

Invariant properties of mycobiont-photobiont networks in Antarctic lichens

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Abstract

Aim: Lichens are often regarded as paradigms of mutualistic relationships. However, it is still poorly known how lichen-forming fungi and their photosynthetic partners interact at a community scale. We explored the structure of fungus-alga networks of interactions in lichen communities along a latitudinal transect in continental Antarctica. We expect these interactions to be highly specialized and, consequently, networks with low nestedness degree and high modularity.

Location: Transantarctic Mountains from 76°S to 85°S (continental Antarctica).

Time Period: Present.

Major Taxa Studied: Seventy-seven species of lichen-forming fungi and their photobionts.

Methods: DNA barcoding of photobionts using nrITS data was conducted in 756 lichen specimens from five regions along the Transantarctic Mountains. We built interaction networks for each of the five studied regions and a metaweb for the whole area. We explored the specialization of both partners using the number of partners a species interacts with and the specialization parameter d' . Network architecture parameters such as nestedness, modularity and network specialization parameter H_2' were studied in all networks and contrasted through null models. Finally, we measured interaction turnover along the latitudinal transect.

Results: We recovered a total of 842 interactions. Differences in specialization between partners were not statistically significant. Fungus-alga interaction networks showed high specialization and modularity, as well as low connectance and nestedness. Despite the large turnover in interactions occurring among regions, network parameters were not correlated with latitude.

Main Conclusions: The interaction networks established between fungi and algae in saxicolous lichen communities in continental Antarctica showed invariant properties along the latitudinal transect. Rewiring is an important driver of interaction turnover along the transect studied. Future work should answer whether the patterns observed in our study are prevalent in other regions with milder climates and in lichen communities on different substrates.

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KEYWORDS

intimate ecological interaction, lichen-forming fungi, symbiosis, Transantarctic Mountains

1 | INTRODUCTION

Lichens, the symbiotic phenotype of lichen-forming fungi (hereafter mycobionts) interacting with photosynthetic partners (green algae and/or cyanobacteria, hereafter photobionts), are the epitome of mutualistic symbioses (Smith & Douglas, 1987). How mutualistic organisms interact with each other to form complex networks is well known for non-symbiotic mutualisms, e.g. plant-pollinators, plant-seed dispersers (Bascompte & Jordano, 2013) but not for symbiotic mutualisms in general (Guimarães Jr et al., 2007; Pires & Guimarães Jr, 2013) and fungal interactions in particular, for which the number of studies focused on the structure of the relationships at a community scale is lower (Jacquemyn et al., 2015; Martos et al., 2012; Montesinos-Navarro et al., 2012; Pölme et al., 2017; Toju et al., 2014). Particularly rare are the studies examining the interaction networks between lichen-forming fungi (mycobionts) and their photosynthetic partners (photobionts) at a community scale (Peksa et al., 2022; Singh et al., 2019; Wagner et al., 2020; Werth, 2012) despite the fact that, with c. 20,000 species, they represent c. 17% of the known fungal species (Feurerer & Hawksworth, 2007; Lücking et al., 2016), cover approximately 8% of Earth's land surface and have a relevant contribution to ecosystem functioning (recently reviewed in Asplund & Wardle, 2017).

The biological intimacy hypothesis predicts high reciprocal specialization and high modularity in interaction networks between organisms with high intimacy, including symbioses (Guimarães Jr et al., 2017; Hembry et al., 2018; Pires & Guimarães Jr, 2013; Thompson, 2005). Further, as specialists are not expected to interact with a subsample of species with which generalists interact, low levels of connectance and nestedness (antinestedness) are hypothesized to characterize highly intimate interaction networks (Guimarães Jr et al., 2007; Toju et al., 2014), as opposed to the highly nested patterns found in low-intimacy mutualistic networks (Bascompte et al., 2003). Indeed, ecological networks depicting intimate interactions between plant and mycorrhizal fungi showed both high modularity and specialization (Chagnon et al., 2012; Montesinos-Navarro et al., 2012; Pölme et al., 2017; Toju et al., 2014). However, patterns of nestedness varied among studies, whereas Chagnon et al. (2012) and Montesinos-Navarro et al. (2012) found higher levels of nestedness than expected in null models, Toju et al. (2014) and Sepp et al. (2019) found antinestedness patterns. With respect to lichens, some observed phenomena such as the change of photobionts even in species with obligate codispersal (Nelsen & Gargas, 2008), the existence of photosymbiodemes, in which the same fungus forms morphologically different thalli depending on whether it is associated with a green alga or a cyanobacterium (Armaleo & Clerc, 1991), or the fact that several lineages of photobionts have been detected within the same thallus (Casano et al., 2011), suggest that fungus-algae interactions may not behave in the same way as other known

symbiotic systems. We are aware of only one study examining nestedness and modularity of fungus-alga interactions at the community level, although it only includes the epiphytic lichens associated with *Ramalina menziesii* fungi (Werth, 2006). This study described the network of fungal species and algal ITS sequence haplotypes to be modular and nested. A further study focused on specialization metrics of myco-photobiont networks and showed that this parameter varied with altitude along an elevational gradient in the Antarctic continent (Wagner et al., 2020). In contrast, Magain et al. (2017) argued that specialization is a species-specific trait independent of environmental conditions. At what extent the network structure of fungus-alga interactions changes along environmental gradients remains poorly unknown. For example, species turnover along the gradient might drastically alter network structure or, alternatively, not to affect it if interactions are rewired between species (Suweis et al., 2013).

Antarctica, the coldest and driest continent, poses a challenge to all organisms due to the extreme environmental conditions. In the c. 0.18% of the ice-free area (Burton-Johnson et al., 2016) bryophytes and, specially, lichen-forming fungi with almost 500 species are the most diverse organisms of the terrestrial macroscopic biota (Convey, 2001; Øvstedal & Smith, 2001, 2009). Two very different biogeographic regions, maritime and continental, are differentiated in Antarctica, with the boundary occurring around 72°S (Peat et al., 2007). In continental Antarctica, the Transantarctic Mountains constitute a latitudinal gradient from 69° to 86°S, that does not, however, translate into a biodiversity gradient (Colesie et al., 2014; Green et al., 2011; Peat et al., 2007; but see Pérez-Ortega et al., in review). Regarding lichen-forming fungi, no more than 35 species are known growing further south than 82°S. The Antarctic terrestrial biodiversity faces a growing pressure due to human disturbance, the introduction of exotic species and pollution (Chown et al., 2012; Hughes & Convey, 2010). Lichens, with their extremely low growth rates in continental Antarctica (Sancho et al., 2007), are prone to suffer the aforementioned effects of global change. Understanding the structure of the interaction networks among lichen-forming fungi and their photobionts may help not only to draw hypotheses about ecological and evolutionary processes (Thompson, 2005) but also to design better conservation plans in the near future. Early studies on photobionts in the Antarctic continent posed the hypothesis that extreme environments would favour species showing lower levels of specialization (Wirtz et al., 2003). Subsequent studies analysing photobiont diversity and mycobiont preferences in two extreme environments such as the McMurdo Dry Valleys (Pérez-Ortega et al., 2012; Wagner et al., 2020) and the Coal Nunatak in Alexander Island (Engelen et al., 2016), revealed a variety of strategies among the analysed species, including high specialization.

The main goal in this study is to characterize the structure of myco-photobiont interaction networks of rock-dwelling lichen

communities along a latitudinal transect in the Transantarctic Mountains (continental Antarctica), one of the longest mountain ranges on Earth (3,500 km) stretching from 72° to 87° S. We build networks for saxicolous lichen communities from five regions along a 76° to 85° S transect, based on DNA barcoding of both biotas (Pérez-Ortega et al., in review), which is a useful tool for standardizing data collection and revealing novel ecological interactions (Derocles et al., 2015; Kelly et al., 2011). In accordance with the biological intimacy hypothesis, we hypothesize that these networks will be characterized by high modularity and specialization and low connectance and nestedness. In addition, based on the hypothesis that specialization is a species-specific trait independent on environmental conditions (Magain et al., 2017 but see Wagner et al., 2020), we expect that the network characteristics are invariant along the latitudinal transect. Finally, we expect a high level of interaction rewiring among localities on the basis of previous evidences of community composition shaped by stochastic and restricted colonization events (Garrido-Benavent et al., 2021; Jones et al., 2015). High rewiring may be compatible with high specialization if the rewiring occurs within modules of highly specialized species.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

A total of 11 localities were sampled in five distinct regions along the southernmost part of the Transantarctic Mountains (77°–85° S; Figure 1). Two nearby localities in Cape Crozier in

Ross Island (77° 31' S, 75–80 m.a.s.l., basaltic rock) were sampled in 2007. In the McMurdo Dry Valleys (78° S) surveys across the Hidden (c. 370 m.a.s.l., metamorphic rock), Garwood (c. 600 m.a.s.l., granite), and Miers (c. 420 m.a.s.l., granite) valleys were carried out during the austral summers of 2009 and 2011. Mount Hope (83° 30' S, c. 210 m.a.s.l., granite) and Mount Kyffin (83° 46' S, c. 735 m.a.s.l., metamorphic rocks) are located at the southern side of Beardmore Glacier. Garden Spur (84° 32' S, c. 380 m.a.s.l., granite) and Waldron Spur (84° 32' S, c. 607 m.a.s.l., granite) are narrow rocky ridges at the lowest end of Shackleton Glacier. Durham Point (85° 32' S, c. 406 m.a.s.l., metamorphic rocks) emerges as a big cliff closed to the confluence of Scott Glacier with the Ross Ice Shelf and it is surrounded by frozen lakes. Sampling in the latter three localities was conducted during January 2011. Complete sampling locality data for each examined specimen is provided in Table S1. There are insufficient meteorological data sets to inform the climate of the Transantarctic Mountains along the Ross Barrier. However, it seems clear that the Beardmore Glacier area and locations further south (Shackleton Glacier and Scott Glacier) receive much more precipitation than locations further north, such as Ross Island or the Dry Valleys. Due to collecting and weather restrictions sampling was not structured but tried to maximize diversity in each of the studied localities. Although caveats may emerge from this type of survey, it allowed us to maximize the diversity achieved per time and to recover a high percentage of the interactions. In order to check whether our sampling may have biased photobiont and/or interaction diversities, and therefore network structure we examined the degree of sampling completeness (see below).

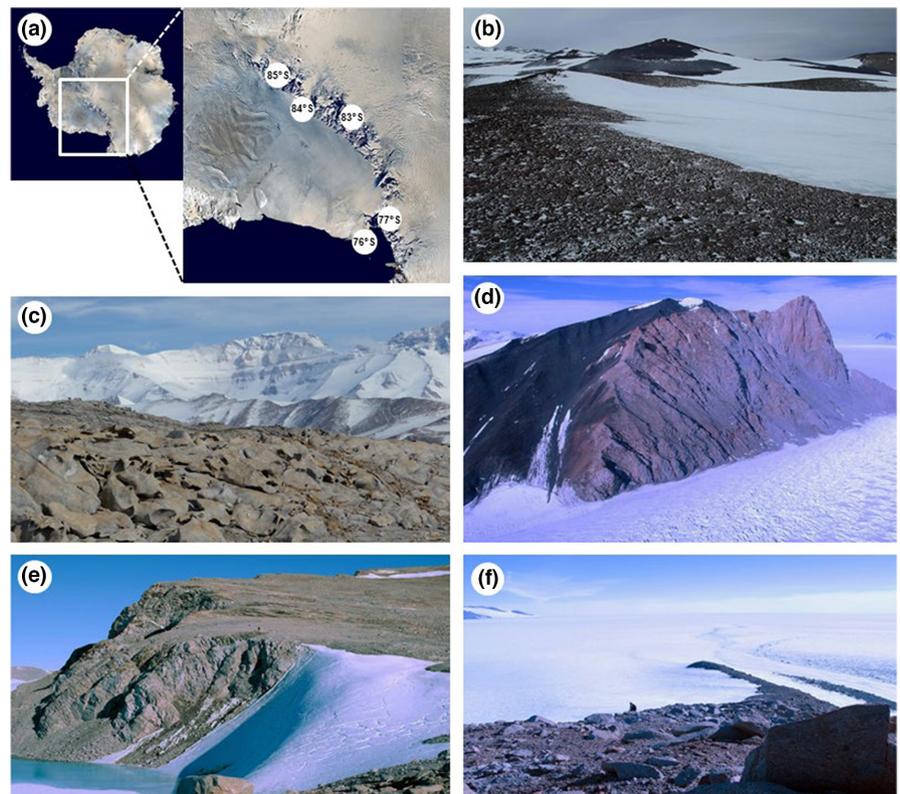


FIGURE 1 (a) Map of Antarctica, the inset and enlarged image represent the Transantarctic Mountains. White circles represent the five areas studied. (b) Cape Crozier, Ross Island. (c) The Altiplano, McMurdo Dry Valleys. (d) Mount Kyffin. (e) Shackleton Glacier, Garden Spur. (f) Durham Point, Scott Glacier. Pictures: A = Wikipedia Commons; 2, 4, 5, 6 = L. G. Sancho; 3: A. de los Ríos.

2.2 | Myco- and photobiont identification

Fungal species delimitation was done as in previous works (Pérez-Ortega et al., 2012, in prep.). Briefly, species boundaries in the 744 lichen samples were inferred with sequence data from the universal barcode for fungi (nrITS, Schoch et al., 2012) and four different, single-locus species-delimitation algorithms, combined with morphoanatomical and chemical data. In total, 76 putative species were recovered from the study area. In addition, we included seven specimens, identified as *Lepraria* sp. 1 in Pérez-Ortega et al. (in review) for which mycobiont's nrITS was not amplified but were unequivocally ascribed to that taxon based on chemical and morphological characters. Five specimens of a sterile species tentatively identified as *Eiglera flavida* were included in the dataset as well. For the identification of the associated photobionts, we mainly the nrITS region for the photobionts of the genera *Trebouxia* and *Asterochloris*. For other genera of photobionts, we used the *rbcL* or the *nrSSU* regions. Specific material and methods regarding photobiont amplification and sequencing are provided in [Supplementary Materials](#). Inferred haplotypes for each of these markers were chosen as interaction units for the photobiont guild. The rationale behind this choice is that species boundaries are not clear for the most frequent photobionts (Leavitt et al., 2015; Muggia et al., 2020), and there is evidence that photobionts isolated from Antarctic lichens, which differ slightly in their nrITS haplotypes, or even the same haplotype may show significantly different ecophysiological responses to environmental conditions (Determeyer-Wiedmann et al., 2019; Sadowsky et al., 2016).

2.3 | Sampling completeness

Since patterns in the network structure may be affected by sampling effort (Jordano, 2016) we estimated the degree of sampling completeness regarding photobiont and interaction diversity. To estimate the level of completeness, for both the regional networks and the whole area (the metaweb), accumulation of photobiont and interaction richness were estimated as sampling effort increased (Chacoff et al., 2012), based on number of mycobiont species and number of specimens. We further analysed sampling completeness for the photobiont diversity associated with each mycobiont species, focusing only on species sampled ≥ 10 times. Sampling effort was measured as the number of a) specimens examined (photobiont and interaction diversities), and b) fungal species studied (photobiont diversity). We computed the Chao2 index which is one of the least biased estimators for small sample sizes (Chao, 1987; Chao et al., 2009) and the Jackknife estimator using the *specpool* function in the R package *vegan* (Oksanen et al., 2013). The degree of completeness was calculated as the ratio between observed/estimated richness*100.

2.4 | Network architecture

Interaction matrices ($i \times j$) were built as follows: matrix rows and columns corresponded to photobionts and mycobionts, respectively.

Matrix cells representing the interaction between photobiont i and mycobiont j were filled with integers representing the frequency of interaction recorded for a particular pair of symbionts. Frequency of interactions is defined in this study as the total number of thalli in which the myco-photobiont combination was retrieved. Matrices were constructed combining localities within each of the five main regions to avoid spurious results due to small-sized networks, and for the whole area (metaweb). Networks were depicted using the command *plotweb* in the R package *bipartite* (Dormann et al., 2008). Symbiont specialization was established calculating the number of different partners from the other guild that one symbiont interacts with (species degree), and the specialization parameter d' , which provides a measure based on the Kullback–Leibler distance of the degree of discrimination that one species displays among all available partners from the other guild (Blüthgen et al., 2006). Both measures were calculated using the function *specieslevel* in the R package *bipartite* (Dormann et al., 2008). Additionally, several parameters were calculated to describe the structure of the myco-photobiont networks: (a) connectance, defined as the ratio between the realized and possible links in the network (Bascompte & Jordano, 2013); (b) nestedness, which is the pattern that arises when specialists from one guild interact with species from the other guild that represent subsets of the species with which the generalists interact. Nestedness was calculated using the index NODF (Almeida-Neto et al., 2008) in its two versions, for presence-absence and quantitative matrices (weighted NODF, wNODF; Almeida-Neto & Ulrich, 2011); (c) the index of interaction asymmetry (Vázquez et al., 2007), which provides an estimation of the dependence of one species on the species of the other guild with which it interacts with. Negative values mean a species depends more on their partners than vice versa, while positive values mean low dependency on their partners; and, finally, d) the network specialization index H_2' (Blüthgen et al., 2006), standardized from 0 (no specialization) to 1 (complete specialization, i.e. one to one interactions). All calculations were carried out using the functions *specieslevel* and *networklevel* in the R package *bipartite* (Dormann et al., 2008). Further, we calculated modularity, the presence of groups of species (modules) preferentially interacting among them and much less with other groups, using the DIRTLPAwb+ algorithm proposed by Beckett (2016) for detecting modularity (Q) in quantitative interaction networks. Due to the stochasticity of the algorithm, modularity and number of modules may vary among runs. Therefore, we retained the highest Q values as the optimum of 20 independent runs. Each run consisted in 10^{10} MCMC steps each. Significance levels for all network parameters but connectance were examined using z-scores. Random matrices (1000, or 500 in case of modularity) were generated from our datasets according to two different null models in the package *bipartite*: the '*r2dtable*' model which implements the Patefield's algorithm keeping row and column sums constant (Dormann et al., 2009; Oksanen et al., 2013) and the more conservative '*vaznull*' algorithm (Vázquez et al., 2007) which let marginal total to vary. The non-sequential '*quasiswap*' algorithm for binary matrices that retains both species and row frequencies (Miklós & Podani, 2004) was used as to create a null model

for binary NODF. z-scores were calculated as $(X_{\text{observed}} - \mu_{\text{null}}) / \sigma_{\text{null}}$, with X_{observed} being the actual value of the parameter, μ_{null} the mean of the parameter for the population of matrices in the null model, and σ_{null} their standard deviation. Finally, p-values for the z-scores were calculated as the number of elements of the null model showing higher or lower values than the observed value divided by the total number of elements in the null model. In order to assess the effect of using photobiont interaction units inferred on the basis of different genomic regions, all calculations were carried out using the whole dataset as well as a subset representing only species for which the photobiont nrITS region was available.

2.5 | Geographic variation of network structure and myco-photobiont interactions

We studied the effect of latitude on network parameters by means of linear models using the *lm* function of the *base* package in R. For each region the southernmost latitude from all collections in the area was chosen for the analyses. Regional means for mycobiont and photobiont degree and specialization d' parameters were used in the analyses as well as z-scores for the analyses of nestedness, modularity and specialization.

We calculated the turnover of myco-photobiont interactions following Poisot et al. (2012). In this framework, beta diversity of species among regions (β_W) and beta diversity of interactions (β_{WN}) are first computed. Interaction beta diversity or interaction turnover between two localities may result from changes in species compositions, i.e. one or both of the species that interacted at one locality are not present at the other locality (β_{ST}), and from the rewiring of interactions between shared species, i.e., species that interacted at one locality are present at the other locality but interact with other partners (β_{OS}), such that $\beta_{WN} = \beta_{ST} + \beta_{OS}$ (Poisot et al., 2012). Measures of beta diversity were calculated according to the equation proposed by Whittaker (1960). This equation returns a value from zero which indicates completely similar species (or interactions) between two areas, and one, completely different species between two areas. Relative contribution of each component of beta diversity was calculated as the ratios β_{ST} / β_{WN} and β_{OS} / β_{WN} (Poisot et al., 2012). Circos graphs, created using the R package *Rcircos* (Zhang et al., 2013), were used to represent interaction turnover between regions, with the width of the ribbons proportional to the variation in interaction.

3 | RESULTS

3.1 | Observed interactions and sampling completeness

In a total of 744 analysed samples belonging to 77 species of mycobionts (Table S1), we found a total of 45 different photobiont haplotypes belonging to the chlorophyte genera *Trebouxia* (39, based on nrITS data), *Asterochloris* (2, nrITS), *Diplosphaera* (2,

rbcl), *Heveochlorella* (1, *rbcl*), and *Myrmecia* (1, nrSSU). The different species delimitation algorithms grouped these haplotypes into an inconsistent number of potential species. GenBank accession numbers for each haplotype are found in Table S3. The number of photobiont haplotypes per region ranged from 19 (77° and 84°S) to 13 (76°S) (Table 1) whereas the number of mycobiont species per region ranged from 34 (77°S) to 16 (85°S). We recorded a total of 842 interaction events in the study area, with 11.4% of the samples analysed presenting two photobionts (Table S1). Latitudinally, the number of interactions ranged from 99 (85°S) to 231 (77°S) (Table 1). All networks showed a low percentage of realized links (Table 1), with connectance ranging from 0.127 (84°S) to 0.205 (76°), and 0.071 for the metaweb.

Sampling completeness differed between both levels analysed (Table S4 and S5). Chao2 and Jackknife estimators yielded similar results, so only Chao2 estimates are presented here. Regarding the total number of photobiont haplotypes, estimates based on the number of specimens showed higher levels of completeness. On average, photobiont richness was well-sampled in all regions as well as for the metaweb, with the lowest percentage of completeness achieved at the area at the highest latitude. The analyses of mycobiont species with ≥ 10 specimens showed that complete photobiont sampling was reached in 14 out of 26 species. *Buellia frigida* and *Lecidea cancriformis*, two widespread species in continental Antarctica, showed the lowest values of completeness. Regarding the diversity of interactions, estimates of completeness ranged from 67.52% at 77°S to 38.08% at 84°S, being the interactions of the whole area relatively well sampled (57.54%).

3.2 | Specialization

Mean species degree for mycobionts ranged from 2.13 ± 0.96 at 83°S to 2.81 ± 2.66 at 85°S (metaweb: 3.22 ± 2.72 ; Table 1). The mycobiont species with the highest number of partners in the metaweb were *Buellia frigida* (13), *Lecanora fuscobrunnea* (12) and *Lecidea cancriformis* (15) (Table S6) which are among the most common species in the region. Mean degree for photobionts ranged from 2.81 ± 2.45 at 85°S to 4.45 ± 5.44 at 83°S (metaweb: 5.51 ± 7.81). Photobiont haplotypes with the highest number of partners in the metaweb were TRE11 (31), TRE12 (26), and TRE27 (33) (Table S7). Although degree means were always higher for photobiont than for mycobionts, differences were not significant in any comparison (Table 1). Mean species specialization (d') for mycobionts ranged from 0.49 ± 0.27 (84°S) to 0.24 ± 0.28 (77°S) (metaweb: 0.34 ± 0.24). At the species level, d' ranged in the metaweb from 1 in highly specialized species such as the two *Lepraria* species or *Sarcogyne privigna* to 0 in species such as *Lecanora expectans* or *Carbonea* sp. 1 (Table S6). For photobionts d' ranged from 0.24 ± 0.20 (85°S) to 0.56 ± 0.28 (84°S) (metaweb: 0.47 ± 0.25). At the strain level d' ranged in the metaweb from 1 in strains such as AST1 and 2 or MYR1 to 0.08 in TRE28 or 0.11 in TRE26 (Table S6). Only the metaweb and the 77°S network showed significant differences among myco- and photobiont d' values (Table 1). The interaction asymmetry index showed values lower than 0 in all cases, indicating a

TABLE 1 Basic network descriptors.

Network	M	P	T	I	I _U	C	M ^{degree} ($\bar{x} \pm SD$)	P ^{degree} ($\bar{x} \pm SD$)	M-U	M _{d'} ($\bar{x} \pm SD$)	P _{d'} ($\bar{x} \pm SD$)	M-U	M _{ia} ($\bar{x} \pm SD$)	P _{ia} ($\bar{x} \pm SD$)	M-U
Metaweb	77	45	122	842	248	0.071	3.221 ± 2.722	5.511 ± 7.812	n.s.	0.341 ± 0.248	0.473 ± 0.253	0.001	-0.35 ± 0.395	-0.223 ± 0.412	0.03
76°	21	13	34	198	56	0.205	2.667 ± 1.56	4.58 ± 4.366	n.s.	0.316 ± 0.28	0.488 ± 0.296	n.s.	-0.253 ± 0.345	-0.16 ± 0.459	n.s.
77°	34	19	53	231	83	0.128	2.441 ± 1.91	4.368 ± 6.094	n.s.	0.243 ± 0.285	0.391 ± 0.296	0.02	-0.435 ± 0.424	-0.213 ± 0.431	0.05
83°	27	16	43	180	56	0.193	2.13 ± 0.968	4.454 ± 5.447	n.s.	0.247 ± 0.236	0.428 ± 0.329	n.s.	-0.399 ± 0.417	-0.257 ± 0.595	n.s.
84°	24	19	43	134	58	0.127	2.417 ± 1.471	3.053 ± 2.656	n.s.	0.491 ± 0.277	0.56 ± 0.276	n.s.	-0.229 ± 0.381	-0.142 ± 0.442	n.s.
85°	16	16	32	99	45	0.175	2.812 ± 2.664	2.812 ± 2.455	n.s.	0.251 ± 0.15	0.241 ± 0.202	n.s.	-0.432 ± 0.541	-0.403 ± 0.542	n.s.

Note: M: Number of mycobiont species in the network; P: Number of photobiont haplotypes; T: Total number of nodes in the network (M+P); I_U: Total number of unique interactions; C: Connectance (I/MP × 100); M^{degree}: Mycobiont species degree, mean ± standard deviation; P^{degree}: Photobiont species degree, mean ± standard deviation (SD); M-U: Mann-Whitney test. M_{d'}: Mycobiont species specialization parameter d'; mean ± standard deviation. P_{d'}: Photobiont species specialization parameter d', mean ± standard deviation. M_{ia}: Mycobiont species interaction asymmetry parameter; mean ± standard deviation. P_{ia}: Photobiont species interaction asymmetry parameter; mean ± standard deviation.

strong, reciprocal dependence of both groups. However, mycobionts always presented lower values than photobionts, which may indicate a greater dependence on photobionts than vice versa. Significant differences between myco- and photobionts were only detected in the metaweb and the 77°S region.

3.3 | Network architecture

Since most patterns found in the subsequent analyses were congruent between both null models used, only the results obtained using the most restrictive *vaznull* model are shown in Table 2 (see results corresponding to the *r2dtable* in Table S8). All analysed quantitative networks (Figure 2) showed lower nestedness values than expected by chance (*wNODF*), except the 85° S network, which was slightly higher than the *vaznull* model (Table 2; Table S8). This pattern of low nestedness is often referred in the literature as antinestedness. *NODF* values calculated for binary networks were broadly consistent with this pattern although z-scores pointed to a much less pronounced pattern (Table S5). All analysed networks exhibited high and significant modularity (Table 2, Table S9). Number of modules ranged from 11 in the metaweb to 4 (85°S) (Figure 3, Figure S1). Network specialization (H_2') was significantly higher than expected by chance in all networks, ranging from 0.665 (84°S) to 0.333(85°S) (Table 2, Table S9). Analyses carried out on the dataset including only nrITS haplotypes (*Trebouxia* and *Asterochloris* haplotypes) yielded almost similar results, discarding a genetic marker effect on the observed patterns (Tables S10-S12).

3.4 | Geographic variation of myco-photobiont interactions

We did not find any significant effect of latitude in any of the species or network parameters studied (Table S13). The beta diversity of interactions was large for all regions (Figure 4a), with a maximum between the 77°S and 83°S regions, which do not share any interaction. The rewiring component (β_{OS}) was significantly greater than the species turnover component (β_{ST}) (*t*-test = 3.531, *df* = 18, *p* < 0.01; Figures 4b,c).

4 | DISCUSSION

In this study we have built interaction networks for saxicolous communities of lichen-forming fungi and their photosynthetic partners in five regions along a latitudinal transect in the Transantarctic Mountains (76–85°S). The architectural properties of the analysed networks were recovered as invariant along that transect.

4.1 | Species level

The number of partners with which myco- and photobionts interact (species degree), varied considerably within each guild along the

TABLE 2 Network weighted nestedness (wNODF), quantitative modularity (Q) and specialization (H_2').

Network	wNODF	wNODF _{vaznull} ($\bar{X} \pm SD$)	z-score	Sig.	Q	N	Q _{vaznull} ($\bar{X} \pm SD$)	z-score	Sig.	H_2'	H_2' _{vaznull} ($\bar{X} \pm SD$)	z-score	Sig.
Metaweb	13.38	22.99 ± 1.96	-4.91	0.000	0.54	11	0.26 ± 0.01	23.07	0.000	0.49	0.25 ± 0.02	14.81	0.000
76°	18.55	35.96 ± 4.45	-3.91	0.000	0.48	6	0.24 ± 0.02	10.04	0.000	0.48	0.22 ± 0.03	7.55	0.000
77°	25.2	31.11 ± 3.8	-1.56	0.055	0.33	9	0.24 ± 0.02	4.53	0.000	0.32	0.22 ± 0.03	3.24	0.000
83°	20.86	31.1 ± 4.65	-2.20	0.005	0.44	5	0.27 ± 0.03	5.75	0.000	0.53	0.3 ± 0.04	5.5	0.000
84°	5.48	13.9 ± 2.41	-3.49	0.000	0.67	9	0.46 ± 0.04	5.62	0.000	0.66	0.43 ± 0.04	6.3	0.000
85°	24.33	24.23 ± 4.27	0.02	0.515	0.43	4	0.33 ± 0.03	3.11	0.000	0.33	0.27 ± 0.043	1.43	0.000

Note: Mean (\bar{X}) and standard deviation (SD) are given for all null models (vaznull) based on 1000 iterations. z-score: $(\text{NODF} - \bar{X}_{\text{nullmodel}}) / \text{SD}_{\text{nullmodel}}$; sig: significance of the z-score. N: number of modules.

whole transect. Although photobionts showed higher mean values than mycobionts, these differences were not statistically significant (Table 1). Interestingly, photobionts showed higher values for the specialization parameter d' . This means that although the average photobiont strain interacts with a larger number of partners than a mycobiont species, these interactions are more selective considering the total number of available partners. There are few studies that have analysed the specialization of fungal-algal relationships in lichen symbioses considering whole communities, and furthermore few have considered the photobiont point of view. Yahr et al. (2004) showed that in Florida scrublands photobiont strains (ITS haplotypes) interacted, on average, with fewer *Cladonia* species compared to the number of photobionts with which those species interacted. However, this pattern may change when photobionts are considered at the species rather than the haplotype level (Magain et al., 2017; Singh et al., 2017; Werth, 2012). Thus, it seems that there are relevant differences in terms of specialization in lichen-forming fungi and their photosynthetic partners depending on the phylogenetic scale used to delimit the photobionts. Increasing evidence from ecophysiological studies points to relevant differences between closely related photobiont ITS haplotypes (Determeyer-Wiedmann et al., 2019; Gasulla et al., 2019; Sadowsky et al., 2016), which would support the use of algal haplotypes as a basis for ecological studies in specialization. It should be noted that specialization in lichen-forming fungi has traditionally been treated from the point of view of specificity, understood as the phylogenetic range of photobionts with which a species interacts (Rambold et al., 1998; Pardo-De la Hoz et al., 2022 for a more modern approach) and selectivity, the local preferences among all compatible photobionts. Our approach focuses on the total number of partners with which a species interacts, independently of their phylogenetic affinities, and on the specialization parameter d' , which quantifies how much a species discriminates when choosing partners among all those available, an analogous measure of selectivity. Our findings show a wide range of specialization strategies, from species with great versatility in the range of compatible algae, such as widely distributed and abundant species like *Lecidea cancriformis* or *Buellia frigida*, to species that show highly specialized interactions, such as the two *Lepraria* species found in the study area, thus supporting the results obtained in previous studies conducted in the lichen communities of the McMurdo Dry Valleys (Pérez-Ortega et al., 2012). Interestingly, these results are contrary to what has been found for fungal-cyanobacteria relationships in cyanolichens from maritime Antarctica (Wirtz et al., 2003) and what has been found for the genus *Protoparmelia*, in which it appears to show a higher degree of specialization in warm areas than in colder areas Singh et al. (2017).

We did not detect interaction asymmetry between myco- and photobionts, and although photobionts had on average higher values, all were below zero, indicating a high dependency among the two guilds. Vázquez et al. (2007) showed that asymmetry is a high prevalence pattern in both mutualistic and antagonistic interactions, with one of the guilds exerting much stronger effect on their partners than the other. Symmetric interactions, as those recorded in all our networks, suggest high potential for ecological and co-evolutionary

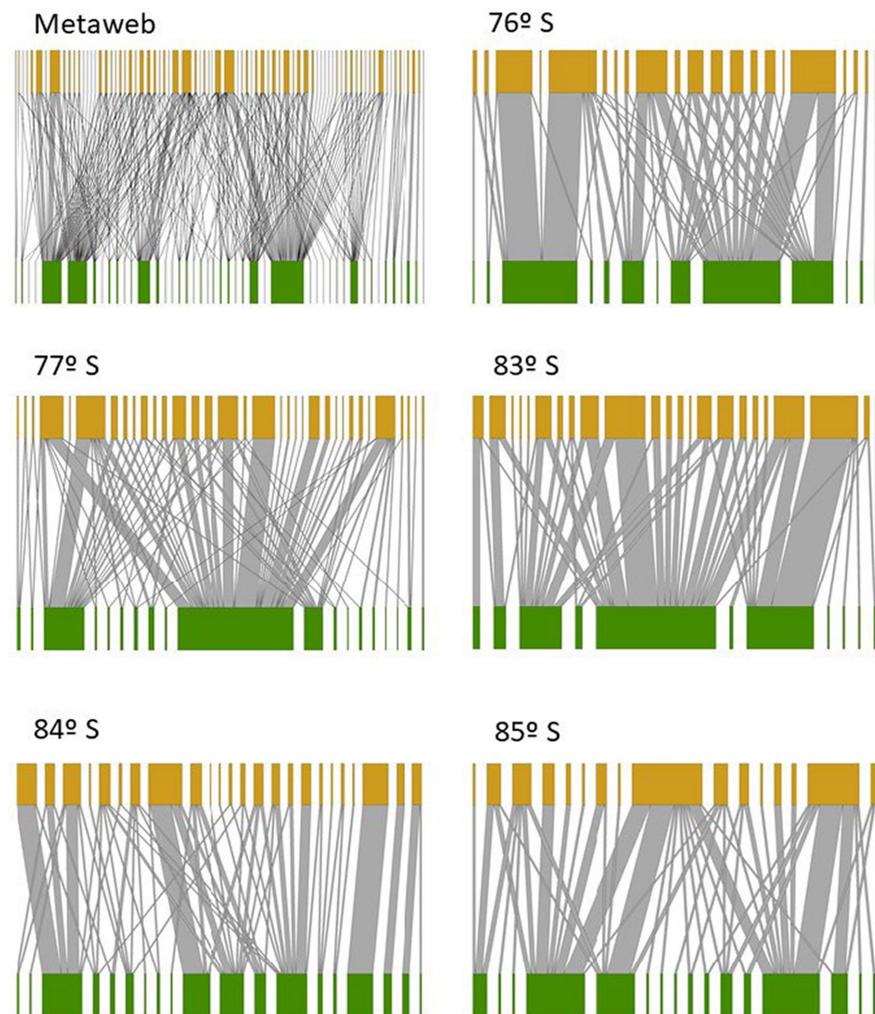


FIGURE 2 Bipartite network showing all interactions recorded on the five regions studied and the metaweb. Orange nodes represent the mycobionts, and green nodes depict the photobionts. Node size is proportional to its abundance in the dataset. Thickness of links is proportional to the interaction frequency between two nodes.

coupling of populations of both bionts (Vázquez et al., 2005), and are highly congruent with the modular structure recovered for all networks and the existence of groups of mycobionts and photobionts that preferentially interact with each other (see below). However, mutual dependence is difficult to reconcile with the existence of free-living populations of photobionts (Mukhtar et al., 1994; Sanders, 2005; but see Ahmadjian, 1988). Chagnon et al. (2018) also found a lack of asymmetry when the interactions between species of the genus *Peltigera* and their cyanobionts were considered at a global scale. Interestingly, this pattern disappeared at the local scale, with local generalist cyanobacteria gathering most of the interactions. We did not find variation between the patterns found and the regional scale and when the whole transect were considered. Asymmetry is largely affected by abundance and species diversity in both guilds (Vázquez et al., 2007) so we could expect different results if photobionts are considered at the species rather than the haplotype level.

4.2 | Network level

All the interaction networks showed similar architectural properties along the latitudinal transect, i.e. low connectance, low

nestedness (both in binary and weighted networks), as well as high modularity and specialization. Sampling completeness of interactions in each region or the metaweb was moderate. The circumstances accompanying sampling in this type of localities (unpredictable and changeable weather with extremely low temperatures and strong winds) prevented more structured and systematic sampling; however, moderate integrity of interactions has been reported in other systems analysed in milder areas (Chacoff et al., 2012), so we believe that the properties reported for the studied networks represent inherent properties rather than sampling artefacts. In addition, most network metrics (nestedness, modularity) are robust to sampling incompleteness, although others like connectance may suffer to a greater extent (Rivera-Hutinel et al., 2012). Low connectance values as those found in our networks have been related with high levels of specialization (Fortuna et al., 2010). Our results are in line with theoretical predictions for organisms interacting with high intimacy, i.e. low connectivity, low levels of nestedness and high reciprocal specialization (modularity; Guimarães Jr et al., 2007; Pires & Guimarães Jr, 2013; Thompson, 2005, 2014). Although high specialization is a typical feature of high intimacy interactions, other biological systems such as in a number of parasites may also present high specialization

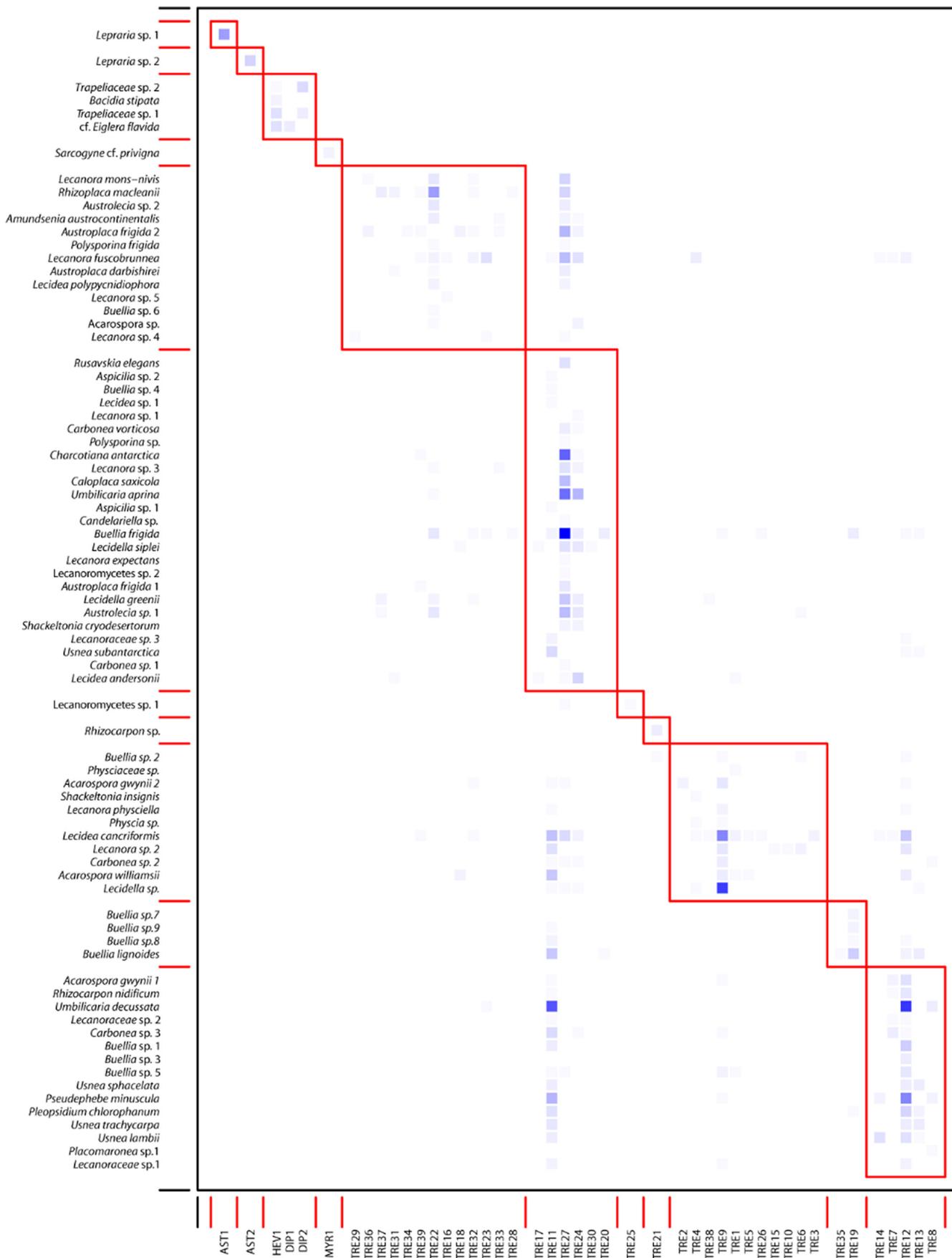


FIGURE 3 Metaweb modularity plot.

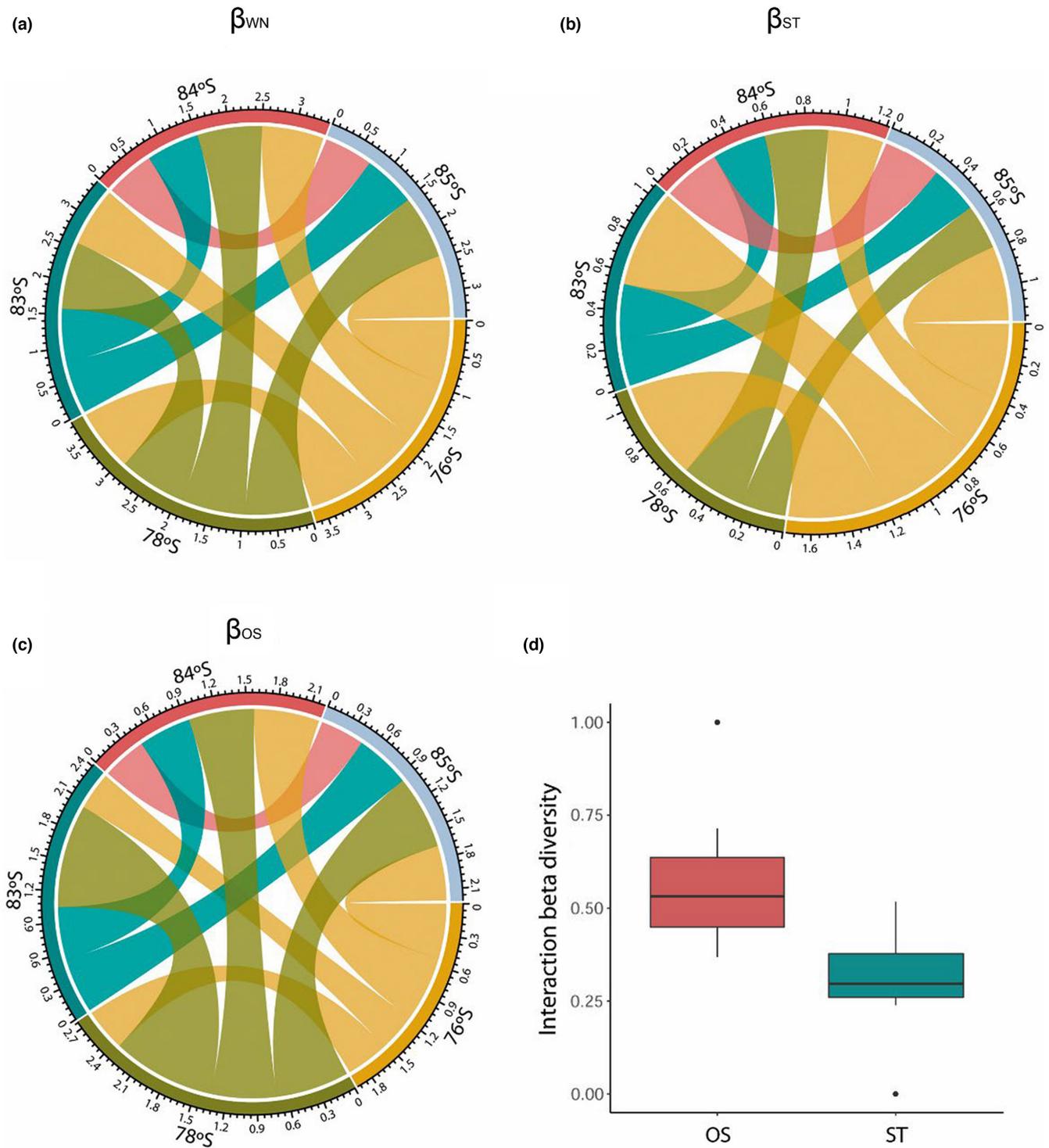


FIGURE 4 Interaction turnover. (a) Total interaction turnover (β_{WN}); (b) Interaction turnover due to changes in species composition (β_{ST}); (c) Interaction turnover due to rewiring (β_{OS}); (d) Boxplot showing differences between β_{ST} and β_{OS} .

without high intimacy (Poulin, 2011; Vázquez et al., 2005). At low connectivity, nestedness and modularity shows a highly negative correlation (Fortuna et al., 2010). Thus, the pattern of high specialization found in our networks, reflected in a significantly modular structure together with the low connectance shown is translated in a low nestedness pattern. In our data set, there are no generalist species groups with which specialists from the other guild also

interact (nestedness), but rather there are several groups of myco- and photobionts (11 in the metabar) that preferentially interact with each other. Interestingly, although a few photobiont haplotypes (TRE11, TRE12, and TRE27) are highly connected and can be considered generalists, the overall pattern is one of high specialization. This could be interpreted to mean that these haplotypes have great versatility in terms of compatibility with different mycobiont

species, but that possibly the interaction fitness is almost never optimal and different mycobiont species prefer locally adapted algal haplotypes. However, these generalist algal haplotypes would assume the important role of connectors of different modules of the networks. Low nestedness and high modularity has been reported in several studies on plant-fungus interactions (Jacquemyn et al., 2015; Martos et al., 2012; Toju et al., 2014, 2018) suggesting that networks of fungi forming symbioses result into fixed network architecture properties (Toju et al., 2018). However, opposite patterns have been also found (Chagnon et al., 2012; Jacquemyn et al., 2011), including some studies on arbuscular mycorrhizae that found both high nestedness and modularity (Montesinos-Navarro et al., 2012) or no structure at all (Encinas-Viso et al., 2016). Pölme et al. (2017) analysed 111 published datasets involving plant-fungal interactions and pointed that orchid-fungal associations have stronger host preferences than ectomycorrhizae, arbuscular mycorrhizae or root endophytes, which results in more modular interaction networks. Nestedness also varied across fungal lifestyles with leaf endophytes being the most nested plant-fungal communities. However, comparisons among groups are difficult because of the different study designs and analytical methods were used to build the interaction networks and the strong effect of singletons (Pölme et al., 2017). Thus, taking into account the great variability of network structure in other fungal groups, the question arises whether the patterns we have found in our fungal-algal networks in Antarctica are general properties of all lichen communities, or whether they are specific to interactions between lichen bionts in this type of extreme environment. Werth (2012), in her study of photobionts in an epiphytic lichen community on *Quercus* in western North America, found that the myco-photobiont network was not nested when mycobionts and photobionts were considered at the species level, but when photobionts were considered at the haplotype level, as in our analyses, the resulting network was significantly nested in the less stringent null models, indicating a clear difference with our saxicolous communities occurring in these extreme habitats. Chagnon et al. (2018) studied the structure of *Peltigera* species in the section *Polydactylon* with their cyanobacteria symbionts at different geographic scales. Although these authors only focused on relationships between species within a genus they found, similar to our findings, that myco-cyanobiont networks were highly modular and showed an antinestedness pattern. The modular structure of our interaction networks is consistent with the lichen guild hypothesis (Rikkinen et al., 2002), i.e., the existence of preferentially interacting groups of mycobionts and photobionts (modules) in lichen communities, which has been observed both in communities of species interacting with cyanobacteria (Kaasalainen et al., 2021; Rikkinen et al., 2002) and for interactions of species interacting with green algae (Peksa et al., 2022). Lichen guilds represent a community-scale phenomenon that is related to substrate and patch characteristics (Peksa et al., 2022; Rikkinen et al., 2002). The presence of modules in interaction networks entails high possibilities of coevolution (Guimarães Jr et al., 2007; Pires & Guimarães Jr, 2013; Thompson, 2005) and future studies

should analyse the coevolutionary structure of interaction networks in lichens.

4.3 | Latitudinal trends and interaction β -diversity

No trend regarding latitude and network parameters were observed although the two southernmost regions showed higher nestedness than the remaining localities, results that may stem from their low species diversity. Overall, interaction turnover between regions was very high, with no interactions shared between the 77° and 83°S. This high turnover could point to low connectivity between regions, however, the higher relevance of rewiring (β_{OS}) in the total turnover, i.e. bionts are shared between localities but interactions differ, points to photobiont switch, either by dispersal of a single biont or change after settlement of vegetative propagules, is high in the studied area. In our study, there is a higher number of species with sexual reproduction (77.92%) in which the fungus disperses individually than species with reproduction by vegetative propagules in which the two bionts are co-dispersed, which may favour turnover of interactions due to rewiring. In addition, dispersal by vegetative propagules may maintain partner interactions at the locality of propagule arrival, but a subsequent photobiont shift may also occur once the propagule has settled (Nelsen & Gargas, 2008). Although high rewiring could correspond to high levels of stochastic dispersion (Romeike et al., 2002), the high specialization and modularity shown in all networks seems to indicate that other underlying causes, such as phylogenetic structure together with environmental filtering promoting a higher abundance of locally adapted genotypes, may explain the observed pattern. In addition, based on microsatellite data the low dispersal of one of the most common species in continental Antarctica, *Buellia frigida*, has been reported (Jones et al., 2015), which could lead to the existence of local modules.

Lichen communities are more dependent on microclimatic than macroclimatic conditions, and this is especially true in continental Antarctica (Sancho et al., 2019). Although microclimate may buffer the impact of expected changes in lichen communities due to global warming (Suggitt et al., 2018), it is likely that global warming will lead to changes that modify community composition as well as myco-photobiont interactions. Future studies should address the role of climate change in altering the structure of interaction networks and their resilience to such changes, as well as whether these changes may pose a threat to the sustainability of interaction and biont diversity in continental Antarctica.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the [Supplementary Material](#) of this article. Photobionts haplotype sequences generated during this study are deposited in Gen Bank.

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BIOSKETCHS

The majority of the authors of this research article (Sergio Pérez-Ortega, Isaac Garrido-Benavent, T. G. Allan Green, Leopoldo G. Sancho and Asunción de los Ríos) have conducted extensive studies on the diversity of lichens in Antarctica over the past few decades, approaching the subject from various angles. Their investigations have encompassed areas such as the physiological adaptations of lichens to the most extreme conditions found on Earth, the relationship between saxicolous lichens and their substrates, the remarkable variety of lichen-forming fungi in Antarctica, resulting in the identification of numerous novel species, and the phylogeography of Antarctic lichen species, shedding light on the origins of the current lichen communities in Antarctica. Furthermore, certain members of the research group (T. G. Allan Green, Leopoldo G. Sancho and Asunción de los Ríos) possess a wealth of experience gained from their involvement in Antarctic expeditions, some spanning over five decades. Finally, the remaining members (Miguel Verdú and Sonia Rabasa) are esteemed ecologists with extensive expertise in the study of ecological interaction networks and statistical analysis.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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