

# Evidence of morphometric differentiation among Antarctic moss populations as a response to local microenvironment

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## ABSTRACT

Studies on phenotypic variation among populations growing in different microenvironments may provide information about plasticity related to environmental pressures, and thus help to elucidate the potential evolutionary forces contributing to the origin and maintenance of diversity in any region. In this study we investigate morphometric variation on a small geographic scale for three species of Antarctic mosses. All species revealed significant differentiation among populations for all evaluated traits. The comparison of morphometric measures of populations of *Polytrichum juniperinum* from Nelson Island and from southern Brazil suggests that the effects of a small geographic scale in Antarctica are the same as a large geographic scale in environments where the climate is more homogeneous and microhabitats have minor influence on vegetation. However, further investigations over a larger area, evaluating more species, and using controlled garden experiments are recommended in order to evaluate the capacity for plasticity of moss species in different climatic conditions and on different geographic scales.

**Keywords:** *Andreae gainii*, *Bryum pseudotriquetrum*, Nelson Island, phenotypic plasticity, *Polytrichum juniperinum*

## Introduction

The ability of some bryophytes to adapt to local conditions is often a key feature of these taxa. Therefore, significant population-level variation in features of life history traits is expected to be observed across environments (Hedderson & Longton 2008). Growth, fecundity, and survivorship are among the traits that directly influences populations' fitness across contrasting microenvironments. In comparison to vascular plants, bryophytes (mosses and liverworts) generally reveal lower infra-specific morphological variation over large spatial scales. However, morphometric analyses are becoming more usual for interpreting infra-specific variation of bryophytes, as in tropical regions where significant phenotypic variation has been observed across wide ranges of moss species distribution (e.g. Pereira *et al.* 2013).

Different environments induce changes in an individual's behavior, morphology and physiology. Such changes are collectively named phenotypic plasticity (Price *et al.* 2003). Phenotypic plasticity may be important for adaptation to heterogeneous environments, and much interest has been shown in understanding the processes affecting plastic morphological features in moss species (Buryová & Shaw 2005). Mosses occur in a diverse range of terrestrial and

aquatic environments, including the Arctic and Antarctic regions. The Antarctic continent is the most untouched region of the planet and presents one of the harshest climatic conditions among the world environments, concerning temperature (annual mean from 0°C to 2°C in the maritime Antarctica and from -30°C to -65°C in the central region; Bednarek-Ochyra *et al.* 2000; Rozema *et al.* 2005), light incidence (e.g. only 15 - 20 weeks of light incidence per year in the Northern Maritime Antarctic; Bednarek-Ochyra *et al.* 2000), water availability (annual precipitation of 300-500 mm, mainly as snow; Rozema *et al.* 2005), UV incidence (the Antarctic polar vortex hinders the outer supply of ozone, leading to severe ozone breakdown at the surface of cold polar stratospheric clouds; Rozema *et al.* 2005) and wind speed (strong katabatic winds make some coastal sites around Antarctica the windiest places in the world; Broeke & Lipzig 2003; Nylen *et al.* 2004). These characteristics and the minor interference of human actions provide the opportunity to access diversity trends and patterns over an area where species dynamics are primarily determined by natural processes (Cannone *et al.* 2013). As a consequence, a substantial increase in the number of scientific publications about Antarctica has been observed over the last 30 years (Stefenon *et al.* 2013) with important emphasis

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in the Biological Sciences. Since bryophytes are the most important terrestrial plant species in Antarctica, botanical studies have focused mainly on this group (Pereira & Putzke 2013).

Mosses cover large areas of Antarctic islands and phenotypic variances among populations growing in different microenvironments may provide information about the plasticity related to the environmental pressure and help to elucidate the potential evolutionary forces contributing to the origin and maintenance of diversity (Pereira *et al.* 2013). Microclimate, including factors such as ground-level wind speed, water availability, and low temperature, has a major influence on Antarctic plants growth (Alberdi *et al.* 2002).

Although Biological Sciences is the area with the higher significance within the world's scientific production regarding the Antarctic continent, botanical studies have a minor contribution to scientific production on this subject (Stefenon *et al.* 2013). A search in the Scopus™ database (<http://www.scopus.com>) using “Antarctic + moss” as search argument in the subjects “Agricultural and Biological Sciences”, “Environmental Sciences” and “Biochemistry, Genetics and Molecular Biology” returned 1,004 studies (as of February 2015). However, no study about morphological differentiation among populations of moss species is recorded within these reports.

Considering this lack of information about morphological differentiation at infra-specific level in Antarctic mosses and the relatively limited evidence for phenotypic variation in bryophyte species (Pereira *et al.* 2013), this study aimed to add basic information about morphometric variability in Antarctic moss species across low ranges of the species occurrence. We expect to find significant morphological variation at short geographic scale among populations of these species because Antarctic vegetation is primarily restricted to microhabitats, which do not reflect the macroclimate of the Continent (Schlensog *et al.* 2013). Therefore, short geographic scale in Antarctic islands may have the same effect of large geographic scale in environments where climate is more homogeneous and microhabitats have minor influence over vegetation.

## Material and Methods

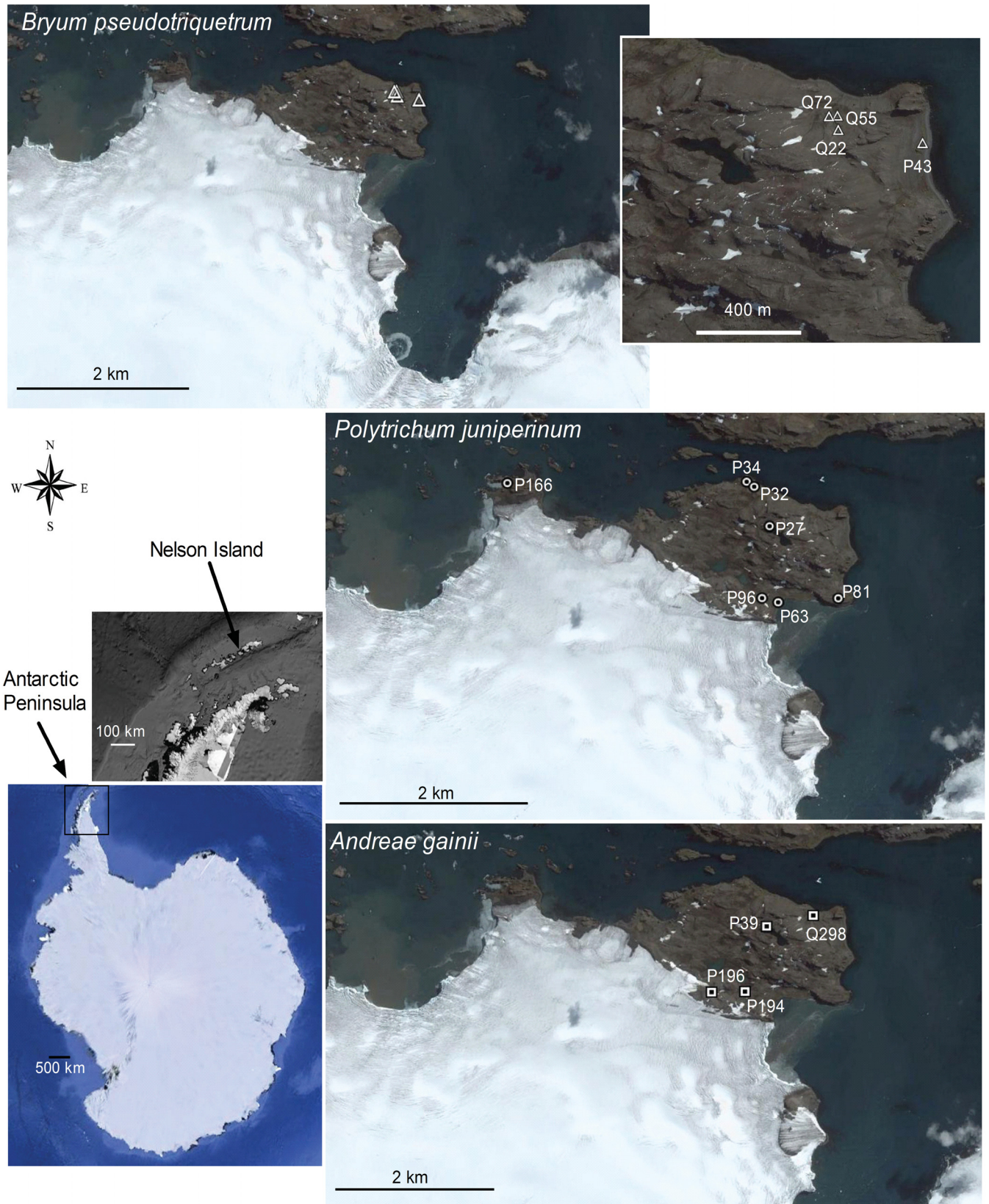
In order to evaluate the phenotypic variation of mosses related to Antarctic environments we firstly compared morphometric traits among Antarctic populations of three species: *Bryum pseudotriquetrum* (Hedw.) P. Gaertn., B. Mey. and Scherb., *Polytrichum juniperinum* Hedw. and *Andreae gainii* Cardot. While *A. gainii* is a species endemic to the Antarctic Continent, *B. pseudotriquetrum* and *P. juniperinum* are widely distributed, occurring in North and South Poles, in temperate areas and in altimontane elevations in South and Central America, Africa and Australasia (Ochyra 1998). In Antarctica, *A. gainii* is found mainly in xeric sites, while *B. pseudotriquetrum* occurs in mesic places (Schlen-

sog *et al.* 2013). *Polytrichum juniperinum* is found in moss carpet, moss hummock and moss tuft formations, in sites where there is soil or deposit of thin sediments without the influence of guano (Pereira *et al.* 2010).

Samples were collected during the Austral summer 2011-2012, in ice-free areas of the Nelson Island (62°14'S, 58°58'W; Fig. 1). This island has an area of about 164.8 km<sup>2</sup>, with a permanent ice cap covering 95% of the island and reaching the ocean along a large part of the island margin (Jiawen *et al.* 1995). Four populations of *Bryum pseudotriquetrum*, seven of *Polytrichum juniperinum* and four of *Andreae gainii* were found in the study area, georeferenced and sampled (Fig. 1).

Complete gametophytes were collected with substrate, conditioned into plastic bags containing silica gel and maintained at room temperature. The specimens were identified using the identification keys provided in Putzke & Pereira (2001) and Ochyra *et al.* (2008). Vouchers were deposited in the Herbarium of the Universidade Federal do Pampa, São Gabriel, RS, Brazil. Samples were rehydrated in the laboratory and 30 gametophytes from each population were randomly selected from the middle of the cushion or tuft for morphometric analyses. Since gametophyte and leaf sizes seem to respond directly to environmental conditions such as light and water availability (e.g. Buyová & Shaw 2005), we focused in measuring these traits. The length of each gametophyte was measured using a digital calliper rule (Mitutoyo) and the length and width of 20 leaves from each gametophyte (totalizing 600 leaves per population) were measured using a stereomicroscope and the software Motic Image Plus<sup>®</sup>. Leaves were sampled from the median portion of the gametophytes. Pairwise population means were compared using a two-tailed *t*-test. For each species, the correlation among populations was evaluated through a multivariate analysis (Principal Component Analysis, PCA) for all morphometric measures combined, using the software PAST 3.04 (Hammer *et al.* 2001). The correlation among the measured traits for each species was determined through pairwise analysis (gametophyte length × leaf length, gametophyte length × leaf width and leaf length × leaf width), using the Pearson correlation index, as implemented in PAST 3.04.

Aiming to compare the morphometric diversity of *P. juniperinum* populations growing in different environments, a multivariate analysis was performed as described above, using morphometric data from the seven Antarctic populations and from six southern Brazilian populations of this species (Tab. 1). The Brazilian populations grow in the states of Rio Grande do Sul (populations CAN, GRA, GXA, PE1 and PE2) and Santa Catarina (LAG), representing a large geographic scale in a region with sub-tropical climatic conditions. Gametophytes and leaves were sampled and measured as described for Antarctic populations. Since leaf width has minor influence in morphometric variation (see results), just measures of gametophyte length and leaf



**Figure 1.** Geographic location of sampled populations of *Bryum pseudotriquetrum*, *Polytrichum juniperinum* and *Andreae gainii* in ice-free areas of the Nelson Island, Antarctic Peninsula. Locations of *Bryum pseudotriquetrum* populations are shown closely in the insert. Images from Google Earth<sup>1</sup>.

**Table 1.** Latitude, longitude and altitude of each sampled populations of *Bryum pseudotriquetrum*, *Andreae gainii* and *Polytrichum juniperinum*.

	Label	Latitude	Longitude
Bryum	Q22	62°14'23.77"S	58°59'08.24"W
	P43	62°14'25.96"S	58°58'45.78"W
	Q55	62°14'21.65"S	58°59'10.95"W
	Q72	62°14'21.58"S	58°59'08.96"W
Andreae	P39	62°14'19.18"S	58°59'15.95"W
	P194	62°14'48.20"S	59°00'43.16"W
	P196	62°14'48.16"S	59°00'29.11"W
	Q298	62°14'19.51"S	58°59'08.59"W
Polytrichum	P27	62°14'23.36"S	58°59'45.23"W
	P32	62°14'08.28"S	58°59'56.54"W
	P34	62°14'06.31"S	59°00'02.34"W
	P63	62°14'51.07"S	58°59'39.78"W
	P81	62°14'51.04"S	58°58'53.22"W
	P96	62°14'22.45"S	59° 01'07.04"W
	P166	62°14'04.89"S	59° 03'08.85"W
	PE1	31°58'17"S	52°43'27"W
	PE2	31°55'32"S	52°53'20"W
	South Brazil	GRA	29°23'19"S
CAN	29°21'57"S	50°50'22"W	
GXA	29°16'13"S	52°34'51"W	
LAG	27°48'40"S	50°28'46"W	

**Table 2.** Mean measurements and standard deviation of the gametophyte length, leaf length and leaf width for each population and each species.

<i>Bryum pseudotriquetrum</i>			
	Gametophyte Length (cm)	Leaf Length (mm)	Leaf Width (mm)
P43	2.45(±0.237) <sup>A</sup>	1.64(±0.32) <sup>B</sup>	0.62(±0.18) <sup>B</sup>
Q22	2.22(±0.230) <sup>A</sup>	1.87(±0.42) <sup>B</sup>	0.49(±0.16) <sup>C</sup>
Q55	1.44(±0.363) <sup>B</sup>	2.01(±0.37) <sup>A</sup>	0.63(±0.13) <sup>B</sup>
Q72	1.13(±0.152) <sup>B</sup>	1.82(±0.28) <sup>B</sup>	0.75(±0.15) <sup>A</sup>
<i>Polytrichum juniperinum</i>			
	Gametophyte Length (cm)	Leaf Length (mm)	Leaf Width (mm)
P96	6.990(±1.328) <sup>A</sup>	6.70(±1.41) <sup>A</sup>	0.499(±0.113) <sup>B</sup>
P32	5.816(±1.290) <sup>B</sup>	6.15(±0.90) <sup>A</sup>	0.594(±0.134) <sup>A</sup>
P166	4.836(±2.089) <sup>C</sup>	4.85(±0.96) <sup>C</sup>	0.574(±0.162) <sup>A</sup>
P63	3.350(±0.665) <sup>D</sup>	4.59(±0.65) <sup>C</sup>	0.429(±0.115) <sup>B</sup>
P27	3.043(±0.580) <sup>D</sup>	4.48(±0.98) <sup>C</sup>	0.595(±0.136) <sup>A</sup>
P81	2.850(±0.592) <sup>E</sup>	4.94(±0.93) <sup>C</sup>	0.469(±0.138) <sup>B</sup>
P34	2.283(±0.522) <sup>E</sup>	5.06(±0.87) <sup>B</sup>	0.506(±0.103) <sup>A</sup>
<i>Andreae gainii</i>			
	Gametophyte Length (cm)	Leaf Length (mm)	Leaf Width (mm)
P196	2.29(±0.473) <sup>A</sup>	0.92(±0.17) <sup>B</sup>	0.35(±0.07) <sup>B</sup>
P194	1.57(±0.219) <sup>B</sup>	0.97(±0.49) <sup>B</sup>	0.37(±0.06) <sup>B</sup>
P39	1.52(±0.179) <sup>B</sup>	0.62(±0.11) <sup>C</sup>	0.24(±0.05) <sup>C</sup>
Q294	1.38(±0.169) <sup>B</sup>	1.62(±0.19) <sup>A</sup>	0.55(±0.32) <sup>A</sup>

Values followed by the same letter in the column are not statistically different at  $\alpha = 5\%$  according to the Student t-test.

length were used in this analysis.

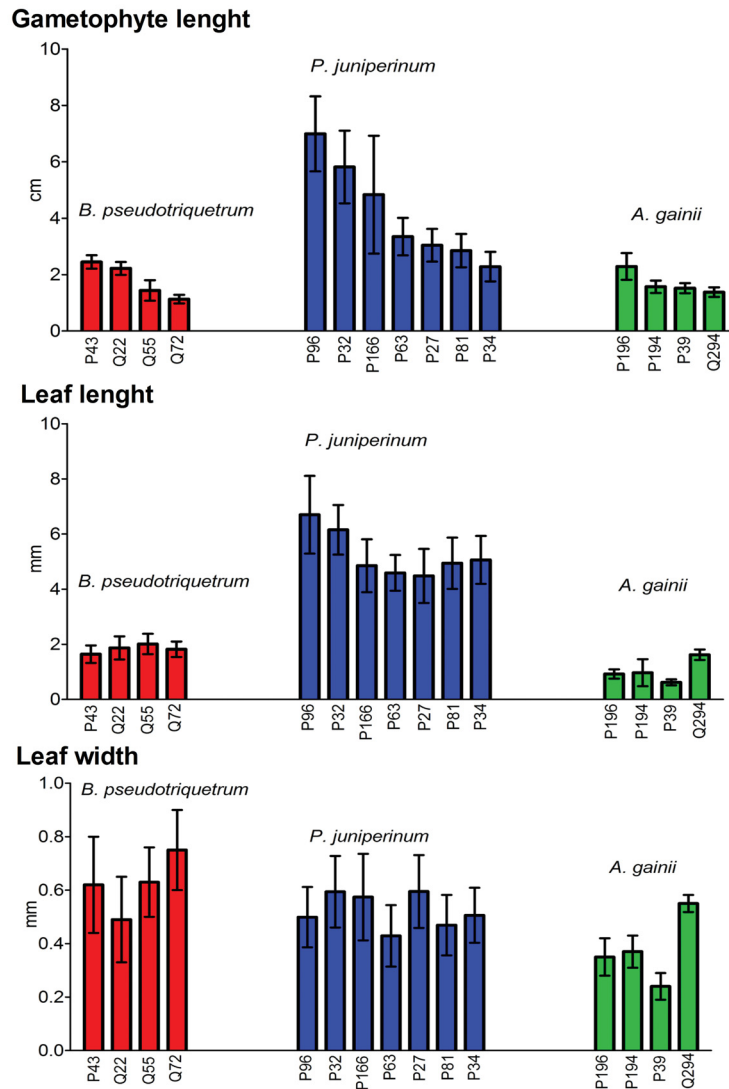
## Results

### Morphometric differentiation among Antarctic populations

For all species, the morphometric measures revealed significant difference among populations in all traits measured ( $p < 0.05$ ; Tab. 2, Fig. 2). In *B. pseudotriquetrum*, gametophyte length ranged from 1.13 cm to 2.8 cm, the leaf length ranged from 1.64 mm to 2.01 mm and the leaf width ranged from 0.49 mm to 0.75 mm. For *P. juniperinum* the longest gametophytes measured 4.84 cm and the shortest measured 2.28 cm. Leaf length ranged from 4.48 mm to 6.70 mm. Leaf width ranged from 0.429 mm to 0.595 mm (Fig. 2). For the populations of *A. gainii*, the gametophyte length ranged from 1.38 cm to 2.29 cm, leaf length ranged from 0.62 mm to 1.62 mm and leaf width ranged from 0.37 mm to 0.55 mm (Fig. 2).

The multivariate analysis of *B. pseudotriquetrum* revealed no clear pattern of population clustering (Fig. 3), with 66.87% of the variation represented in the first axis and 33.10% in the second axis. Gametophyte length variation was mainly represented in PCA1 (loading coefficient 0.98) and leaf length variation in PCA2 (loading coefficient 0.92). For *P. juniperinum*, the first axis represented 95.4% of the variation, whilst the second axis represented 4.5% (Fig 3). As for *B. pseudotriquetrum*, variation in gametophyte length was mainly represented in the PCA1 and variation in leaf length in the PCA2, both with loading coefficient 0.92. For populations of *A. gainii*, the multivariate analysis revealed 96.5% in the first axis and 3.5% in the second axis. Different from the other species, the PCA1 was mainly represented by variation in leaf length (loading coefficient 0.75) and the PCA 2 by variation in gametophyte length (loading coefficient 0.78).

The correlation between the gametophyte length and leaf length was negative for *B. pseudotriquetrum* and *A. gainii* ( $r = -0.57$ ,  $p = 0.42$  and  $r = -0.33$ ,  $p = 0.66$ , respectively),



**Figure 2.** Mean sizes of gametophyte length, leaf length and leaf width for Antarctic populations of *Bryum pseudotriquetrum*, *Polytrichum juniperinum* and *Andreae gainii* from Nelson Island. Bars are the standard deviation for each population.

but highly positive ( $r = 0.85$ ,  $p = 0.001$ ) for *P. juniperinum*. The same pattern was observed for the correlation between gametophyte length and leaf width ( $r = -0.73$ ,  $p = 0.27$  for *B. pseudotriquetrum*;  $r = -0.29$ ,  $p = 0.71$  for *A. gainii* and  $r = 0.27$ ,  $p = 0.56$  for *P. juniperinum*). The correlation between leaf length and leaf width was slightly positive for *B. pseudotriquetrum* ( $r = 0.09$ ,  $p = 0.90$ ) and *P. juniperinum* ( $r = 0.11$ ,  $p = 0.82$ ) and markedly high for *A. gainii* ( $r = 0.99$ ,  $p = 0.003$ ).

#### Morphometric differentiation among Antarctic and Brazilian populations of *P. juniperinum*

In the multivariate analysis of Antarctic and Brazilian populations of *P. juniperinum*, 86.7% of the variation was expressed in axis 1 and 13.3% in axis 2 (Fig. 4A). The gametophyte length is the main responsible for the variation

in the first axis (loading coefficient 0.94), while leaf length is the main factor for the variation expressed in the second axis (loading coefficient 0.94). Populations GRA and CAN, from southern Brazil, revealed a symptomatic differentiation in comparison to the other populations in relation to leaf length (axis 2; Fig. 4A and Tab. 3). On the other hand, the Antarctic populations P27, P34, P63 and P81 differentiated from the other populations concerning gametophyte length (axis 1; Fig. 4A and Tab. 3).

## Discussion

Although all Antarctic populations evaluated in this study grow in the same sub-Antarctic island and all measures recorded are within the range reported by Ochyra *et*

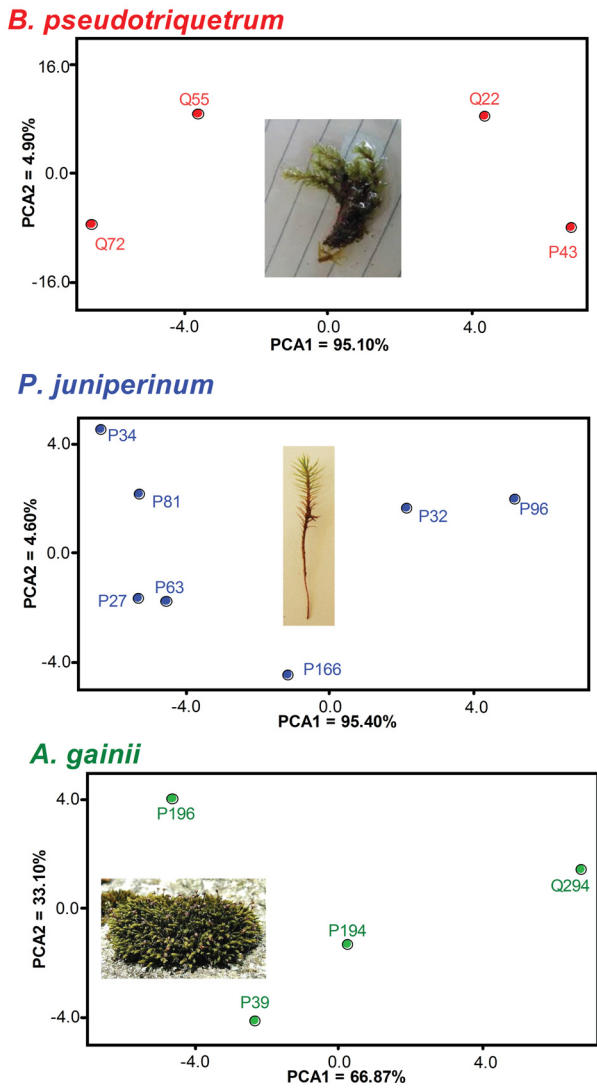


Figure 3. Principal Component Analysis (PCA) based on measures of gametophyte length, leaf length and leaf width for populations of *Bryum pseudotriquetrum*, *Polytrichum juniperinum* and *Andreae gainii* from Nelson Island.

al. (2008) for Antarctic populations of these species, such significant morphometric differences among populations may have an adaptive significance. Plasticity is considered an evolutionary adaptation to environmental variation that occurs within the lifespan of an individual organism. It is understood to be genetically controlled, heritable and of potential importance to species' evolution (Nicotra *et al.* 2010).

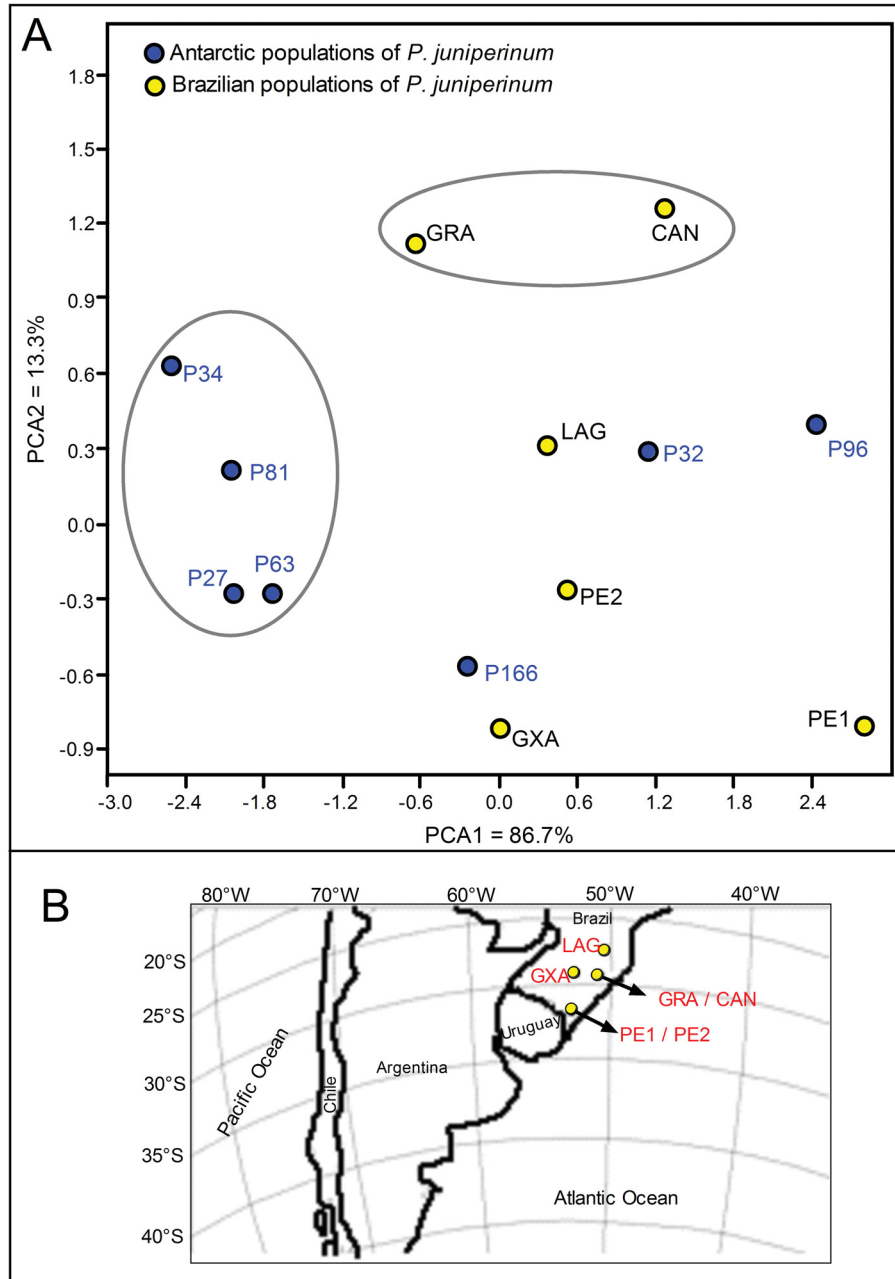
Structured morphological variation among bryophyte populations is infrequent (Pereira *et al.* 2013). However, our survey revealed significant morphological differentiation among moss populations of Nelson Island. Pereira *et al.* (2013) also observed significant phenotypic variation in the widespread Neotropical moss *Syrrhopodon leprieurii* Mont. in Central and South America. Buryová & Shaw (2005) evaluated the phenotypic plasticity of the moss *Philonotis*

*fontana* by comparing size of gametophyte and leaves and found significant difference among populations for both characters, detecting the existence of significant effects of water stress on leaf length. In the Antarctic Continent, the harsh climatic conditions include air temperatures below freezing, strong winds, light varying from total darkness to total sunlight and little amount of free water. These conditions are a challenge for Antarctic live forms and the phenotypic plasticity exhibited by bryophytes may represent an alternative strategy over genetic differentiation to enable growth in such a range of environments (Skotnicki *et al.* 2000; Buryová & Shaw 2005).

Genetic differentiation at DNA level was reported for populations of the Antarctic moss species *Bryum pseudotriquetrum* (Skotnicki *et al.* 1998), *Sarconeurum glaciale* (Skotnicki *et al.* 1999; Selkirk *et al.* 1998), *Pohlia nutans* (Skotnicki *et al.* 2002) and *Ceratodon purpureus* (Skotnicki *et al.* 2004; Clark *et al.* 2009). Overall, these studies focused mainly in dispersion distance estimations, although genetic variation related to local adaptation was not completely discarded (e.g. Skotnicki *et al.* 1998). The levels of genetic diversity observed were supposed to be primarily effect of mutation and protection to the harsh Antarctic environment (Skotnicki *et al.* 1998; 1999; 2004). Such protection against the extreme climatic conditions influences also the morphological characteristics as the type of moss growth (Skotnicki *et al.* 1998). Since neighbor populations seems to be largely originated from clonal reproduction for all studied species (Skotnicki *et al.* 1998; 1999; 2002; 2004; Selkirk *et al.* 1997; Clark *et al.* 2009), the significant differentiation observed in our morphometric analysis may be interpreted as a response to microclimatic environmental differences at short scale, counterweighing low genetic diversity in near populations.

The studied populations of *B. pseudotriquetrum* and *P. juniperinum* have the gametophyte length as the main variable responsible by the differentiation, while for *A. gainii*, leaf length was the main factor. In Antarctica, snow cover is an important microclimatic factor in protecting plants from windblown ice and sand particles (Alberdi *et al.* 2002). During the growing season, without the snow cover in ice-free areas, the moss populations are suitable to windblown ice and sand particles, causing damages in the leaves and consequently, reducing the photosynthesis area. In such a case, an increase in leaf surface supporting more exposure to light and maximizing photosynthesis is linked to competitive strategies. When the plants produce more photosynthates they can invest in processes such as growth and maintenance, enhancing survival rates (Andrade *et al.* 2013). Therefore, bigger leaves guarantee higher photosynthetic area, even after injury. On the other hand, populations that suffer such injuries in a lower intensity guarantee the same photosynthetic capacity with smaller leaves.

The multivariate analysis composed by Antarctic and Brazilian populations of *P. juniperinum* revealed low morphometric differentiation between regions, although a



**Figure 4.** Comparison of Antarctic and Brazilian populations of *Polytrichum juniperinum*. (A) Principal Component Analysis (PCA) based on morphometric measures of gametophyte and leaf length. (B) Geographic location of south Brazilian populations.

**Table 3.** Mean measurements and standard deviation of the gametophyte length and leaf length for Brazilian populations of *P. juniperinum*.

Population	Gametophyte length (cm)	Leaf Length (mm)
LAG	5.11 ( $\pm 1.18$ )	5.97 ( $\pm 0.71$ )
PE1	7.75 ( $\pm 1.78$ )	5.73 ( $\pm 0.98$ )
PE2	5.43 ( $\pm 1.05$ )	5.40 ( $\pm 1.00$ )
GXA	5.16 ( $\pm 0.63$ )	4.76 ( $\pm 0.82$ )
CAN	5.60 ( $\pm 1.24$ )	7.10 ( $\pm 0.99$ )
GRA	3.72 ( $\pm 1.26$ )	6.30 ( $\pm 1.08$ )

group of Antarctic populations present shorter leaves and two Brazilian populations revealed somewhat longer leaves in comparison to the total sample. However, comparing the plotting pattern of Antarctic populations (short geographic scale) and of Brazilian populations (large geographic scale; Fig. 4B), the relationship among populations is quite similar. This similarity supports the hypothesis that short geographic scale in Antarctica (Nelson Island) has the same effect of large geographic scale in environments where climate is more homogeneous and microhabitats have minor influence over vegetation (South Brazil). However, we tested this hypothesis for just one species (*P. juniperinum*) and these conclusions should be corroborated also through other species. Further investigations covering a wider area, evaluating more species and using controlled garden experiments are needed in order to evaluate the plasticity capacity of moss species under different climatic conditions and different geographic scales. Moreover, connecting such morphometric investigations with genetic analysis may largely improve our knowledge about the influence of ecological factors leading to plant adaptation and selection.

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