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Neighbourly Dispute at the Edge of Life: Species Interactions Among Antarctic Mosses

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ABSTRACT

Question: The stress gradient hypothesis predicts that extreme environments favour positive over negative species interactions, that is, facilitation over competition. However, along the Antarctic Peninsula (maritime Antarctic), we observed indirect evidence of competitive interactions among moss species, leading to the question of whether mosses compete even under harsh abiotic conditions for plant growth.

Location: Lagoon Island and Anchorage Island, northern Marguerite Bay, Antarctic Peninsula (67° S 68° W).

Methods: In a laboratory experiment based on simulated Antarctic field conditions, we used the locally dominant moss, *Sanionia uncinata*, in combination with three other native moss species to compare lateral growth rates between individual clumps and species combinations. The experiment included species associations collected directly from the field as well as experimentally assembled combinations.

Results: After one simulated growing season, *S. uncinata* showed increased growth in all combinations, whereas all other species decreased in surface area, demonstrating contramensalism—an interaction in which one species is positively and the other negatively affected.

Conclusions: While the underlying mechanisms cannot be confirmed, the results indicate that significant interactions do occur between moss species under simulated Antarctic conditions and should therefore be taken into account, alongside strong abiotic drivers, to understand moss community assembly in extreme environments such as those of the Antarctic.

1 | Introduction

Species interactions play an important role in shaping vegetation communities across many different ecosystems (Yang et al. 2022). In line with general life history strategy theories (Grime 1977; Southwood 1977), the stress gradient hypothesis

(SGH) proposes that biotic interactions will shift from competition to facilitation with increasing stress, because species in stressful environments, such as desert, polar or alpine biomes, will direct energy investment towards survival rather than competition (Bertness and Callaway 1994). The role of species interactions is often considered to be limited to facilitation in

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extreme environments, for example, through accumulation of water and nutrients or providing shelter, with competition generally regarded as insignificant (Hogg et al. 2006; Brooker et al. 2008). However, this hypothesis was challenged by Michalet et al. (2014), who illustrated the collapse of facilitation in extremely cold, dry and eroded environments with high solar exposure (Michalet et al. 2006; Koyama and Tsuyuzaki 2013) and a switch from facilitation to competition in water-limited ecosystems (Tielbörger and Kadmon 2000; Maestre and Cortina 2004). Furthermore, Caruso et al. (2013) demonstrated the existence of competitive interactions (even though quantitatively minor) in Antarctic terrestrial communities, which face some of the most extreme conditions. In addition, a study on vegetation in the Sahara by Noumi et al. (2015) found competition to weaken with increasing drought stress, but facilitation was not observed. In line with these findings, a recent comprehensive overview of plant interactions worldwide (Yang et al. 2022) concluded that competition was the fundamental driver of plant communities globally, identifying no strong latitudinal or climatic patterns and suggesting that local factors may be better predictors of plant interactions than macroclimate.

A limited number of studies have focused on interactions among moss species, especially *Sphagnum* mosses, reporting mostly competition (Mulligan and Gignac 2002; Hájek and Adamec 2009; Mälson and Rydin 2009; Spitale 2009; Bu et al. 2013; Udd et al. 2016; Liu, Bu, Mallik, Chen, et al. 2020; Liu, Bu, Mallik, Rochefort, et al. 2020; Cheng et al. 2023) and, less frequently, facilitation (Mulder et al. 2001; Liu, Bu, Mallik, Chen, et al. 2020; Liu, Bu, Mallik, Rochefort, et al. 2020; Cheng et al. 2023). However, in studies specifically addressing a water stress gradient, the SGH was not supported, finding no switch from competition to facilitation towards the dry end of the gradient (Spitale 2009) or, alternatively, a switch from facilitation to competition (Bu et al. 2013). Antarctic mosses can face the coldest, driest and windiest conditions on Earth

(Convey et al. 2008), and competition has been considered unimportant in moss communities along the Antarctic Peninsula (Smith 1972), as in Antarctic terrestrial communities more generally (Convey 1996; Hogg et al. 2006). Conversely, studies focussing on species interactions in Antarctic communities involving vascular plants have reported or inferred both facilitation and competition (Krna et al. 2009; Casanova-Katny and Cavieres 2012; Atala et al. 2019). However, no experimental studies have been carried out to investigate the interactions between moss species in this environment, and the limited long-term monitoring available does not address species interactions, leaving the role of species interactions between Antarctic moss species poorly explored.

In the Maritime Antarctic, we observed moss species growing closely together, often appearing to compete for suitable space between rocks (Figure 1). To test if such competitive interaction can occur between Antarctic moss species, we paired *Sanionia uncinata*, a widespread and common moss species in the Maritime Antarctic (Ochyra et al. 2008), with three other commonly occurring native moss species (*Andreaea regularis*, *Brachythecium austrosalebrosum*, *Pohlia nutans*) and grew the species combinations in the laboratory under conditions representative of one Antarctic growing season. We compared moss lateral growth in the combinations with that for each species grown alone. Because moss interaction outcomes have been found to differ between field and laboratory conditions for the same species combinations (Liu, Bu, Mallik, Chen, et al. 2020), we included intact species combinations from the field (collected when growing in close physical contact) as well as combinations assembled in the laboratory, as there was no option to study them long term in the field. Based on our field observations and widespread reports of *S. uncinata*'s dominance in the field (Ochyra et al. 2008), we hypothesised (1) that interspecific competition plays a role in Antarctic moss community assembly and (2) that *S. uncinata* has a competitive advantage over less abundant species.



FIGURE 1 | Moss species *Henediella heimii* (upper) and *Bartramia patens* (lower) growing closely together between rocks in the Antarctic, demonstrating the potential for interaction at the boundary of physical contact. Photos: Seringe Huisman.

2 | Terminology, Materials and Methods

2.1 | Terminology

In the introduction, we used the broad terms competition and facilitation to indicate negative versus positive species interactions, because the original SHG was formulated at this level (Bertness and Callaway 1994). Subsequently, more refined types of interactions, including combinations of competition and facilitation, were acknowledged in the context of the SGH (Callaway and Walker 1997; Maestre et al. 2009). Goldberg (1990) described interaction definitions based on all possible combinations of outcomes between two species, considering the effect of the interaction on each species (positive (+), negative (−) or neutral (0)). Halvorsen (2012) refined this terminology, leading to the framework we adopted in this study to define more specific interaction outcomes, defined in Box 1. While competition in the strictest sense is constrained to (−/−) outcomes (Box 1), we refer to all outcomes including negative effects on one species as ‘competitive interactions’, considering that the negatively affected species is essentially hampered by the presence of the other species. Figure 2 illustrates the potential outcomes based on our experimental design.

2.2 | Sample Collection

Moss samples were collected in February 2022 on Lagoon Island (67°35′ S 68°14′ W) and Anchorage Island (67°36′ S 68°12′ W), located close to each other in Ryder Bay (northern Marguerite Bay) off the west coast of the Antarctic Peninsula (Figure 3). Both islands are rocky, sparsely vegetated and partly covered by semi-permanent snow and ice fields (Convey and Smith 1997). The vegetation mainly consists of lichen communities, with the fruticose lichen *Usnea antarctica* being most prominent, but valleys and rock crevices support isolated patches of several moss species. *Sanionia uncinata* is the most abundant species, followed by species representing *Andreaea*, *Brachythecium* and *Pohlia*. The vegetation is snow-covered for at least 6 months during the austral winter and occasionally during the summer. The average winter and summer air temperatures range from

−20°C to −5°C and 0°C to 5°C, respectively (Tang et al. 2018), and solar radiation in summer is generally high, reaching 2000 PPFd (Lud et al. 2003). Annual precipitation is 150 mm/year, falling mostly as snow (Tang et al. 2018).

2.3 | Interaction Experiments

We included three species pairs of *S. uncinata* with another native species: *S. uncinata* vs. *Andreaea regularis*, *S. uncinata* vs. *Brachythecium austrosalebrosum* and *S. uncinata* vs. *Pohlia nutans* (Ochyra et al. 2008). All of these species form dense cushions or continuous carpets in the field (Fowbert 1996). Six ‘natural’ samples were collected per species pair, where the two species shared a boundary of physical contact in the field. These combinations differed in size and shape, as a function of the natural habitats from which they were obtained, but all were a maximum of 7 cm across. Only the combination of *S. uncinata* and *B. austrosalebrosum* was found in more extensive natural patches, from which combinations of ~7 cm diameter were taken. In addition to these natural combinations, 12 individual samples of each species were collected to assemble six new combinations per species pair in the laboratory and six monospecific samples to give control comparison. The combination of *S. uncinata* vs. *B. austrosalebrosum* was sampled on Anchorage Island, whereas the combinations of *S. uncinata* with *P. nutans* and *A. regularis* were sampled on Lagoon Island, based on the presence of the species and our responsibility to not sample > 1% of any local species population. All samples were carefully lifted from the underlying rocks by hand, transferred into sample bags and kept at −18°C during the remainder of the field season (±2 months). After transportation, the samples were kept at −5°C until preparation for the experiment described below.

2.4 | Experimental Design

All natural combinations ($n=6$), assembled combinations ($n=6$) and monospecific samples ($n=6$) were carefully placed in an individual circular plastic container (7.5 cm wide and 3 cm

BOX 1 | Interaction definitions based on the positive (+), neutral (0) or negative (−) outcome for each species in an interspecific interaction (Goldberg 1990).

(−/−)	Competition	Competition in the strictest sense, that is, a negative effect on both species that can be symmetric or asymmetric. A classic example is resource competition
(−/0)	Amensalism	An unspecific type of interaction that is not dependent on the species characteristics, but rather morphological presence, for example, a larger tree preventing sunlight from reaching a plant below
(0/+)	Commensalism	Also called facilitation, for example, epiphytes that benefit from their host tree without negatively affecting the tree
(+/+)	Mutualism	An interaction beneficial to both species, for example, mycorrhizal fungi that benefit from plant sugars while providing the plant with nutrients
(+/-)	Contramensalism	Interaction outcome that is positive for one species and negative for the other, also referred to as antagonism. For example, bryophytes using another species as substrate, where the species on top benefits (the beneficiary species) and the substrate species is hampered. A special case is parasitism, where the beneficiary species is completely dependent on the negatively affected host species

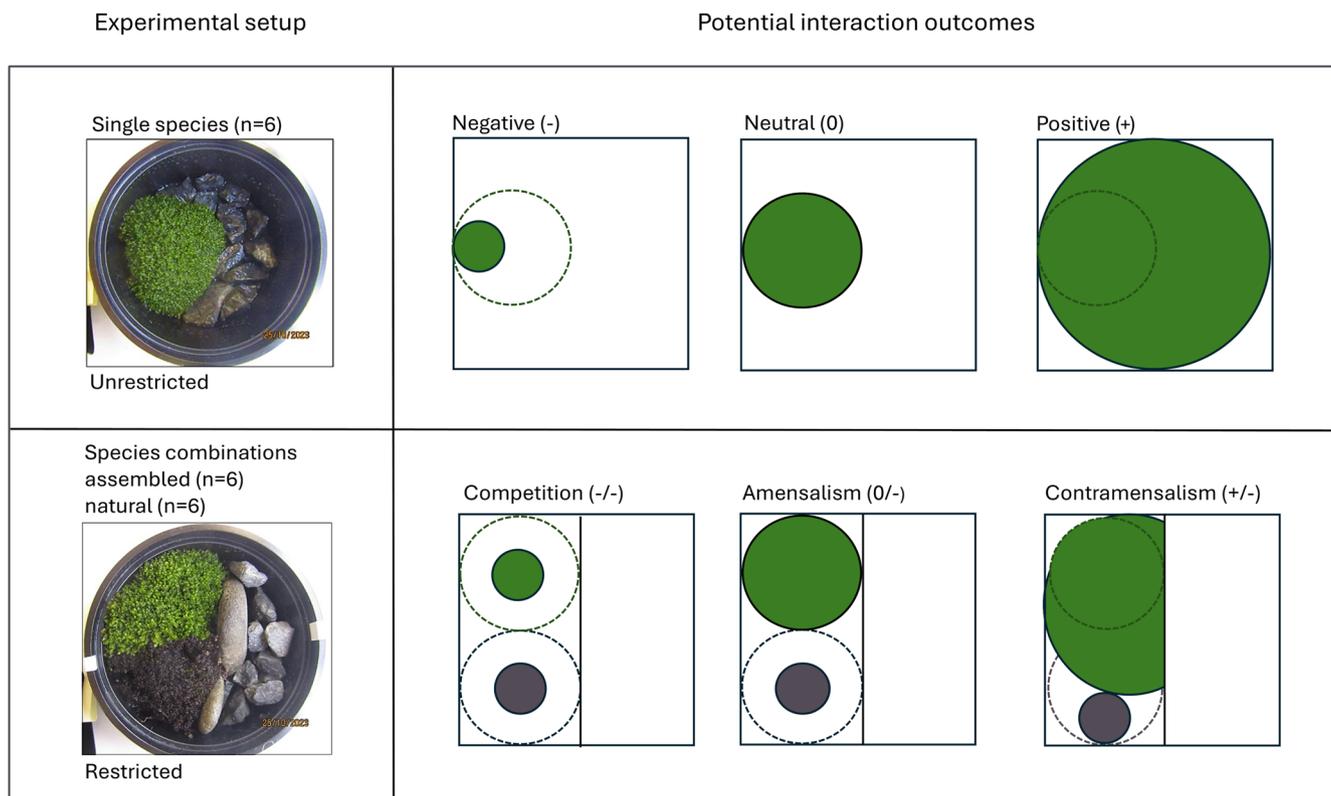


FIGURE 2 | Experimental set-up including pictures from *Sanionia uncinata* alone in an unrestricted setting, and an assembled combination of *S. uncinata* and *Andreaea regularis* in a restricted setting, with the potential interaction outcomes indicated for both settings (following Goldberg 1990). In the first two interaction scenarios, *A. regularis* could also remain the same size, leading to a reverse case of amensalism (-/0) or a completely neutral/non-existent interaction (0/0).

high) (Figure 2). The natural combinations were transferred in their original shape, the assembled combinations were created by carefully placing two clumps of different species together that were roughly equal in size and height, making sure the samples were in contact along the central boundary. Mimicking the limited space available in natural rock crevices (Figure 1), and to ensure that the mosses could only grow in the direction of the other species at the ‘competition boundary’, any surrounding spaces were filled with small stones (Figure 2). These were first carefully cleaned and autoclaved for 15 min at 120°C to avoid contamination. The monospecific samples were all placed in an individual container and not restricted in their lateral expansion, but a thin layer of flat stones was placed at the bottom of the containers to prevent excessive evaporation compared to the other containers, representing the non-competitive situation (Figure 2).

All containers were placed in a 2°C climate chamber (THEBO Horeca) with RIVA Cold refrigeration units (Rivacold srl—Vallefoglia, Italy) under light emitting diode (LED) lamps (Hortilight Sunfactor 270; 405 W). After an acclimation period of 2 weeks under low light, the lights were set to follow a daylength regime through the months representative for an Antarctic summer, based on field photosynthetically active radiance (PAR) measurements from Anchorage Island (Bokhorst et al. 2007, 2022) (Appendix S1). Each month was slightly shortened for the purpose of the experiment, resulting in a total growth season of 15 weeks. The containers were placed randomly under the lights and rotated twice a week to randomise their positions on

the shelf. Twelve additional *S. uncinata* samples of similar size with temperature loggers (I-Button, Maxim integrated) placed within the moss were used to track temperature fluctuations throughout the experiment. Moss temperature remained within the mean ambient fluctuations measured in the field (diurnal range 0°C–7°C; Bokhorst et al. 2022). The samples were watered with tap water twice a week, with the total water amount added not exceeding local precipitation levels of 150 mm/year (Tang et al. 2018). Relative humidity was kept between 60% and 90%, with drier conditions during the day (high light intensity) and more humid conditions during the night (no/low light), again conforming with field conditions (Bokhorst et al. 2008).

2.5 | Growth Measurements and Data Analyses

To assess the growth of the mosses, we quantified percentage change in surface area. Photographs were taken from above using a Canon powershot SX 210 camera at the start and end of the experiment. Moss surface areas were measured using ImageJ software (Schneider et al. 2012). The percentage change in area was then calculated by comparing surface area differences between the start and end of the experiment.

To identify whether lateral growth was affected by the presence of other species, we compared the percentage surface change for each species between growing alone, in natural combinations and assembled combinations. Due to the small sample sizes ($n=6$), non-normal distributions and unequal variances,

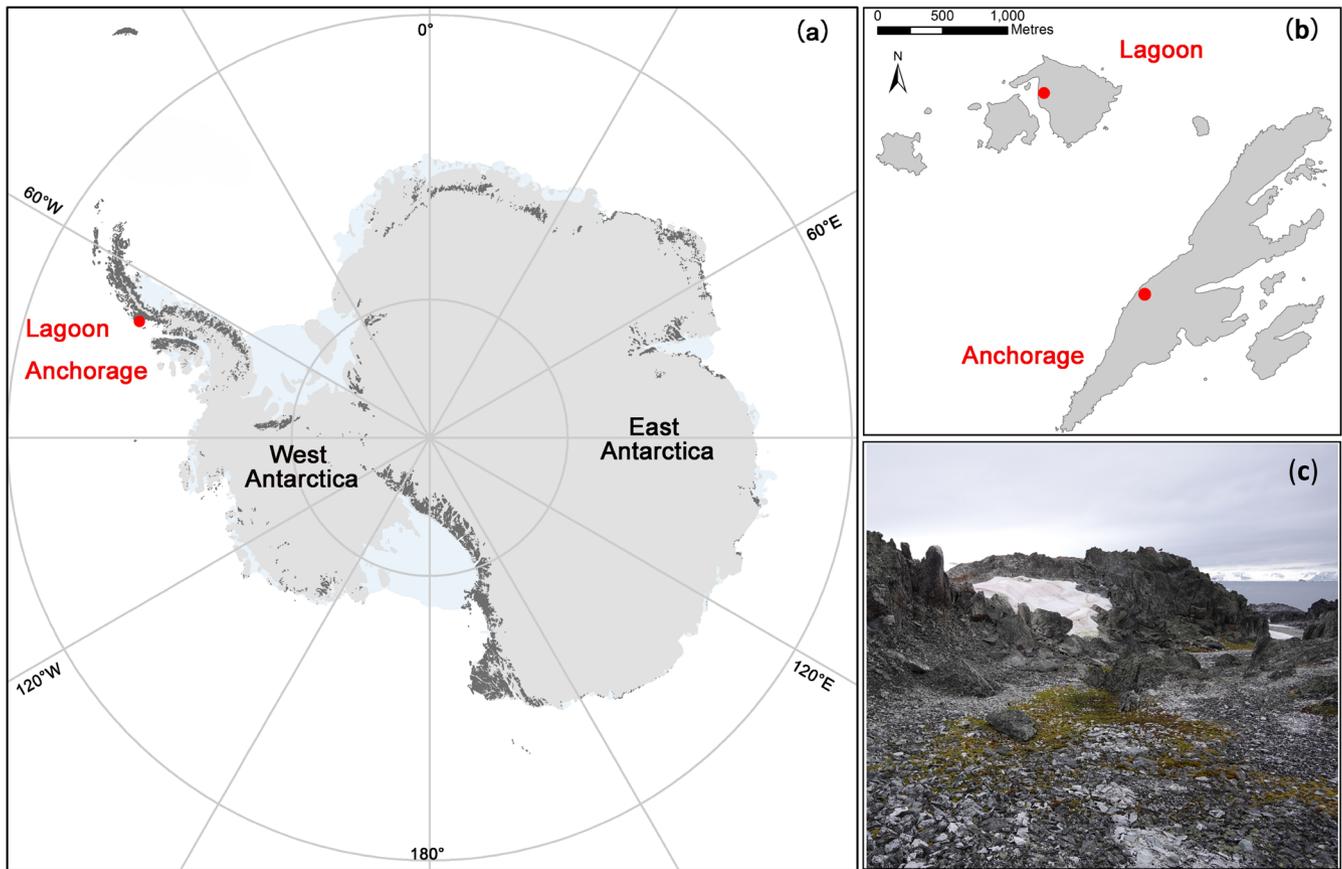


FIGURE 3 | (a) Locations of Lagoon Island and Anchorage Island (67°S 68°W) along the Antarctic Peninsula, (b) sampling locations on the islands and (c) typical moss cover on Lagoon and Anchorage islands.

non-parametric tests were applied. Kruskal–Wallis tests were performed for the sets with three groups (alone, natural and assembled combinations), followed where significant by a Dunn's test for pairwise comparisons between groups. For interspecific comparison per combination (i.e., only two groups) Wilcoxon rank-sum tests were performed (also known as Wilcoxon–Mann–Whitney test). For this test, *R* reports *W* as the test statistic (R Core Team 2023), however, this value is comparable to the *U* statistic that is commonly reported and should not be confused with the *W* statistic of the Wilcoxon–signed rank test for paired samples. All statistical analyses were performed in *R* version 4.2.3 (R Core Team 2023).

3 | Results

The surface area of *S. uncinata* increased in combination with all other species compared to when growing alone (increase of between 10% and 60%), while all other species decreased in the combinations (decrease of between 20% and 70%) (Figure 4a–f). The effect was strongest in the natural combinations and significant in most cases (Figure 4a–f). Compared to growing alone, where *S. uncinata* hardly increased in surface area, the Kruskal–Wallis (KW) and subsequent Dunn's tests (Dt) showed that *S. uncinata* area increased significantly when growing in natural combinations with *A. regularis* (KW $p=0.007$; Dt $p=0.006$) and *P. nutans* (KW $p=0.039$; Dt $p=0.033$), and marginally non-significantly with *B. austrosalebrosus* (KW

$p=0.095$) (Figure 4a,c,e). At the same time, *A. regularis* and *B. austrosalebrosus* decreased significantly in the natural combinations with *S. uncinata* compared to when growing alone (KW $p=0.002$; Dt $p=0.001$ and KW $p=0.004$; Dt $p=0.007$, respectively), whereas *P. nutans* showed a smaller, non-significant decrease (KW $p=0.160$) (Figure 4b,d,f).

When considering interspecific outcomes, that is, which of the two species grew more in each combination, *S. uncinata* showed greater growth (up to 50%; $p < 0.05$) in all natural combinations, whereas all other species decreased by up to 50% (Appendix S2c). In the assembled combinations, no significant differences were apparent between the species ($p > 0.05$) (Appendix S2b).

4 | Discussion

In support of our hypotheses, the experiment showed that competitive interactions can play a role between Antarctic mosses, and that *S. uncinata* has an advantage over the other three species tested. *Sanionia uncinata* showed an increase when growing in combination with all other species, especially in the natural combinations, compared to growing alone (Figure 4a–f), indicating a benefit from the interaction, while the other species were negatively impacted and declined compared to growing alone, demonstrating a case of contramensalism (+/–). Not all combinations showed significant effects, but the tendency was similar for all species pairs, and a longer growing period would

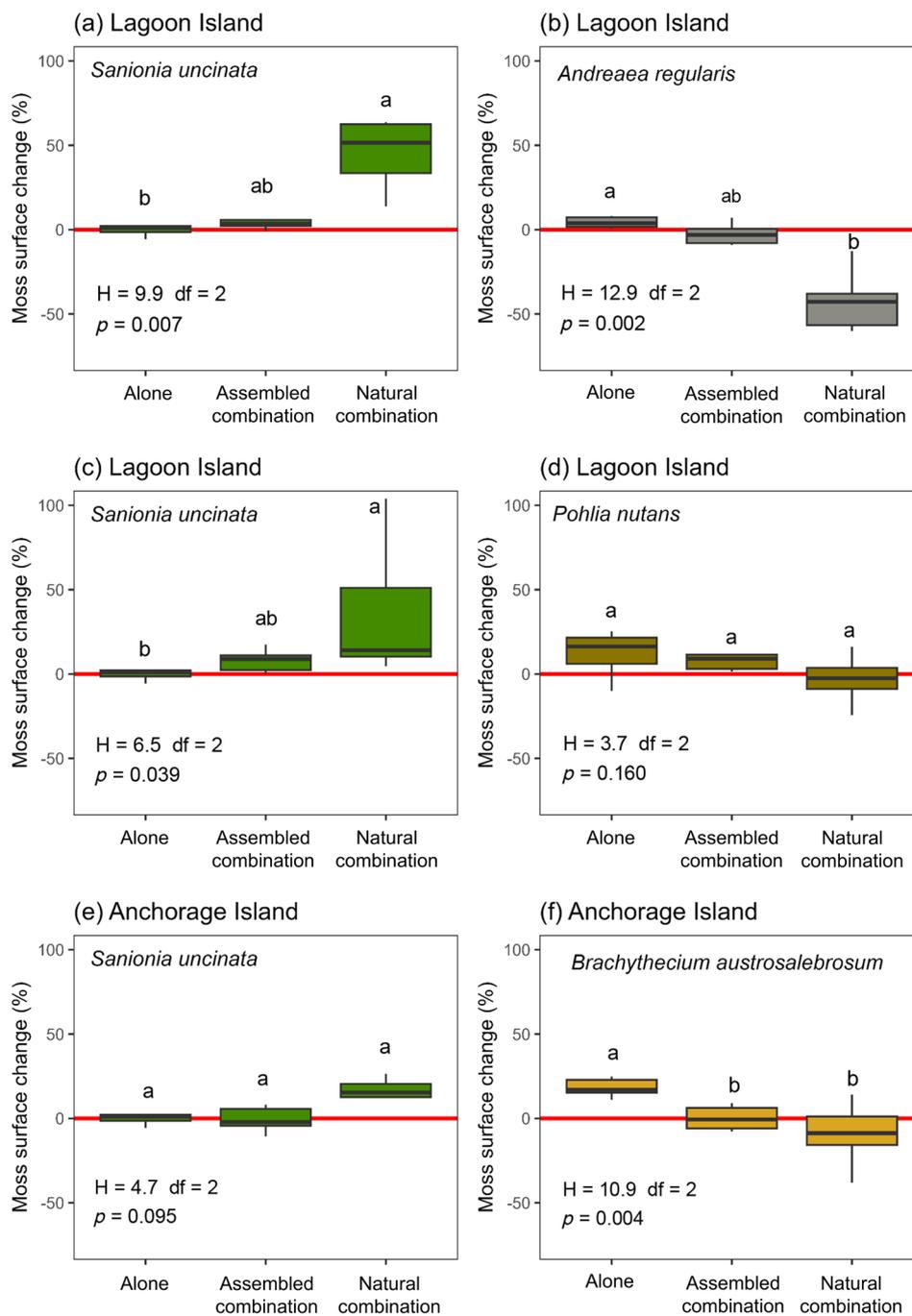


FIGURE 4 | Percentage surface area changes of Antarctic moss species collected on Lagoon Island (a–d) and Anchorage Island (e, f) growing alone versus when in physical contact with other species, after a 15-week experimental period. Panels are paired horizontally, with the left panel (a, c, e) showing *Sanionia uncinata* growing either alone or within each respective paired combination, and the right panel (b, d, f) showing the response of the three other native species tested growing either alone or with *S. uncinata*. Panels a–f show values of the Kruskal–Wallis test for all groups, letters above the boxes indicate significant differences between specific groups ($p < 0.05$, Dunn's test). Box plots are based on six replicate experimental units.

likely have increased the effect size. These results provide confirmation that Antarctic moss communities are not solely driven by species adapted to the abiotic conditions provided by that habitat, as suggested by Smith (1972), but that biotic interactions also contribute (cf. Caruso et al. 2013). It also opens up the possibility of successional stages in vegetation development, defined by interspecific interactions, in this case with *S. uncinata* demonstrating the potential for replacing other species in the process.

Our findings contradict the original SGH, which predicts competitive interactions to disappear in more extreme environments (Bertness and Callaway 1994). However, our data appear to support one of the alternatives to the SGH provided by Michalet et al. (2014), the switch from facilitation to competition at the extreme end of a water gradient, due to the inevitable competition for water. This alternative hypothesis was also supported by Bu et al. (2013), who observed a change from facilitation to competition between two *Sphagnum* mosses under drought conditions.

Although our study did not specifically include a water gradient, the field and laboratory circumstances reflect those of an environment acknowledged to face repeated periods of drought stress. Here, mosses only survive where liquid water is periodically available (Pannowitz et al. 2003; Schroeter et al. 2017). Suitable habitat is often limited and an increase of one species will automatically mean a decrease of adjacent species, as reflected in our experimental setup (Figures 1 and 2). In this context, the observed positive effect on *S. uncinata* (i.e., *S. uncinata* performing better when in combination than alone) within a restricted setting will inevitably result in competition for space. As these circumstances are not unique to the Antarctic but also occur, for instance, on rocky outcrops on high mountains or in desert settings, we propose the switch from facilitation to competition due to limited space as another alternative to the SGH.

The competitive advantage of *S. uncinata* demonstrated here could be a result of its superior water holding capacity (Gimingham and Smith 1971). This superior capacity could facilitate the capture of moisture from neighbouring mosses, a mechanism also reported in dry alpine shrub interactions (Schöb et al. 2014). Such an ability would be consistent with *S. uncinata* performing better when in combination with other species than when growing alone. In addition, growth form could have played a role, with *S. uncinata* being a pleurocarpous moss with more loosely arranged, branching shoots and creeping, weft-like growth, while the acrocarpous *A. regularis* forms more compact cushions or turfs with short, upright shoots. However, in the harsh Antarctic environment, *S. uncinata* often only grows short shoots as well, showing a more compact structure compared to when growing in mild conditions, resembling the acrocarpous growth form more closely (Figure 2). We therefore do not think growth form was the determining factor in the interaction outcome.

The assembled combinations did not show significant effects, raising the question of which factors 'prime' the natural combinations to enable the competitive effect to become apparent. While our study did not focus on identifying underlying mechanisms, potential factors could include allelopathic (Liu, Bu, Mallik, Rochefort, et al. 2020) or microbial effects (Holland-Moritz et al. 2018) that require an 'intact' initial species combination. To investigate these mechanisms and address contrasting outcomes between laboratory and field conditions (Liu, Bu, Mallik, Chen, et al. 2020), further studies should include natural and assembled combinations in both laboratory and field conditions. In addition, longer timescales and more species combinations, including more growth forms and combinations without *S. uncinata*, could determine if competitive exclusion takes place or an equilibrium is reached, and whether a competitive hierarchy can be established.

5 | Conclusions

In this first experimental study on species interactions between Antarctic mosses, we found that *S. uncinata* increased in surface area in combination with other species compared to when growing alone, while the other species performed less well in combination with *S. uncinata*, demonstrating contramensalism. These findings indicate that, apart from abiotic factors, species interactions are likely to be an important driver of moss community structure and may, in particular, help explain the

current dominance of *S. uncinata*. In-depth research is now required to understand the underlying mechanisms, preferably with the inclusion of a wider range of species and growth forms, and through long-term field experiments under current and predicted future climatic regimes. Understanding the role of these interactions, and gauging their overall importance in the field, is essential to understanding moss community composition in the unique Antarctic environment.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in the [Supporting Information](#) of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Diurnal patterns in photosynthetically active radiation (PAR) during an Antarctic summer. PAR values reflect mean diurnal values. **Appendix S2:** Pairwise comparisons (Wilcoxon rank-sum tests) of horizontal growth rates (%) of Antarctic moss species from Lagoon and Anchorage. **Appendix S3:** Dataset. **Appendix S4:** Metadata for the dataset (Appendix S3). **Appendix S5:** R-code.