Myco- and photobiont associations in crustose lichens in the McMurdo Dry Valleys (Antarctica) reveal high differentiation along an elevational gradient

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Abstract

Climatically extreme regions such as the polar deserts of the McMurdo Dry Valleys (78° S) in Continental Antarctica are key areas for a better understanding of changes in ecosystems. Therefore, it is particularly important to analyze and communicate current patterns of biodiversity in these sensitive areas, where precipitation mostly occurs in form of snow and liquid water is rare. Humidity provided by dew, clouds, and fog are the main water sources, especially for rock-dwelling crustose lichens as one of the most common vegetation-forming organisms. We investigated the diversity and interaction specificity of myco-/photobiont associations of 232 crustose lichen specimens, collected along an elevational gradient (171–959 m a.s.l.) within the McMurdo Dry Valleys. The mycobiont species and photobiont OTUs were identified by using three markers each (nrITS, mtSSU, *RPB1*, and nrITS, psbJ-L, COX2). Elevation, positively associated with water availability, turned out to be the key factor explaining most of the distribution patterns of the mycobionts. Pairwise comparisons showed *Lecidea cancriformis* and *Rhizoplaca maclearii* to be significantly more common at higher elevations and *Carbonea vorticosa* and *Lecidea polypycnidophora* at lower elevations. Lichen photobionts were dominated by the globally distributed *Trebouxia* OTU, *Tr_A02* which occurred at all habitats. Network specialization resulting from myco-/photobiont bipartite network structure varied with elevation and associated abiotic factors. Along an elevational gradient, the spatial distribution, diversity, and genetic variability of the lichen symbionts appear to be mainly influenced by improved water relations at higher altitudes.

Keywords Crustose lichens · Specificity · Spatial patterns · Polar desert · Foehn winds · Humidity

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Introduction

The McMurdo Dry Valleys (MDV) in Southern Victoria Land, Continental Antarctica, are characterized by an environment that is exceptional even for Antarctica: it is extremely arid and cold, which makes it hostile for most organisms. Thus, life is rare within the valleys of this polar desert, and only few life forms can cope with these extreme conditions (e.g., Adams et al. 2006; Pointing et al. 2009). The main limiting factor for life within the MDV is water availability with fog, clouds, dew, and ephemeral melting water of snow patches having important effects on the climatic conditions (Pannewitz et al. 2005; Adams et al. 2006; Green et al. 2007; Stichbury et al. 2011). Among the most diverse macro-organisms present in the MDV are lichens. Lichens represent a classic example of symbiosis, consisting of a fungus (mycobiont) and one or more photosynthetic partners (photobiont). When completely desiccated, lichens

are dormant and can survive unfavorable conditions for long periods (Kappen and Valladares 2007; Green 2008). Consequently, they are able to colonize rocks and boulders above melting streams or in the vicinity of snow patches, even in such extreme environments as the MDV (e.g., Hertel 2007; Ruprecht et al. 2010, 2012a; Schroeter et al. 2010; Green et al. 2011b; Sancho et al. 2017). The most successful species are green-algal lichens, as they do not depend on the presence of liquid water for reactivation and can be active below zero degrees, in contrast to cyanobacterial lichens that appear to be completely absent in continental Antarctica (Lange et al. 1986; Schlensog et al. 1997; Kappen 2000; Seppelt et al. 2010; Green et al. 2011a).

Several studies on mycobiont–photobiont interactions in lichens have shown that green-algal as well as cyanobacterial lichenized fungi can show considerable photobiont variability and can have more than one photobiont and even combine green alga and cyanobacteria (Nelsen and Gargas 2009; Otalora et al. 2010; Wornik and Grube 2010; Fernández-Mendoza et al. 2011; Henskens et al. 2012; Ruprecht et al. 2014; Engelen et al. 2016). Low photobiont specificity and a high ability to accept different photobionts might be a survival strategy and extend the ecological range of lichens (Wirtz et al. 2003; Blaha et al. 2006; Ruprecht et al. 2012a; Leavitt et al. 2015; Dal Grande et al. 2017). Furthermore, photobiont selection appears to be influenced by abiotic factors like climate (Beck et al. 2002; Yahr et al. 2006; Fernández-Mendoza et al. 2011; Peksa and Skaloud 2011). At the local scale (for instance along elevational gradients), this may translate into habitat-specific photobiont switches (Vargas Castillo and Beck 2012). Above all, temperature has often been identified as a key factor for photobiont selection of lichens in Antarctica (Kappen and Valladares 2007; Green 2008; Ruprecht et al. 2012a). In warmer regions, myco-/photobiont interactions show increased specificity leading to one-to-one interactions in contrast to more generalist interactions in colder environments (Singh et al. 2017). Thus, it appears that symbiotic interactions in lichens can react very sensitively to environmental change although this conclusion is based on a small database, and these responses have been investigated only in a few species (Colesie et al. 2014b; Allen and Lendemer 2016; Sancho et al. 2017). In general, there is agreement that climatic changes will influence the diversity, abundance, and growth of lichens (Sancho et al. 2017) and that lichens therefore represent excellent bioindicators for processes associated with global warming (Alatalo et al. 2015; Allen and Lendemer 2016; Bassler et al. 2016; Sancho et al. 2019).

Over the last decades, studies on elevational gradients have re-emerged because the species composition changes remarkably with elevation suggesting a species-specific adaptation to different environmental conditions (Grytnes et al. 2006). They provide steep ecological transitions (e.g.,

in temperature, humidity, and UV radiation) over short distances (Körner 2007; Keller et al. 2013) and several studies suggest that the structure and diversity of communities, the abundance and distribution of species, and ecosystem properties and processes can change along elevational gradients (Wolf 1993; Körner 2003; Grytnes et al. 2006; Bassler et al. 2016; Dal Grande et al. 2017; Junker and Larue-Kontic 2018). For lichens, elevational gradients are reported to show large changes in species composition (Leavitt et al. 2015; Dal Grande et al. 2017), habitat-specific photobiont switches (Vargas Castillo and Beck 2012), and/or microclimatic partitioning of ecologically differentiated fungal and algal gene pools (Nadyeina et al. 2014).

This study focuses on saxicolous crustose lichens in continental Antarctica which are associated with green micro alga as photobionts. In general, these lichens are slow growing and restricted to microhabitats on rock surfaces (Hertel 1998), but nevertheless, due to their poikilohydric nature, they are well adapted to habitats with high insolation and with rapid fluctuations in temperature and water availability (Lange 1997, 2000; Green et al. 2002; Schroeter et al. 2011). Most of the lichens analyzed here belong to the “lecideoid” lichen group (Hertel 1984) and these species are assigned to the generic name *Lecidea sensu* Zahlbruckner (1925) but they do not necessarily belong to the genus in its strict sense. Due to their inconspicuous growth form, distinguishable only by a few small morphological traits such as spore size and ascus type, the identification of these lichens is difficult even under best growing conditions (Ruprecht et al. 2020). Extreme climate conditions in cold deserts result in reduced development of the thallus such as chasmolithic growth, a lack of ascomata, or sparsely developed ascospores, all features that hamper identification and even the detection of the specimens in the vast landscape (Hertel 2009; Ruprecht et al. 2010). Nevertheless, these pioneers on rocks and pebbles (Hertel 1984, 1987) belong to one of the most abundant species groups in continental Antarctica (Hertel 2007; Ruprecht et al. 2010, 2012b) and are, therefore, an excellent study system to investigate changes in symbiotic associations along gradients. The present study covers lecideoid lichen species of the genera *Carbonea* Hertel, *Lecanora* Ach., *Lecidella* Körb., *Rhizoplaca* Zopf, and the genus *Lecidea* Ach s.str. (Hertel 1984) plus, in addition, lichen samples of the genera *Austrolecia* Hertel, *Buellia* De Not., and *Huea* C.W. Dodge & G.E. Baker which were included, because they often have a similar appearance.

The aim of this study was to analyze the spatial pattern and factors that might affect the distribution of both symbiotic partners within the MDV. We addressed the following objectives: (1) to confirm and extend our knowledge of the abundances of the myco- and photobiont species that have been found by previous, less extensive studies, (2) to investigate the variability of myco-/photobiont interactions, in

particular, analyze the level of selectivity by using network statistics, and (3) to study for mycobionts, photobionts and lichens the relationships with abiotic and climatic factors such as elevation and water status.

Materials and methods

Study area and sampling sites

This study was conducted as part of the New Zealand Terrestrial Antarctic Biocomplexity Survey (nzTABS, <https://nztabs.ictar.aq>), which was initiated during the International Polar Year 2007–2008, and drew a diverse range of international expertise to profile the biology, geochemistry, geology, and climate of the MDV. The study is among the most comprehensive landscape-scale biodiversity surveys undertaken and includes nearly all trophic components found in the MDV ecosystem (Lee et al. 2019). Sampling of soils and biological communities was carried out over two successive Austral summers (2009/10, 2010/11). The geographic area within which lichen samples were collected was the southern part of the MDV (total area: 22,700 km², ice-free area: 4500 km²; Levy 2013; Fig. 1a, b). The landscape is a mosaic of glacially formed valleys with intervening high ground, ice-covered lakes, ephemeral streams, arid rocky soils, ice-cemented soils, and surrounding glaciers along the steep scree and boulder slopes (Fig. 1b–d; Doran et al. 2002; Stichbury et al. 2011; Yung et al. 2014). There are four main valleys (Miers Valley, Garwood Valley, Hidden Valley, and Marshall Valley) and some other extensive ice-free areas (Shangri-La). The topography ranges from sea level to more than 2000 m a.s.l. with granite being the dominant rock type on the ridges and hills, while the valley floors are covered with glacial drift. The valleys have the typical glaciated form with a U-cross-section with steep sides, often with scree slopes, which reach up to around 600 m in height. To the west, the valleys are separated from the polar plateau by the Royal Society Range that has peaks over 4000 m a.s.l. in height. To the east, the valleys open out onto the Ross Ice Shelf, which represents a climatically maritime influenced location within the MDV, despite the absence of ice-free sea at any time of the year (Yung et al. 2014).

Climate of the McMurdo Dry Valleys

The climate of the MDV is, for several reasons, classified as that of a polar desert. First, the mountains at the west are sufficiently high to block seaward flowing ice from the East Antarctic ice sheet from reaching the Ross Sea. In addition, the Transantarctic Mountains provide a precipitation shadow, causing an extremely low humidity and lack of snow or ice cover in the MDV (Monaghan et al. 2005).

Annual precipitation is < 50 mm a⁻¹ water equivalent, with precipitation decreasing away from the coast (Fountain et al. 2010). The major source of liquid water is the seasonal melting of perennial snowbanks and glaciers (Stichbury et al. 2011; Head and Marchant 2014) but, in most cases, this water is not available for lichens that inhabit rock surfaces above the surrounding ground level. MDV climate is best known from the northern valleys, particularly Taylor Valley, because of the McMurdo Long-Term Ecological Research programme (McMurdo LTER) that has been active since 1993 (<https://www.mcmlter.org>). The valley floors of the MDV show annual mean temperatures that range from – 30 to – 15 °C and typically have fewer than 50 days a⁻¹ where average temperatures exceed 0 °C (Doran et al. 2002; Ochrya 2008; Colesie et al. 2014b). There is agreement that the air temperature lapse rate is close to 1 °C decline per 100 m elevation rise, as well as an increase with distance inland from the coast of 0.09 °C per 1 km (McKay 2015). The aspect of the valley slopes has an important impact: north facing slopes are warmer and dryer, south facing slopes are cooler and wetter (Yung et al. 2014). The wind regime is strongly topographically channeled and directed mainly up- or downvalley. During summer, easterly valley winds dominate, due to differential surface heating between the low albedo valley floors and the high albedo ice to the east (Mckendry and Lewthwaite 1990). In winter, wind direction is typically more variable. Cold air pools associated with light winds and very low minimum temperatures (– 50 °C) often occupy topographic low points of the valleys during winter (Doran et al. 2002).

Almost all climate information comes from studies on the valley floors. There are, however, conditions that tend to produce a major difference in water regime between valley floors and intervening mountain ranges. First, there is a tendency at higher elevations for greater snowfall and higher humidity, as shown by the presence of clouds at higher elevations (Fig. 1d). Second, there is the regular occurrence within the valleys of what have traditionally been regarded as katabatic winds (Mckendry and Lewthwaite 1990; Ayling and McGowan 2006) but which are now suggested to be foehn winds albeit generated in a slightly different manner to the classic northern hemisphere foehns (Speirs et al. 2010). In the Taylor Valley, for example, these winds are easily recognizable by their sudden arrival, high intensity (around 15 m s⁻¹), rapidly rising temperature (by around 25 °C to reach about 0 °C), and rapidly falling relative air humidity to around 20% (Speirs et al. 2010). These foehn winds also occur in the southern valleys with an example from Miers Valley (Online Resource 2a) showing almost identical characteristics to those in the Taylor Valley. Foehn winds are extremely drying with air vapor pressure deficit rising about 50 times from 0.01 kPa (– 30 °C, 80% RH) to 0.49 kPa (0 °C, 20%

Fig. 1 **a** Antarctic continent; investigated area marked with red rectangle (Natural Earth, Qgis), **b** MDV sampling sites defined in four areas (<https://www.gpsvisualizer.com>), **c** Garwood Valley and field

camp, **d** Garwood Valley with incoming cloud bank, **e** *Lecidea cancriformis*, **f** *Rhizoplaca macleanii*, **g** *Austrolecia* sp. 1

RH). They are also topographically constrained within the valleys and can apparently reach altitudes up to almost 500 m (Speirs et al. 2010). The net result of the higher elevation cold, moister air, and the extremely drying foehn winds within the valleys is that the wetness availability gradient is strongly non-linear and, for the purposes of our analyses, we defined an elevational threshold of about

600 m a.s.l. which marks the upper limit of the steeper valley sides.

Sample sources

The present study includes 232 lichen samples (lecidoid lichen species of the genera *Carbonea*, *Lecanora*, *Lecidella*,

Rhizoplaca, *Lecidea*, and additionally *Austrolecia*, *Buellia* and *Huea*, which have a similar appearance under these extreme climate conditions) collected in four different areas (Hidden Valley, Miers Valley, Shangri La, and Garwood Valley) at 153 different localities with a range of aspects (N-facing slopes, flat areas, and plateaus) and elevations (171–959 m a.s.l.; Fig. 1a–g, Table 1). 154 specimens were collected between the years 2009 and 2011 by Ulrike Ruprecht and Roman Türk and are deposited at the herbarium of the University of Salzburg (SZU, Online Resource 1a). An additional 78 lichen samples from the same area were obtained from the study of Pérez-Ortega et al. (2012) excluding specimens of the genera *Acarospora*, *Caloplaca*, *Polysporina*, *Sarcogyne*, and *Umbilicaria* (see Online Resource 1b).

Please note that for most of the data evaluations, mycobionts, and photobionts were treated separately. In some analyses (noted in text), only mycobiont species with $n \geq 10$ (*min10MycSp*) were used, while others included only photobiont haplotypes with $n \geq 10$ (*min10PhoHap*).

DNA-amplification, purification, and sequencing

Total DNA was extracted from the thallus and/or apothecia by using the DNeasy Plant Mini Kit (Qiagen) following the manufacturer's instructions. For all samples, we sequenced and amplified the internal transcribed spacer (ITS) region of the mycobionts' and photobionts' nuclear ribosomal DNA (nrITS). We also amplified additional markers: for the mycobionts the mitochondrial small subunit (mtSSU) and the low-copy protein coding marker RPB1 and, for the photobionts, the chloroplast-encoded intergenic spacer (psbJ-L) and part of the cytochrome oxidase subunit 2 gene (COX2). This was done using newly developed specific primers and PCR-protocols in our project framework (Ruprecht et al. 2020).

For amplifying nrITS of the mycobiont, we used the primers ITS1 (White et al. 1990), ITS1F (Gardes and Bruns 1993), ITS1L (Ruprecht et al. 2020), ITS4 (White et al.

1990), ITS4L (Ruprecht et al. 2020), and for the photobiont 18S-ITS uni-for (Ruprecht et al. 2012a), ITS1T (Kroken and Taylor 2000), ITS1aT (Ruprecht et al. 2014), ITS4T (Kroken and Taylor 2000), and ITS4bT (Ruprecht et al. 2014). For the marker mtSSU, the primers CU6 (<https://nature.berkeley.edu/brunslab/tour/primers.html>), mrSSU1 (Zoller et al. 1999), mtSSU for2 (Ruprecht et al. 2010), and mtSSU rev2 (Ruprecht et al. 2010) and for *RPB1*, fRPB1-C rev (Matheny et al. 2002), gRPB1-A for (Matheny et al. 2002), and RPB1_for_Lec (Ruprecht et al. 2020) were chosen. For the marker COX2, COXIIIf2 and COXIIr (Lindgren et al. 2014) and COX sense (Ruprecht et al. 2020) and for psbJ-L, psbF (Werth and Sork 2010), psbL-sense and psbJ-antisense (Ruprecht et al. 2014) were used. All reactions were performed as described in (Ruprecht et al. 2020). Unpurified PCR products were sent to Eurofins Genomics/Germany for sequencing.

Phylogenetic analysis

The sequences of the different marker regions listed above were assembled and edited using Geneious version 6.1.8 (Kearse et al. 2012) and aligned with MAFFT v7.017 (Katoh et al. 2002) for both symbionts. For the photobiont, the classification and labeling of the different operational taxonomical units (OTUs) followed the concept of Leavitt et al. (2015), using automatic barcode gap discovery (ABGD; Puillandre et al. 2012) implemented in the reevaluated study by Ruprecht et al. (2020).

Phylogenetic relationships of the samples of the present study were calculated from the sequences of the marker nrITS, because the other markers could not be amplified in a sufficient quantity for all species, as well as intraspecific variation was in most of the cases too low, if available; therefore, they were excluded in all following analyses using sequence data.

A maximum likelihood analysis was calculated with the IQ-TREE web server (Trifinopoulos et al. 2016), using the

Table 1 Site descriptions and specifics of the four regions defined within the MDV, including the range of the coordinates of the sampling sites and areas, minimum, maximum, and mean values of the elevation of the sampling sites, and the number of lichen samples per area

	Sampling area	Range of coordinates of sampling sites	Min., max., and mean of elevation of sampling sites (m a.s.l.)	Number of sampling sites	Number of lichen samples
Area 1	Hidden Valley	S 78.12°–78.17° E 163.62°–163.81°	361, 911, 645	39	53
Area 2	Miers Lake	S 78.10°–78.11° E 163.69°–163.86	171, 597, 477	28	42
Area 3	Shangri-La	S 78.05°–78.08° E 163.71°–163.87°	411, 890, 656	30	51
Area 4	Garwood Valley	S 78.02°–78.05° E 163.80°–164.10°	319, 959, 593	56	86

model selection algorithm ModelFinder (Kalyaanamoorthy et al. 2017). The Bayesian information criterion (BIC) selected for the best-fit model for the mycobiont alignment TN+I+G4 and for the photobiont K2P+I. Branch supports were obtained with the implemented ultrafast bootstrap (UFBoot) (Minh et al. 2013) (number of bootstrap alignments: 1000, maximum iteration: 1000, minimum correlation coefficient: 0.99). Additionally, a SH-aLRT branch test (Guindon et al. 2010) was performed. Each branch of the resulting tree was assigned with SH-aLRT as well as UFBoot supports; the branches with SH-aLRT < 80% and/or UFBoot < 95% were collapsed by adding the command `minsupnew 80/95` to the script.

Haplotype analysis

We determined the haplotypes (h) of the different mycobiont species and photobiont OTUs by using the function `haplotype()` of the R package `pegas` (Paradis 2010) (note: the function only takes into account transversions and transitions but ignores insertions and deletions). For *min10MycoSp* species and photobiont OTUs with $h \geq 2$ and at least two haplotypes with $n \geq 3$ (*Lecidea cancriformis*, *Lecidella greenii*, *Rhizoplaca macleanii*, and photobiont OTU *Tr_A02*), haplotype networks were computed, using the function `haploNet()` of the R package `pegas` (Paradis 2010). The frequencies were clustered in 10% ranges, for example, the circles of all haplotypes making up between 20 and 30% have the same size. The haplotypes were color-coded according to their spatial distribution.

Analysis of spatial distribution

To analyze how the distribution of the lichen specimens correlated with abiotic factors, the sampling sites of the different lichen species or haplotypes in the investigated areas were compared with respect to their environmental specifics. For this, we tested the variables elevation, latitude, longitude, and the BIOCLIM variables generated by Wagner et al. (2018) providing a spatial resolution of 1 km. Since only elevation with its accompanying abiotic factors such as humidity and temperature had an effect on the data. The other variables could not be suitably assessed due to the relatively small area (data not shown). To assure a minimum group size of ten sample points, the tests only included the *min10MycoSp* species and *min10PhoHap* haplotypes.

We used nonparametric multiple comparisons for relative effects (`mctp-test`; function `mctp()` of the R package `npcomp` (Konietschke et al. 2015), which conducts pairwise comparisons of all possible combinations. Considering the photobionts contain four OTUs with only two of them including more than ten individuals, the elevation of the sample sites of these two most dominant photobiont

OTUs (*Tr_A02* and *Tr_S15*) was additionally compared by conducting a nonparametric t -test, using the R function `np.t.test()` of the package `npcomp` (Konietschke et al. 2015).

Analysis of mycobiont–photobiont associations

The associations between mycobiont and photobiont haplotypes were analyzed by computing bipartite networks, using the R function `plotweb()` of the package `bipartite` (Dormann et al. 2008). For the bipartite network including mycobiont species and photobiont haplotypes, the indices H_2' and d' (Blüthgen et al. 2006) were calculated. Both indices are derived from Shannon entropy. H_2' characterizes the degree of complementary specialization or partitioning among the two parties of the entire bipartite network, while d' describes the degree of complementary specialization at species or haplotype level. They both range from 0 for the most generalized to 1 for the most specialized case and were computed using the R functions `H2fun()` and `dfun()` of the package `bipartite` (Dormann et al. 2008).

Phylogenetic species diversity of the interaction partners was quantified by calculating a number of further metrics listed in Table 2, including the indices net relatedness index (NRI), phylogenetic species variability (PSV), and phylogenetic species richness (PSR).

Analysis of DNA polymorphism

For each identified mycobiont and photobiont species with more than one sample, we calculated the haplotype as well as the nucleotide diversity using p -distances with `DnaSP v5` (Librado and Rozas 2009). Gaps and missing data were excluded. We focused on h/n (number of haplotypes, h , divided by number of samples, n , per species), hd (haplotype diversity, the probability that two randomly chosen haplotypes are different; Nei 1987), and π (nucleotide diversity, average number of nucleotide differences per site between two randomly chosen DNA sequences; Nei and Li 1979).

In order to analyze the dependence of haplotype and nucleotide diversity values on elevation, we used the defined threshold of 600 m a.s.l. The h/n , hd , d' , and PSV of those *min10MycoSp* species with mean values above this threshold were grouped together and then compared to those species with mean values below 600 m a.s.l., using the R function `nonpartest()` of the package `npmv` (Ellis et al. 2017), which performs nonparametric comparisons of multivariate samples. (note: π , NRI, and PSR were excluded because of high correlations ($r \geq 0.85$) with h/n (π), hd (π), d' (π), and PSV (NRI and PSR).

Table 2 Diversity metrics compared in this study, citations and descriptions of each, and the used R functions

Metric	Definition	Citations	Description and interpretation of values	R function, R package
d'	Specialization index	Blüthgen et al. (2006)	Degree of interaction specialization at species level (values range from 0 = most generalized case to 1 = most specialized case)	dfun(), bipartite (Dormann et al. 2008)
NRI	Net relatedness index	Webb et al. (2002)	Comparison of phylogenetic distances among all members of a community (pos. values = phylogenetic clustering; neg. values = phylogenetic evenness)	ses.mpd(), picante (Kembel et al. 2010)
PSV	Phylogenetic species variability	Helmus et al. (2007)	Degree to which species in a community are phylogenetically related (values range from 0 = increased relatedness to 1 = decreased relatedness)	psd(), picante (Kembel et al. 2010)
PSR	Phylogenetic species richness	Helmus et al. (2007)	PSV multiplied by species richness SR (number of species in a sample); SR after discounting species relatedness (values range from 0 = increased relatedness to SR = decreased relatedness)	psd(), picante (Kembel et al. 2010)

Results

Phylogenetic analysis

The molecular phylogenies for the mycobiont (Online Resource 2b) and the photobiont (Online Resource 2c) are based on the marker nrITS, because the additional markers (mycobiont: mtSSU, *RPB1*; photobiont: psbJ-L, COX2) were not available in a sufficient quantity for all species, partly because of the implementation of the dataset (solely ITS) of (Pérez-Ortega et al. 2012). Besides, the available sequences showed for mtSSU, *RPB1*, and COX2, in most of the cases, very low or no variation within their taxonomical units. Only the highly variable region of the IGS (psbJ-psbL) shows mere 79.3% identical sites and an elongated sequence part on the 5' end of the IGS in contrast to northern hemispheric specimen for the OTU *Tr_A02* (Online Resource 1c). This finding is supported by a cultured specimen from Antarctica (NCBI Acc.num.: MH818851; Ruprecht et al. 2020). Unfortunately, only six sequences of 202 specimens are available. However, they are an important resource for future studies, as they contain the only multilocus information for this region. Both analyses include only accessions from the study sites (Online Resource 1a, b) to present the various species and diversity levels.

Mycobiont

The final data matrix for the phylogeny comprised 232 single sequences of the marker nrITS with a length of 610 bp and included sequences of the families *LECANORACEAE*, *TELOSCHISTACEAE*, *CATILLARIACEAE*, *CALICIACEAE*, and *LECIDEACEAE*. The phylogenetic tree was midpoint rooted and shows a total of 25 strongly supported clades on species level, assigned to eight genera. The backbone is not supported and therefore the topology will not be discussed. The genera *Huea*, *Austrolecia*, *Buellia*, and *Lecidea* are clearly assigned to their family level and are strongly supported. The genera *Carbonea*, *Lecidella*, and *Rhizoplaca* assigned to the family *LECANORACEAE* each form highly supported clades, but do not form an independent clade. The clade of the genus *Lecanora* is divided in five species (*L. cf. mons-nivis*, *L. fuscobrunnea*, *L. sp. 1*, *L. sp. 2*, and *L. sp. 3*), *Carbonea* in three species (*C. vorticosa*, *C. sp. URM1*, and *C. sp. 2*), *Austrolecia* in three species (*A. sp. 1*, *A. sp. 2*, and *A. sp. 4*), *Buellia* in four species (*B. frigida*, *B. sp. 1*, *B. sp. 2*, and *B. sp. 3*), and *Lecidea* in seven species (*L. andersonii*, *L. cancriformis*, *L. lapicida*, *L. polypycnidophora*, *L. sp. 5*, *L. sp. 6*, and *L. UCR1*). The samples allocated to the genera *Lecidella*, *Rhizoplaca*, and *Huea* were, in each genus, monospecific (*L. greenii*, *Rhizoplaca macleani*, and *Huea sp. 1*). The taxonomical assignment of the obtained sequences was

especially based on the concept of (Pérez-Ortega et al. 2012) which was extended accordingly, as well as on the following literature: Ruprecht et al. (2010, 2012b, 2020).

Photobiont

The final data matrix for the phylogeny comprised 222 single sequences of the marker nrITS with a length of 578 bp. The phylogenetic tree was midpoint rooted and shows four strongly supported clades, all of them belonging to the genus *Trebouxia*. They were assigned to OTU level using automatic barcode gap discovery (ABGD; Puillandre et al. 2012) according to Leavitt et al. (2015) and were included in the reevaluated dataset of Ruprecht et al. (2020). The OTUs were assigned to *Tr_A02*, *Tr_S02*, *Tr_S15*, *Tr_S18*. The OTU *Tr_A02* was by far the most common, being present in 202 (91%) of our 222 samples. Photobiont sequences taken from Pérez-Ortega et al. (2012) which were labeled only with numbers were included in our system of assigning the haplotypes to the appropriate OTUs (Ruprecht et al. 2020) and therefore renamed.

Haplotype analysis

The following analyses were based on the nrITS sequences of myco- and photobionts. The number of haplotypes differed significantly between myco- and photobionts. We identified 48 different mycobiont but only 17 different photobiont haplotypes. The most frequent mycobiont haplotype was *Lecidella greenii*_h01 with 28 samples, the most frequent photobiont haplotype was *Tr_A02*_h01 with 87 samples. Additionally, some of the mycobiont species appear to be more diverse (number of different haplotypes) than others. Figures 2 and 3 show bar charts that give the number of samples per mycobiont species/photobiont OTU per area and per haplotype.

Three different mycobiont species (*L. cancriformis*, *L. greenii*, and *R. macleanii*) and the most common photobiont OTU (*Tr_A02*) met the required criteria defined above for the construction of haplotype networks ($h \geq 2$ and at least two haplotypes with $n \geq 3$). In Fig. 4, the respective haplotype networks show the spatial location within the four areas. As shown in Fig. 2 for mycobiont species/photobiont OTUs, the distribution again turned out to be rather uniform, with most of the haplotypes found in all of the four areas.

Analysis of spatial distribution

For 12 of the 28 pairwise comparisons for the mycobionts species (*min10MycoSp*) and photobiont haplotypes (*min10PhoHap*), the mctp tests (pairwise comparisons of all possible combinations) for elevation showed significant differences, which are also visually recognizable when

Fig. 2 Number of samples per species/OTU and area (cf. Fig. 1b). **a** mycobiont species (total sample size: $n = 232$), **b** photobiont OTUs (total sample size: $n = 222$)

comparing the maps of the sample locations where the sample locations for each species are shown separately with varying colors indicating their elevations (*min10MycoSp* and *min10PhoHap* summarized in the respective OTUs; Online Resource 2d). The pairs with significant differences as well as the associated p -values are given in Online Resource 1d.

For the photobionts, the mctp test showed significant differences for only for two of the six pairwise comparisons (*Tr_A02*_h01 and *Tr_A02*_h03, *Tr_A02*_h01, and *Tr_S15*_h01 and, in each case, *Tr_A02*_h01 has lower elevation values; Online Resource 1d). The nonparametric t -test for comparing the elevation of the sample locations on OTU level resulted in a significant difference between the two groups for *Tr_A02* and *Tr_S15* ($p = 0.005$) with sampling sites of the OTU *Tr_S15* being higher.

Figure 5 shows the elevational distribution of the different mycobiont species and photobiont OTUs at their sample sites for *min10MycoSp* species and *min10PhoHap* haplotypes. The mycobiont species *L. cancriformis* and *R. macleanii* had a significant tendency to higher elevations, while *Carbonea vorticosa*, *Lecidea polypycnidophora*, and *L. greenii* had a significant tendency to lower elevations. One haplotype of the photobiont, OTU *Tr_S15*, was restricted

Fig. 3 Number of samples per species/OTU and haplotype. **a** Mycobiont species (total sample size: $n = 232$), **b** photobiont OTUs (total sample size: $n = 222$)

to higher elevations. The remaining mycobiont species and photobiont haplotypes have an intermediate distribution.

Analysis of mycobiont–photobiont associations

The bipartite network was calculated for all associations between the mycobiont species (*min10MycoSp*; lower level) and the respective photobiont haplotypes (higher level; Fig. 6). The H_2' (overall level of complementary specialization of all interacting species) of this network shows a low value of 0.226, which indicates a network with mostly generalized interactions (as opposed to specialized). This was mainly caused by the dominant occurrence of the three most abundant haplotypes (h01–h03) of the most common photobiont OTU *Tr_A02* (91% of 222 accessions). All mycobiont species were additionally associated to a variety of other and less abundant haplotypes (h04–h13) of this OTU *Tr_A02*. Furthermore, some of the mycobionts were associated with accessions of the distantly related OTUs *Tr_S02*, *Tr_S15*, and *Tr_S18*. The network matrix shows the number of associations between the mycobiont species and photobiont haplotypes (Online Resource 1e). The individual d' values (complementary specialization at species or haplotype level) are ranging from 0 to 1 and are presented in Table 3.

Species richness of mycobiont vs. photobiont

The number of different symbiotic partners at haplotype level (SR) as a function of the number of mycobiont haplotypes (h in Table 3) is illustrated in Fig. 7 for the *min10MycoSp* species. We found that highly variable mycobionts are tendentially, albeit not significantly, associated with a higher number of photobiont haplotypes (Pearson correlation: $t_6 = 2.41$, $p = 0.053$, $r = 0.70$).

Analysis of DNA polymorphism and nonparametric comparisons of multivariate samples

Analyses of DNA polymorphism and nonparametric comparisons of multivariate samples were achieved for *min10MycoSp* and *min10PhoHap* including the parameters h/n (number of haplotypes, h , divided by number of samples, n , per species), hd (haplotype diversity), and π (nucleotide diversity), d' (specialization index), NRI (net relatedness index), PSV (phylogenetic species variability), SR (species richness), and PSR (phylogenetic species richness; Table 3).

The lowest values of hd and π were developed by four mycobiont species of *min10MycoSp* (*C. vorticosa*, *L. polypycnidophora*, *L. greenii*, and *Huea* sp. 1) which occur at the lowest and intermediate elevations. In contrast, species that were found only at the higher elevations (*R. macleanii*, *L. cancriformis*) showed the opposite behavior and had the highest values for hd and π . These results were supported by nonparametric tests of the different haplotype and nucleotide diversity values which showed a significant difference between *min10MycoSp* samples below the threshold of 600 m a.s.l. (*C. vorticosa*, *Huea* sp. 1, *L. polypycnidophora*, and *L. greenii*) and those above (*Austrolecia* sp. 1, *Buellia frigida*, *L. cancriformis*, and *R. macleanii*) in terms of h/n , hd , d' , and PSV (ANOVA type test p -value: 0.009). The scatterplots of the indices as a function of elevation as well as the Pearson correlation coefficients are presented in Online Resource 2e.

Discussion

The McMurdo Dry Valleys at 78° S in Victoria Land, Antarctica, are known as the largest continuous ice-free landscape on the continent and are mostly colonized by lithic and soil-related microbial communities (Pérez-Ortega et al. 2012; Bottos et al. 2014; Colesie et al. 2014a; De Los Rios et al. 2014; Yung et al. 2014; Lee et al. 2019). The only comprehensive evaluation to date for saxicolous lichens was that of Pérez-Ortega et al. (2012) which showed a high number of mycobiont species (26) and, in contrast, a low number of photobiont species (four). Here, we use a new and much larger dataset focused specifically on the lecideoid

Fig. 4 Haplotype networks of those mycobiont species/photobiont OTUs with $h \geq 2$ and at least two haplotypes with $n \geq 3$: **a** *Lecidea cancriformis*, **b** *Lcidella greenii*, **c** *Rhizoplaca macleanii*, and the photobiont OTU *Tr_A02*, **d** showing the spatial distribution within Area 1 to Area 4 (cf. Figs. 1b, 2). Roman numerals at the center of

the pie charts refer to the haplotype IDs, italic numbers next to the pie charts to the total number of samples per haplotype. The circle sizes reflect relative frequency within the species/OTU; frequencies were clustered in ten, so that, for example, the circles of all haplotypes making up between 20 and 30% have the same size

lichen group but also included some other species with similar morphologies in the same and adjacent areas and the respective data of Pérez-Ortega et al. (2012; Fig. 1b). A total of 25 mycobiont species were identified with a composition that was mostly similar to the previous study but including a few additional specimens (*Lecanora fuscobrunnea*, unknown *Lecidea* and *Buellia* species). They were all associated with the same set of common photobionts (four species), dominated (91%) by the more recently reclassified OTU *Trebouxia* A02 (Leavitt et al. 2015), equivalent to the species *T. sp.* URA2 (Ruprecht et al. 2012a). The evaluation of Pérez-Ortega et al. (2012) included not only the same set of lecideoid and morphologically similar lichen genera (*Lecidea*; *Carbonea*, *Lecanora*, *Lcidella*, *Rhizoplaca*;

Austrolecia; *Buellia*; *Huea*) as investigated in this study, but also five additional lichen genera (*Acarospora*; *Caloplaca*; *Polysporina*; *Sarcogyne*; *Umbilicaria*).

In our study, we found that the different mycobiont species and photobiont OTUs within the MDV appear to be relatively evenly distributed across all four primary sample sites (Fig. 2), which is in basic agreement to the previous study. However, our results show distinct patterns for distribution, genetic diversity, and specificity. These results contrast with Pérez-Ortega et al. (2012) where the distribution of mycobionts and photobionts was independent of elevation and other abiotic factors. A clear trend has now emerged showing that the distribution of species/OTUs is significantly related to elevation, using 600 m a.s.l. as a defined

Fig. 5 Boxplots showing the elevation of the sample sites of the *min10MycoSp* species and *min10PhoHap* haplotypes. Numbers in italics refer to sample sizes. The elevational threshold of 600 m a.s.l. is highlighted with a dashed line

Fig. 6 Bipartite network including the *min10MycoSp* species as well as the haplotypes of their associated photobionts with an $H_2' = 0.226$. Rectangles represent species, and the width is proportional to the

number of samples. Associated species are linked by lines, whose width is proportional to the number of associations

Table 3 Diversity (left) and specificity indices (right) for the different mycobiont species and photobiont OTUs

	<i>n</i>	<i>h</i>	<i>h/n</i>	<i>hd</i>	π	<i>d'</i>	<i>NRI</i>	<i>PSV</i>	<i>SR</i>	<i>PSR</i>
Mycobiont species										
<i>Austrolecia</i> sp. 1	28	3	0.107	0.204	0.00069	0.053	− 0.127	0.454	8	3.636
<i>Austrolecia</i> sp. 2	2	2	1.000	1.000	0.00791	0.140	–	–	1	–
<i>Austrolecia</i> sp. 4	1	1	1.000	–	–	0.000	–	–	1	–
<i>Buellia frigida</i>	16	4	0.250	0.350	0.00098	0.105	2.210	0.029	6	0.173
<i>Buellia</i> sp. 1	6	1	0.167	0.000	0.00000	0.014	− 0.784	0.670	3	2.011
<i>Buellia</i> sp. 2	1	1	1.000	–	–	0.000	–	–	1	–
<i>Buellia</i> sp. 3	1	1	1.000	–	–	0.036	–	–	1	–
<i>Carbonea</i> sp. 2	6	2	0.333	0.333	0.00073	0.163	− 0.354	0.511	4	2.046
<i>Carbonea</i> URm1	3	1	0.333	0.000	0.00000	0.000	0.895	0.011	2	0.023
<i>Carbonea vorticosa</i>	11	1	0.091	0.000	0.00000	0.064	0.895	0.011	2	0.023
<i>Huea</i> sp. 1	17	1	0.059	0.000	0.00000	0.120	1.266	0.023	3	0.069
<i>Lecanora</i> cf. <i>mons-nivis</i>	3	1	0.333	0.000	0.00000	0.305	0.819	0.046	2	0.092
<i>Lecanora fuscobrunnea</i>	3	2	0.667	0.667	0.00129	0.391	− 1.239	1.000	2	2.000
<i>Lecanora</i> sp. 1	1	1	1.000	–	–	0.366	–	–	1	–
<i>Lecanora</i> sp. 2	6	1	0.167	0.000	0.00000	0.048	1.285	0.015	3	0.045
<i>Lecanora</i> sp. 3	6	2	0.333	0.533	0.00104	0.254	1.590	0.025	4	0.099
<i>Lecidea andersonii</i>	1	1	1.000	–	–	0.366	–	–	1	–
<i>Lecidea cancriformis</i>	18	6	0.333	0.719	0.00388	0.595	− 1.273	0.665	6	3.990
<i>Lecidea lapicida</i>	1	1	1.000	–	–	0.000	–	–	1	–
<i>Lecidea polypycnidophora</i>	10	1	0.100	0.000	0.00000	0.059	0.895	0.011	2	0.023
<i>Lecidea</i> sp. 5	1	1	1.000	–	–	1.000	–	–	1	–
<i>Lecidea</i> sp. 6	3	2	0.667	0.667	0.01028	0.147	–	–	1	–
<i>Lecidea</i> UCR1	2	2	1.000	1.000	0.00193	0.491	0.866	0.023	2	0.045
<i>Lecidella greenii</i>	34	2	0.059	0.299	0.00062	0.049	0.027	0.415	5	2.074
<i>Rhizoplaca macleanii</i>	51	9	0.176	0.692	0.00185	0.155	2.528	0.033	7	0.234
Photobiont OTU										
<i>Tr_A02</i>	202	11	0.054	0.659	0.00174	0.367	1.235	0.485	42	20.375
<i>Tr_S02</i>	4	2	0.500	0.500	0.00189	0.721	− 0.336	0.441	2	0.882
<i>Tr_S15</i>	14	1	0.071	0.000	0.00000	0.493	− 0.965	0.529	7	3.705
<i>Tr_S18</i>	2	1	0.500	0.000	0.00000	0.344	− 1.188	1.000	2	2.000

n number of sequences, *h* number of haplotypes, *h/n* quotient of *h* and *n*, *hd* haplotype diversity, π nucleotide diversity, *d'* specialization index, *NRI* net relatedness index, *PSV* phylogenetic species variability, *SR* species richness, *PSR* phylogenetic species richness

Fig. 7 Scatterplot of the species richness (*SR*) of photobiont haplotypes dependent on the number of haplotypes (*h*) of each *min10MycoSp* species (*Carbonea vorticosa* and *Lecidea polypycnidophora* share the same coordinates) including the Pearson correlation coefficient (*r*)

threshold dividing higher and lower sites. The mycobiont species *C. vorticosa*, *L. polypycnidophora*, and *L. greenii* were found almost exclusively below and *L. cancriformis* and *R. macleanii* above the threshold (Fig. 5), which was supported by mctp-tests for pairwise comparisons (Online Resource 1d).

In contrast, the dominant photobiont OTU *Tr_A02* is distributed everywhere while the remaining and distantly related OTUs (*Tr_S02*, *Tr_S15* and *Tr_S18*) are mostly restricted to the higher elevated habitats (cold and humid; Fig. 5, Online Resource 2c). This result is in agreement with Dal Grande et al. (2018), who reported clear elevational preferences for some *Trebouxia* taxa at the OTU level at a mountain range in central Spain covering an elevational gradient of 1400 m. He suggested that elevation plays a prominent role in shaping the community structure of these algae. The distribution of *Tr_S15* (equivalent to the species *T. URa1*), only occurring in the cold and humid areas was surprising because the first specimen of this species described was found at the climatically most extreme and dry habitats in the Darwin area at 80° S (Ruprecht et al. 2012a). However, lichen photobionts seem to have clear ecological preferences and niche differentiations. This was also shown for various *Asterochloris* lineages (TREBOUXIOPHYCEAE) which have diverging preferences in terms of rain and sun exposure (Peksa and Skaloud 2011) while Nadyeina et al. (2014) reported elevational partitioning in the distribution of different gene pools of the photobiont of the lungwort lichen *Symbiochloris reticulata* (TREBOUXIOPHYCEAE; Škaloud et al. 2016). In general, several studies suggest a strong genetic association of lichen-associated algae with climatic factors and substrate (e.g., Yahr et al. 2006; Fernández-Mendoza et al. 2011; Vargas Castillo and Beck 2012), and this has been interpreted as evidence for ecological specialization (Ruprecht et al. 2012a; Muggia et al. 2014).

The mycobiont species *min10MycoSp* not only show clear spatial differentiation with respect to elevation for species and OTUs but also for variables expressing the genetic diversity and specialization towards both symbiotic partners. A higher elevation correlates with a higher number of haplotypes (*hd*) and an increased nucleotide diversity (π) which leads to a greater intraspecific diversity within the mycobionts (Table 3). These differences are also partially reflected by a higher *d'*, PSV, PSR, and a low NRI which show a low relatedness to the co-occurring photobiont, associated with the rarely occurring and highly differentiated other OTUs *Tr_S02*, *Tr_S15*, and *Tr_S18*. Consequently, mycobionts with a high genetic diversity have a higher number of interacting partners. These findings are partially supported by the study of Singh et al. (2017), who reported climate as a selective pressure in terms of increased specificity of myco-/photobiont interactions.

Our study has also shown that there is a trend that highly variable mycobionts are associated with a larger number of photobiont haplotypes (Fig. 7). If we focus on the species which are significantly distributed either below or above the threshold of 600 m a.s.l., three main scenarios emerged: (1) mycobionts with low genetic diversity (*C. vorticosa*, *L. polypycnidophora* and *L. greenii*) are associated with one photobiont OTU *Tr_A02* and were found in only the lower area; (2) a mycobiont with a high genetic diversity (*R. macleanii*) is still solely associated to one photobiont OTU (*Tr_A02*) and is only located at the high elevated areas; and (3) the mycobiont with the highest genetic diversity (*L. cancriformis*) is associated with the highest number of photobiont OTUs, in the high elevation sites. These findings are in agreement with the known distribution of *L. greenii* (solely associated with *Tr_A02*), which, so far, have only been reported for sites in the more northern parts of the Ross Sea region and have never been found at the most extreme southern environments like the Darwin area (Ruprecht et al. 2012a, b). In contrast, *L. cancriformis* is one of the most widespread lichens, being distributed all over Continental Antarctica and is associated with all known photobiont species (Castello 2003; Ruprecht et al. 2010, 2012a).

The above results suggest that the mycobionts are dependent on the availability of climatically adapted photobionts. However, the mycobionts seem to have also their unique climate specific preferences because they do not always make use of the whole climate niche of the associated photobionts. This seems to be the case for, e.g., *L. greenii* which is associated with the widely distributed photobiont (*Tr_A02*), but only occurring in the milder parts of the Ross Sea region. These findings are only partially in line with previous studies on macro lichens (e.g., Romeike et al. 2002; Wirtz et al. 2003) that suggest that in extreme environments like the Antarctic continent there might be a selection pressure against photobiont specificity so that more versatile mycobionts are favored. Flexibility concerning the partner choice has been considered as an adaptive strategy to survive harsher environmental conditions (Leavitt et al. 2013; Engelen et al. 2016; Singh et al. 2017; Werth and Sork 2010).

To explain the myco- and photobiont distribution, we need to understand what abiotic factors control terrestrial life in these polar ecosystems. For the MDV, Lee et al. (2019) state clearly that one of the most important factors governing the distribution of taxa in the MDV is temperature, which is accepted to be inversely correlated to elevation (McKay 2015). However, much less is known about the conditions for wetness and humidity. The available wetness index for the MDV quantifies the expected wetness of a unit within the watershed by calculating the amount of possible water flowing into that unit from estimated snow fall (Stichbury et al. 2011). For rock associated lichens this is not relevant, because they are not connected to this source of water.

They are, therefore, dependent on moisture provided by the very low precipitation, infrequent melting snow (Head and Marchant 2014), and humidity provided by dew, incoming fog, and clouds from the sea. Additionally, it is now clear that the occasional foehn wind events cause severe drying within the valleys at altitudes up to 500 m. At higher elevations there is cold and moister air and this establishes a strong moisture availability gradient with elevation (Speirs et al. 2010; Fig. 1d). Our results suggest that our defined elevation threshold of about 600 m a.s.l. is a reasonable level which marks the shift from lower, dryer to higher, more humid conditions. Habitat aspect is also known to be important. Yung et al. (2014) described large differences with respect to just aspect for their chasmoendolithic microbial communities at Miers Valley. Similar results were also reported for the more maritime site, Botany Bay (Seppelt et al. 2010). We did not find any impact of other topographical features such as distance to coast, slope, aspect, and substrate. The collection sites were mainly N-facing or on plateaus, our transects were narrow and consistently only five to ten km inland plus the underlying rock in the whole area is granite and the investigated lichens are restricted to siliceous rock (Ruprecht et al. 2010, 2012b). However, our sampling was equally distributed below and above the threshold of 600 m a.s.l., so the differences found for species distribution, genetic diversity, and specificity appear to be due to the changing climate conditions, particularly moisture, along the elevational gradient.

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Compliance with ethical standards

Conflict of interest We hereby declare that there are no ethical issues or conflicts of interest.

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