and *Colobanthus*, could have enhanced ecophysiological performance or expanded their distributions southwards (Torres-Mellado et al. 2011; Molina-Montenegro et al. 2012). In this regard, it is very important to address the potential role of mosses or lichens as nurse species facilitating the establishment of vascular plants during the early stages of succession.

In this study, we tested for positive associations between cushions of the widespread lichen *U. antarctica* and co-occurring plant and lichen species in the Maritime Antarctic. Specifically, we evaluated: (1) how frequently other species grow associated with *U. antarctica* compared to adjacent bare soil, (2) whether survival of seedlings of *Deschampsia* is increased when planted within cushions of *U. antarctica* compared to bare soil, and (3) how the presence of *U. antarctica* affects microclimate conditions (temperature, nutrient availability and soil moisture). Research was carried out in two replicate sites located at King George Island, South Shetland Islands.

## Methods

### Study sites and study species

The study was conducted in two sites 2 km apart in King George Island, South Shetlands (Site 1: 62°11′ S, 58°56′ W; Site 2: 62°11′ S, 58°59′ W). Mean annual temperature is −2 °C, with averages of −7 and 1 °C for the coldest and warmest month, respectively, and mean annual precipitation of 700 mm (data from Bellinghausen base, 62°12′ S, 58°55′ W; www.weatherbase.com). Antarctic soils have a high content of coarse mineral particles and total organic carbon, low C/N ratio and acidic pH. Local enrichment of nutrients is due to input by seabirds

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(Beyer et al. 2000). Site 1 was located 75 m from coastline on a north-facing slope of 21° inclination. Site 2 was located 90 m from the coastline on a north-facing slope of 34°. Both sites have little runnels, and vegetation is distributed on dry gravelly ground and rock ledges.

The plant community in King George Island is composed of the vascular plants *Colobanthus quitensis* (Caryophyllaceae) and *Deschampsia antarctica* (Poaceae) and a wide variety of cryptogams that typically colonize unfrozen areas near the ice sheet, including macrolichens forming cushions such as *U. antarctica* (Fig. 1) and *U. aurantiaco-atra*, smaller lichens and mosses (Komárková et al. 1990; Ochyra 1998; Øvstedal & Smith 2001).

### Species association patterns

Vegetation sampling was done during January 2010, i.e. at mid-growing season. In each study site a total of 50 *U. antarctica* cushions (50–70 cm diameter) were randomly chosen. A 50-cm diameter metallic hoop was placed over each selected *U. antarctica* cushion, and all plant species growing within the hoop were recorded. The same procedure was followed when the hoop was randomly located on bare ground, at least 0.5 m away from the cushion. Cushions of *U. antarctica* and samples in the bare ground were selected with the aid of a random number table converted to hexadecimal degrees indicating the direction (degrees from magnetic north) in which the first cushion that met our size criteria was selected.

### Survival experiment

Transplant experiments were performed with adult individuals of *Deschampsia* collected in the study area. All plants appeared healthy and were growing in ice-free zones close to the coastline. Each individual plant was excavated together with the soil around the roots (ca. 500 g) and kept well watered in a plastic box for 12 h until the transplant. Plant status was visually assessed just before the transplant in order to include undamaged individuals only. At each study site, five *Deschampsia* individuals were planted within each of ten randomly selected *U. antarctica* cushions and each of ten randomly selected points on the bare ground. We selected cushions of 50–70-cm diameter, visually healthy and with a crown cover above 75%. All cushions and bare ground samples were separated by least 5 m. All individuals used for the survival experiment were planted at least 10 cm apart from each other. Transplants were carried out during the 2010–2011 growth season and transplant survival was evaluated after 1 mo.

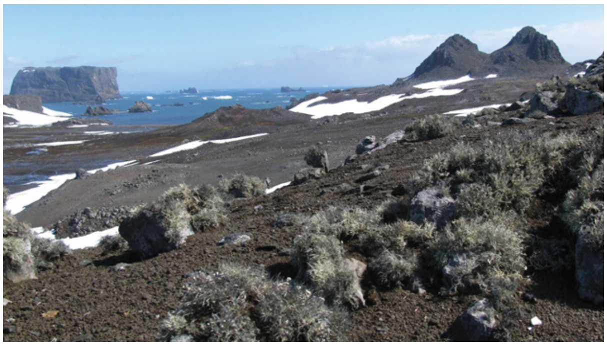

**Fig. 1.** Individuals of the lichen *Usnea antarctica* in the study area (King George Island, South Shetlands, Maritime Antarctica).

### Microclimate measurements

To assess whether *U. antarctica* cushions could ameliorate microclimatic conditions beneath their canopies, we measured temperature, soil moisture and nutrient content within and outside cushions at both study sites. In addition, we recorded a daily cycle of temperature and photosynthetic active radiation (PAR) within and outside cushions of *U. antarctica*. Finally, a water loss experiment was performed to evaluate whether water loss is lower beneath cushions than in open areas.

We recorded temperature on ten randomly selected cushions at 1-cm height above the ground surface within each cushion and on ten points at 1-cm height above the ground surface on bare ground adjacent to each cushion. At each selected point, temperature was measured in the first 1 cm of substrate with a CHY-110 non-contact infrared thermometer (0.01 °C resolution). Measurements were taken between 12:00 and 14:00 h on 11 January, which was a typical day in terms of climate conditions, and were made simultaneously in the two microhabitats (cushions and surrounding bare ground).

Soil moisture (soil matric potential) was measured beneath and outside *U. antarctica* cushions during the mid-growth season (January 2010) in ten randomly selected cushions of similar size (80–100-cm diameter) and at ten points on the bare ground adjacent to each cushion. At each sampling point, a soil tensiometer (2725 series Jet Fill Tensiometer; Soil Moisture Equipment Corp., Santa Barbara, CA, US) was dug into the soil to 10-cm depth. Tensiometers were placed at 10:00 h and, after a stabilization period of 2 h, the soil matric potential was recorded.

We compared nitrogen availability between seven *U. antarctica* cushions and seven randomly selected points on the bare soil. A soil sample of 10-cm depth (ca. 300 g) was taken beneath cushions and on bare ground. Soil samples were stored in hermetic plastic bags and sent for analyses to determine the concentration of nitrate ($NO_3^-$) and ammonium ($NH_4^+$) following the colorimetric techniques proposed in Robarge et al. (1983) and Longeri et al. (1979), respectively. All samples were analysed in the

Laboratory for Soil Analyses (Agronomy Faculty, Universidadde Concepción), where total nitrogen content ($NO_3^-$ plus $NH_4^+$) was estimated.

To characterize daily microclimate variation within cushions of *U. antarctica* and their surrounding environment, we measured temperature and PAR on 15 January, which was a typical day during the growing season in terms of climate conditions. We randomly selected five cushions, and five points in the surrounding environment. At each of these cushions and points in the bare ground, we measured temperature and PAR at 1-cm height above ground surface with a CHY-110 non-contact infrared thermometer (0.01 °C resolution) and Li-250 light meter (LiCor, Lincoln, NE, US), respectively. Measurements were taken every 2 h between 08:00 and 20:00 h, and registrations on the two microhabitats (cushions and surrounding environment) were made simultaneously in order to obtain comparable data.

We compared differences in evaporative water loss beneath *U. antarctica* cushions and in bare ground. At each site, 14 semi-transparent white cloth mesh bags (10 cm × 10 cm) were filled with commercial vermiculite, fully hydrated (water saturated) and weighed. Seven bags each were placed within and outside *U. antarctica* cushions. After 3 h in the field, bags were recovered and re-weighed to estimate the mass of water loss through desiccation within and outside *U. antarctica* cushions.

### Data analysis

The hypothetical nurse effects of *U. antarctica* on Antarctic flora were evaluated by analysing differences between the occurrence of each species within *U. antarctica* cushions and their occurrence in open areas. To this end, we used generalized linear models (GLM; Crawley 2007) with binomial probability distribution. The null hypothesis of no effect of cushions on species occurrence was assessed using *z*-tests, except for over-dispersed data, where we used *t*-tests (quasi-binomial GLMs). These GLMs were performed for each study site separately because there were four species that were not shared between sites. Factorial ANOVAs were used to assess differences in *Deschampsia* transplant survival, as well as differences in microclimatic variables (temperature, soil moisture, nitrogen availability) and evaporative water loss between microhabitats (outside vs within cushions) and sites (site 1 vs site 2). Daily microclimate variation within cushions of *U. antarctica* and their surrounding environment was analysed with repeated measures using ANOVA. All response variables fulfilled ANOVA assumptions (survival data were arc-sin transformed prior to analysis). Comparisons between treatments were made using Tukey HSD tests. ANOVAs were performed using Statistica (v. 6.0; Statsoft, Tulsa, OK, US) and GLMs were made with the R 2.8.0 software (R Development Core Team 2008; R Foundation for Statistical Computing, Vienna, AT).

## Results

### Species association patterns

A total of 13 and 11 species were recorded either outside or within *U. antarctica* cushions in sites 1 and 2, respectively (Table 1). In site 1, five out of 13 species (38.5%) were positively associated with *U. antarctica* cushions (Table 1), and in site 2 four out of 11 species (36.4%) were more frequently associated with *U. antarctica* cushions. When data from both sites were pooled, another three species (*Placopsis contortuplicata*, *Psoroma hypnorum* and *Sanionia* spp.) were found to be significantly associated with *U. antarctica* cushions. In contrast, *U. aurantiaco-atra* was more frequent outside *U. antarctica* cushions than within them at both sites (Table 1).

### Survival experiment

Survival of experimental *Deschampsia* plants after 1 mo was significantly higher within cushions of *U. antarctica* than outside them at both study sites (Table 2). At site 1 survival was three times higher in *U. antarctica* cushions than in bare ground, while at site 2 it was two times higher (Fig. 2). There were no differences in plant survival between sites (Table 2).

### Microclimate

Mean temperature above ground within *U. antarctica* cushions was 1.2 °C and 1.1 °C higher than on bare ground in sites 1 and 2, respectively (Fig. 3a, Table 3). Soil moisture was nearly 6% higher beneath *U. antarctica* cushions than outside them at both sites, the differences being significant (Fig. 3b, Table 3). Mean nutrient content of the soil beneath *U. antarctica* cushions was approximately two-fold higher than on bare ground at both sites (Fig. 3c, Table 3).

Averaging temperatures each hour, maximum temperatures within both cushions of *U. antarctica*, as well as in the surrounding environment, were recorded between 12:00 and 16:00 h, whereas minimum temperatures were detected at 08:00 and 20:00 h (Fig. 4). Repeated measures ANOVA indicated differences in temperatures and radiation between microsites and over time and a significant interaction between time and site (Table 3). Most of the time, cushions maintained higher mean temperatures than the surrounding environment, but cushions of *U. antarctica* maintained lower radiation than open areas over the full daily cycle (Fig. 4). Interaction between microsites and time was significant. While strong increases in both

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**Table 1.** Frequencies of occurrence of plant species within and outside cushions of the lichen *Usnea antarctica* (Parmeliaceae) at two sites in Maritime Antarctica. M, moss; L, lichen.

| Species | Site 1 | | | | | Site 2 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Outside | Within | | z/t | P | Outside | Within | | z/t | P |
| *Andreaea* sp. (Andreaeaceae) M | 2 | 16 | + | −3.09 | **0.002** | 3 | 13 | + | 3.54 | **<0.001** |
| *Brachythecium* sp. (Brachytheciaceae) M | 0 | 3 | | −0.01 | 0.992 | | | | | |
| *Caloplaca sublobulata* (Teloschistaceae) L | 3 | 27 | + | −4.41 | **<0.001** | 3 | 24 | + | 4.05 | **<0.001** |
| *Cladonia metacorallifera* (Cladoniaceae) L | 3 | 32 | + | −5.01 | **<0.001** | 3 | 19 | + | 3.41 | **<0.001** |
| *Placopsis contortuplicata* (Agyriaceae) L | 1 | 4 | | −1.28 | 0.202 | 2 | 7 | | 1.63 | 0.107 |
| *Polytrichum* sp. (Polytrichaceae) L | | | | | | 1 | 3 | | 0.96 | 0.338 |
| *Psoroma hypnorum* (Pannariaceae) L | 2 | 5 | | −1.13 | 0.263 | 2 | 6 | | 1.39 | 0.167 |
| *Rhizocarpon geographicum* (Rhizocarpaceae) L | 1 | 2 | | −0.01 | 0.995 | 1 | 3 | | 0.96 | 0.338 |
| *Rhizoplaca melanophthalma* (Lecanoraceae) L | 4 | 31 | + | −4.91 | **<0.001** | 4 | 20 | + | 3.27 | **<0.001** |
| *Sanionia* sp. (Amblystegiaceae) M | 0 | 3 | | −0.01 | 0.992 | 2 | 6 | | 1.39 | 0.167 |
| *Stereocaulon alpinum* (Stereocaulaceae) L | 0 | 3 | | −0.01 | 0.992 | | | | | |
| *Umbilicaria antarctica* (Umbilicariaceae) L | 1 | 8 | + | −2.05 | **0.004** | 2 | 8 | | 1.84 | 0.069 |
| *Umbilicaria* sp. (Umbilicariaceae) L | 2 | 3 | | −0.45 | 0.635 | | | | | |
| *Usnea aurantiaco-atra* (Usneaceae) L | 9 | 2 | – | + 2.05 | **0.040** | 9 | 2 | – | 2.03 | **0.022** |

Significant differences are highlighted in bold (*P*-values, after GLMs; see text for details of the statistical analyses). **+** = significant positive association with *U. antarctica*; − = significant negative association.

**Table 2.** ANOVA of the survival of *Deschampsia antarctica* plants on cushions of the lichen *Usnea antarctica* at two sites in Maritime Antarctica. The main effects were microhabitat (outside vs within cushions) and site (site 1 vs site 2).

| Source of variation | df | MS | F | P-value |
|---|---|---|---|---|
| Microhabitat (M) | 1 | 1.88 | 36.83 | <0.001 |
| Site (S) | 1 | 0.07 | 1.36 | 0.252 |
| M × S | 1 | 0.01 | 0.35 | 0.556 |
| Error | 36 | 0.05 | | |

temperature and radiation between 12:00 and 16:00 h were recorded for both microsites; sharper increases within and outside cushions, respectively, accounted for the interaction (Fig. 4, Table 3).

The short-term experiment on evaporative water loss showed significantly higher water loss on bare ground than on *U. antarctica* cushions at both study sites (Fig. 5, Table 3). This difference was higher at site 1 than at site 2 (59% vs 43%; Fig. 5, Table 3).

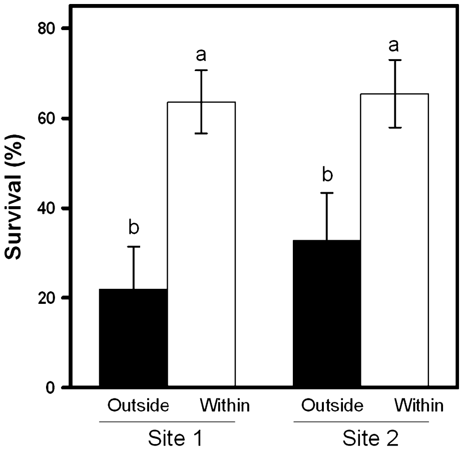

**Fig. 2.** Survival (%) of *Deschampsia antarctica* plants 1 mo after transplant outside (black bars) and within (white bars) *Usnea antarctica* cushions at two sites in Maritime Antarctica. Bars are means ± SE. Different letters indicate significant differences (*P* < 0.001, Tukey test).

## Discussion

Theoretical models (Bertness & Callaway 1994; Brooker & Callaghan 1998; Bruno et al. 2003) and empirical studies (Molina-Montenegro et al. 2005; Lortie & Callaway 2006; LeRoux & McGeoch 2008) have shown that positive interactions are more common than negative (competitive) interactions in stressful environments. Spatial pattern analyses are commonly used to infer the nature of interactions among organisms (Haase 2001; Tirado & Pugnaire 2003; Molina-Montenegro et al. 2005). Our analysis of spatial association between species indicates that the dominant cushion lichen, *U. antarctica*, has predominantly positive effects on other species in the harsh environments of Maritime Antarctica. Five out of 13 species at two sites in King George Island were positively associated with cushions of the widespread lichen *U. antarctica*, while only one species (*U. aurantiaco-atra*) showed a negative association with *U. antarctica* cushions. The latter suggests a competitive interaction between the congeneric macrolichens, probably because of similar ecological niches. Nonetheless, the fact that *U. antarctica* is a very widespread lichen in Antarctic ecosystems (Walker 1985; Schroeter et al. 1995;

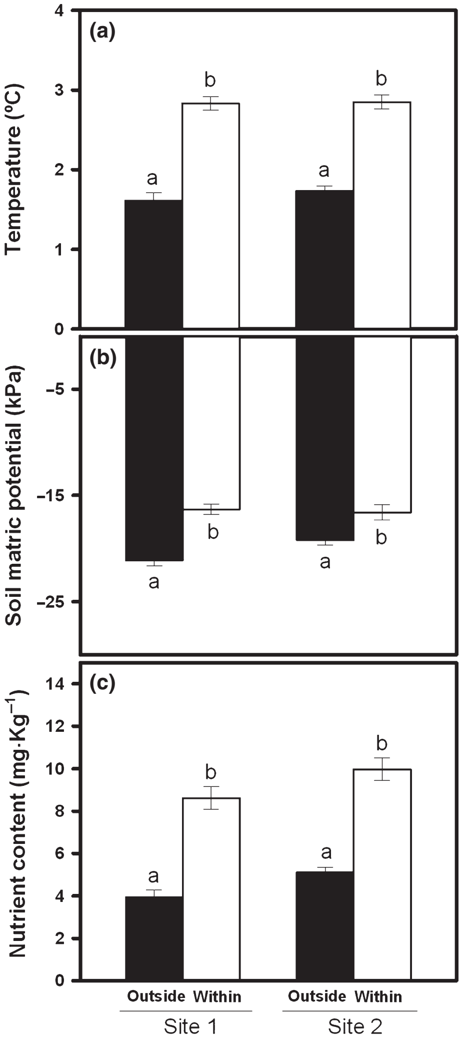

**Fig. 3.** Microclimate variables measured outside (black bars) and within (white bars) *Usnea antarctica* cushions at two sites in Maritime Antarctica. Bars are means ± SE. Different letters indicate significant differences ($P < 0.001$, Tukey test). (**a**) Soil temperature (°C), (**b**) soil moisture (soil matric potential, kPa), and (**c**) soil nutrient content (mg $NO_3^-$ plus $NH_4^+$ kg$^{-1}$).

**Table 3.** ANOVAs of microclimate variables (temperature, soil moisture, nitrogen availability, daily cycles of temperature and radiation) and experimental water loss on cushions of the lichen *Usnea antarctica* in Maritime Antarctica. The main effects were microhabitat (outside vs within cushions) and site (site 1 vs site 2) or time.

| Source of variation | *df* | MS | *F* | *P*-value |
|---|---|---|---|---|
| Temperature | | | | |
| Microhabitat (M) | 1 | 13.68 | 188.38 | <0.001 |
| Site (S) | 1 | 0.05 | 0.67 | 0.417 |
| M × S | 1 | 0.02 | 0.34 | 0.561 |
| Error | 36 | 0.07 | | |
| Soil moisture | | | | |
| Microhabitat (M) | 1 | 136.90 | 46.06 | <0.001 |
| Site (S) | 1 | 6.40 | 2.15 | 0.151 |
| M × S | 1 | 12.10 | 4.07 | 0.051 |
| Error | 36 | 2.97 | | |
| Nitrogen availability | | | | |
| Microhabitat (M) | 1 | 59.19 | 38.26 | <0.001 |
| Site (S) | 1 | 0.21 | 0.13 | 0.717 |
| M × S | 1 | 2.40 | 1.55 | 0.224 |
| Error | 24 | 1.54 | | |
| Daily temperature cycle | | | | |
| Microhabitat (M) | 1 | 271.66 | 309.76 | <0.001 |
| Time (T) | 6 | 5.80 | 116.82 | <0.001 |
| M × T | 6 | 1.21 | 24.38 | <0.001 |
| Error | 48 | 0.04 | | |
| Daily radiation cycle | | | | |
| Microhabitat (M) | 1 | 576.92 | 17143.71 | <0.001 |
| Time (T) | 6 | 28.96 | 504.67 | <0.001 |
| M × T | 6 | 69.96 | 12.19 | <0.001 |
| Error | 48 | 5.73 | | |
| Water loss experiment | | | | |
| Microhabitat (M) | 1 | 3.36 | 59.68 | <0.001 |
| Site (S) | 1 | 0.72 | 12.84 | <0.001 |
| M × S | 1 | 0.44 | 7.76 | 0.010 |
| Error | 24 | 0.05 | | |

Øvstedal & Smith 2001) and one of the largest (Øvstedal & Smith 2001), together with the evident facilitation provided by their cushions to almost two-thirds of the co-occurring species, strongly suggests that such a negative interaction between *Usnea* species does not limit the role of *U. antarctica* as a major nurse plant in Maritime Antarctica.

Moreover, if the relative importance of positive interactions actually increases with environmental stress, as has been found in high-altitude environments (Callaway et al. 2002; Cavieres et al. 2002; Yang et al. 2010; but see Onipchenko et al. 2009) and sub-Antarctic ecosystems (LeRoux & McGeoch 2008), then greater nurse effects of *U. antarctica* cushions may be expected in the more southern, harsher habitats of the Antarctic Peninsula. Our study sites probably represent the most extreme end of a cold–harsh continuum as can be found on Earth, and we found strong facilitation. Thus our results are not consistent with the idea that intensity of facilitation wanes at the most stressful ends of such gradients (sensu Michalet et al. 2006).

Relative importance of facilitation can change with ontogeny as well as with stress levels (Miriti 2006). For example, Krna et al. (2009) showed a decrease in biomass accumulation of *Deschampsia* when grown associated with neighbouring species compared to when grown alone, suggesting competition more than facilitation. Our results, however, show positive effects of *Usnea* on short-term survival of adult transplants of *Deschampsia*. This suggests that effects of inter-specific interactions may be in different directions when examining different aspects of demography (e.g. establishment, recruitment, survival or growth rates) or different time frames.

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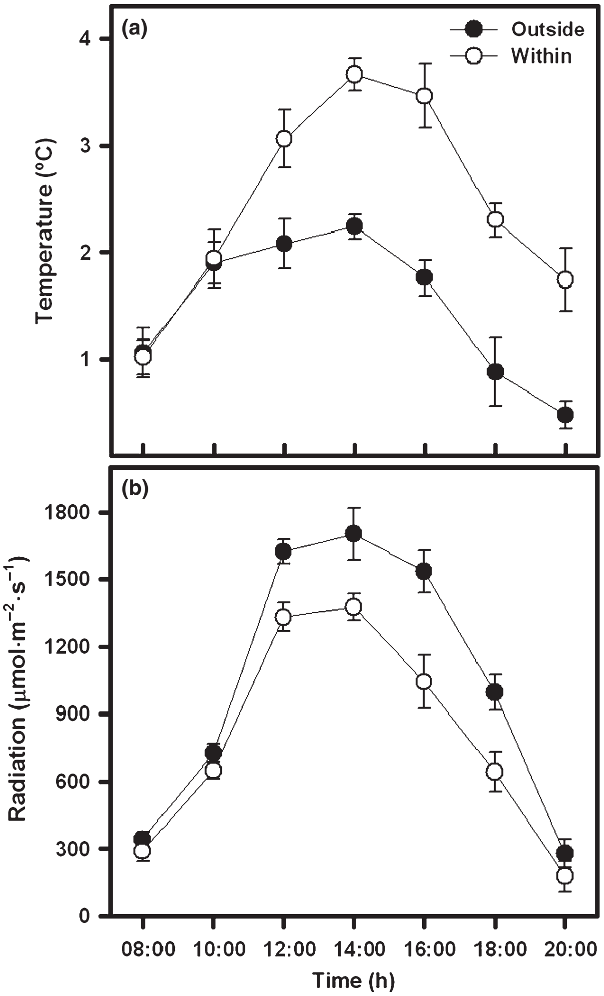

**Fig. 4.** Daily cycle of temperature (°C) and photosynthetic active radiation ($\mu mol \cdot m^{-2} \cdot s^{-1}$) measured outside (black circles) and within (white circles) *Usnea antarctica* cushions. Bars are means ± SD.

The two Antarctic vascular plants (*Colobanthus* and *Deschampsia*) were not recorded in the samplings. However, both are present on King George Island (Komárková et al. 1990) and *Deschampsia* was found growing a few meters distant from the *U. antarctica* cushions studied (M. A. Molina-Montenegro, pers. obs.). Smith (2003) has suggested that nesting skuas and terns can act as vectors for vegetative dispersal of *Deschampsia* by accidentally transporting tillers that may subsequently root and establish in moss carpets; the same process may apply to lichen cushions. Recently, Torres-Mellado et al. (2011) recorded new plant populations of *Deschampsia* in the Shetland Island, with an increasing plant number and vegetation cover growing in association with moss–lichen communities, suggesting an expansion of this plant species in recent times. Hence, *Deschampsia–Usnea* interaction could be particularly important if *Deschampsia* is becoming more broadly distributed, as suggested previously. Although, in the data, *Deschampsia* is not present in *U. antarctica* cushions, future association cannot be ruled here. The two Antarctic flowering plants (*Colobanthus* and *Deschampsia*) were not recorded in the samples. This is somewhat surprising because *Deschampsia* is present in the community, but likely this species needs a more moist soil for establishment. Nevertheless considering that evaporative water loss is reduced within cushions of *U. antarctica* and current trends of climate change show an increase in the soil water, the association *Usnea–Deschampsia* should become more common over time.

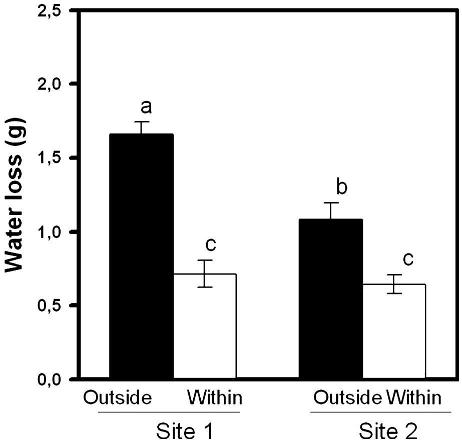

**Fig. 5.** Evaporative water loss (g) measured outside (black bars) and within (white bars) *Usnea antarctica* cushions in two sites in the Maritime Antarctica. Bars are means ±SE. Different letters indicate significant differences ($P < 0.001$, Tukey test).

The nurse effects of *U. antarctica* herein verified are likely due to the amelioration of microclimatic conditions within the cushions compared to adjacent bare ground, including increased temperature and soil moisture, decreased high radiation and evaporative water loss, and increased nutrient availability, as has been reported for other cushion plants (Cavieres et al. 2007; Yang et al. 2010). These abiotic factors may be critical for survival of Antarctic plants in different ecological scenarios (Beyer et al. 2000; Robinson et al. 2003; Wasley et al. 2006; Bokhorst et al. 2007; Convey et al. 2008). It is important to recall that, as stated by Robinson et al. (2003), Antarctic vegetation lives at the physiological limits of survival and therefore even slight changes to growth conditions are likely to have a significant impact. Instead, Tallowin & Smith (1977) noted that the vulnerability of the overwintering green shoots to wind and snow abrasion was reduced in *Festuca contracta* by a large amount of standing dead leaves, but this probably does not apply to *Deschampsia* because it carries less than 15% of its dry weight as attached dead leaves. However, plants of *Deschampsia* may avoid such detrimental effects of wind and snow by association with *U. antarctica* cushions, suggesting that the increase in resources would be not only the mechanism for facilitation, but also provide shelter, presumably due to protection from desiccation by wind, which will constitute another key mechanism for its establishment.

*Deschampsia* is currently seldom found in continental Antarctica (Robinson et al. 2003), and in Maritime Antarctica it is distributed in sandy, mineral-rich sites with some supply of meltwater, often associated with mosses and close to bird nesting areas where nutrient availability is high (Komárková et al. 1985, 1990). Importantly, significant fluctuations of temperature and rainfall typical of continental habitats may limit the distribution of *Deschampsia*, which is particularly susceptible to water shortage (Komárková et al. 1990). However, the enhancement of microclimatic conditions by cushions of macrolichens such as *U. antarctica*, together with the increase in ice-free areas suitable for plant establishment in the Antarctic Peninsula due to recent warming (Alley et al. 2005; Vaughan 2006; Convey et al. 2008) will affect the distribution of *Deschampsia*. In this sense, climate amelioration by cushions of *U. antarctica* may permit expansion of distribution of *Deschampsia*; if so, lichen cushions may provide microsite conditions most amenable to establishment of new populations.

Lichens are a life form adapted to thrive under the very harsh environmental conditions of Antarctic ecosystems (Øvstedal & Smith 2001). Surprisingly, to our knowledge, the hypothetical nurse effects of lichens on Antarctic vegetation had not been addressed before. The macrolichen *U. antarctica* is a major component of the Antarctic landscape, and the extent of its role in maintaining local species richness and promoting range expansions deserves further research. In a climate change scenario (IPCC 2007), it is important to understand how the Antarctic flora could respond to novel environmental conditions and whether this process could be affected by plant–plant interaction. Mechanistic approaches to nurse effects, such as those carried out in the present study, would improve our ability to predict the response of the target organisms to specific changes in microhabitat conditions.

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