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Research Article

RESEARCH ARTICLE

# Diversity and dispersal capacities of a terrestrial algal genus *Klebsormidium* (Streptophyta) in polar regions

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**One sentence summary:** Our analyses revealed the presence of two different distribution patterns which are supposed to characterize both macroorganisms and protists. On the one hand, we demonstrated unlimited dispersal and intensive gene flow within one of the inferred lineages (superclade B). On the other hand, there was a significant decrease of species richness towards the poles.

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## ABSTRACT

The distribution of microbial eukaryotes (protists) has been frequently discussed during the last two decades. The ubiquity hypothesis assumes the lack of latitudinal gradients in protist diversity due to their unlimited global dispersal. In this study, we examined the diversity and distribution of the very common, globally distributed green algal genus *Klebsormidium* across climatic zones, focusing on the polar regions. We tested whether (i) there is comparable diversity among the polar and temperate regions, and (ii) whether a spatial genetic differentiation occurs at the global scale. We collected a total of 58 Arctic, Antarctic and temperate strains, and genetically characterized them by sequencing the *rbc*L gene and two highly variable chloroplast markers. Our analyses revealed the presence of two different distribution patterns which are supposed to characterize both macroorganisms and protists. On the one hand, we demonstrated unlimited dispersal and intensive gene flow within one of the inferred lineages (superclade B). On the other hand, the majority of *Klebsormidium* clades showed rather a limited distribution. In addition, we detected a significant decrease of species richness towards the poles i.e. the macroecological pattern typical for macroorganisms. Species within a single protist genus may thus exhibit highly contrasting distribution patterns, based on their dispersal capabilities, which are usually shaped by both intrinsic and extrinsic factors.

**Keywords:** bipolar distribution; genetic diversity; *Klebsormidium*; phylogeography; polar regions

## INTRODUCTION

The distribution of microalgae is a major topic of modern microbial research (Caron 2009; Gast 2015). Two opposite hypotheses have been proposed: the ubiquity model (Finlay, Esteban and Fenchel 1996; Finlay 2002), which emphasizes the cosmopolitan distribution of protists; and the moderate endemicity model (Foissner 1999, 2006), which admits the existence of endemic species with limited distribution. Some authors proposed that the small organism size, large population sizes and high dispersal potential of eukaryotic microorganisms would lead to high gene flow across large geographical scales, resulting in an ubiquitous species distribution in suitable environments (Finlay 2002; Fenchel and Finlay 2004). Large population sizes would be expected to prevent local extinction and

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result in undisturbed population diversity (Fenchel and Finlay 2004), leading to high local genetic diversity (Mes 2008). In addition, intensive gene flow would constantly erase genetic diversity among populations, leading to a relatively low global diversity and undifferentiated populations (Fenchel and Finlay 2004).

Another consequence of the ubiquity hypothesis is that, as a result of global dispersal, latitudinal gradients in diversity should be weak or absent once ecological controls are factored out (Hillebrand and Azovsky 2001; Finlay and Fenchel 2004). However, there are only a few studies testing the presence of latitudinal gradients in eukaryotic microorganisms, moreover they are largely incongruent. Whereas Hillebrand and Azovsky (2001) showed that latitudinal gradients of species richness are largely absent for diatoms and presumably also for other unicellular and small multicellular organisms, the studies of Vyverman *et al.* (2007) and Siver and Lott (2012) showed these gradients on freshwater diatoms and silica-scaled chrysophytes, respectively. On the contrary, large organisms like plants and vertebrates show an obvious strong decrease of species richness towards the poles (see overview in Huston 1994). In addition, there should be significant differences in diversity between the poles due to the contiguous nature of the terrestrial Artic landmass with a temperate landmass at lower latitudes. Conversely, terrestrial Antarctica is a large isolated continent with small outlying sub-Antarctic islands. There, high polar ecosystems are biologically unique, with a more central role for bryophytes, lichens and microbial photoautotrophs over that of vascular plants. The biggest diversity differences between the poles are known in vascular plants where 2218 species are recorded for the Arctic, but just two species for Antarctica (Pointing *et al.* 2015). Similar differences were also found in bryophytes and lichens, which constitute the major plant cover in the polar regions. Whereas ca 900 mosses and liverworts have been described from the Arctic (Walker *et al.* 2005), Antarctica hosts only ca 125 species covering a small fraction of the total land area (Seppelt and Green 1998). For lichens, about 1750 species are known from the Artic, with 8%–10% of these species being endemic (Dahlberg and Bultmann 2013). On the contrary, ca 380 lichen species have been recorded in Antarctica (Øvstedal and Smith 2001), with about 21% of these being endemic taxa (Hertel 1988; Sancho *et al.* 1999).

Based on their cosmopolitan distribution and high dispersal, the diversity of microbial photoautotrophs should be comparable through the various regions (Pearce *et al.* 2009). Indeed, the estimated total number of species occurring in the Arctic was comparable to the diversity estimated for Antarctica (Pointing *et al.* 2015). However, this assumption has never been tested directly for whole microbial communities. Usually, the composition of polar microbial flora has been investigated separately either in Antarctica (e.g. Seaburg *et al.* 1979; Broady 1986, 1996; Pankow, Haendel and Richter 1991; Broady and Smith 1994; Mataloni, Tell and Wynn-Williams 2000; Cavacini 2001; Fermani, Mataloni and Van de Vijver 2007) or the Arctic region (Kaštovská *et al.* 2005, 2007; Stibal, Šabacká and Kaštovská 2006; Matuła *et al.* 2007). Similarly, the currently available molecular data are very fragmentary, consisting of a number of isolated taxonomic and ecophysiological studies on individual taxa, such as various diatom species (Sabbe *et al.* 2003; Vyverman *et al.* 2010; Souffreau *et al.* 2013), green algae (Lesser *et al.* 2002; Pocock *et al.* 2004; Pichrtová *et al.* 2013; Pichrtová, Hájek and Elster 2014), xanthophytes (Broady, Ohtani and Ingerfeld 1997; Rybalka *et al.* 2009), ciliates (Petz *et al.* 2007), dinoflagellates (Montresor *et al.* 2003; Rengefors *et al.* 2008, 2015; Rengefors, Logares and Laybourn-Parry 2012) and lichen symbionts (Romeike *et al.* 2002; Fernández-Menroza *et al.* 2011; Domaschke *et al.* 2012). The majority of studies suggested a bipolar distribution of the investigated microautotrophs (Darling *et al.* 2000; Montresor *et al.* 2003; Fernández-Menroza *et al.* 2011; Domaschke *et al.* 2012). However, Petz *et al.* (2007) demonstrated that only 13% of ciliate species showed a bipolar distribution. Strunecký, Elster and Komárek (2010) even observed no similarities between the poles when investigating the diversity of the cyanobacterial genus *Phormidium*. In the most recent evaluation of protist diversity in the polar regions, Wolf *et al.* (2015) found a rather small overlap between the Arctic and Antarctica, ranging from 5.5% to 14.5% depending on the group investigated.

There is still a fruitful debate concerning the endemicity of protist organisms in polar regions. For example, identical cyanobacterial taxa have been reported from the Arctic, Antarctica and alpine lakes (Jungblut *et al.* 2005), while the existence of endemic species has been proposed within the cyanobacterial genus *Phormidium* (Strunecký, Elster and Komárek 2010). Some polar cyanobacteria occupying highly cryptic habitats, such as hypolithic substrates, may have been genetically isolated for an evolutionarily long time (Bahl *et al.* 2011). In diatoms, morphological studies suggested the existence of at least 40% endemic taxa in some Antarctic areas (Schmidt, Mäusbacher and Müller 1990; Sabbe *et al.* 2003). Currently, combined molecular, ecological and morphological studies have indicated far greater microbial endemism than previously assumed (Vyverman *et al.* 2010). Souffreau *et al.* (2013) presumed that cosmopolitan Antarctic diatom species are in fact species complexes, possibly containing Antarctic endemics with low-temperature preferences. However, in contrast to diatoms and cyanobacteria, the green algal component of microbial mats has remained virtually unstudied. The available data are largely restricted to morphological taxonomic inventories on the continent, such as Victoria Land (Cavacini 2001; Adams *et al.* 2006), the Antarctic Peninsula (Mataloni and Pose 2001) and maritime Antarctica (Fermani, Mataloni and Van de Vijver 2007; Zidarova 2007). Broady (1996) suggested that the vast majority of Antarctic terrestrial green algae are cosmopolitally distributed. However, this prediction has yet to be studied by modern molecular techniques.

In this study, we examined the diversity and distribution of the filamentous green algal genus *Klebsormidium* in the polar regions. The genus *Klebsormidium* is very common and diverse in temperate zones (Rindi and Guiry 2004; Rindi, Guiry and López-Bautista 2008; Rindi *et al.* 2011; Škaloud and Rindi 2013; Mikhailyuk *et al.* 2015; Ryšánek, Hrčková and Škaloud 2015), but data about its occurrence in polar regions are still very scarce. The majority of its occurrence records comprises simple notes about their presence in various algal assemblages (Mataloni, Tell and Wynn-Williams 2000; Cavacini 2001; Kaštovská *et al.* 2005, 2007; Stibal, Šabacká and Kaštovská 2006; Fermani, Mataloni and Van de Vijver 2007; Matuła *et al.* 2007).

The general aim of this study was to test whether there exists comparable diversity among the polar and temperate regions in green algal eukaryotic microorganisms. We used the genus *Klebsormidium* as a model evolutionary lineage of ubiquitous terrestrial protists. In addition, to test for the presence of spatial genetic differentiation at the global scale, we investigated the population structure of a selected globally distributed lineage by sequencing fast evolving cpDNA molecular markers.

## MATERIALS AND METHODS

### Sampling site and cultivation methods

During the period from 1989 to 2014, a total number of 12 expeditions were organized to investigate the diversity of algae and cyanobacteria in polar regions. Six expeditions were carried out at different Arctic and Antarctic regions, respectively, resulting in collecting over 500 samples in total (Table S1, Supporting Information). All samples were cultivated on Petri dishes on 1.5% agar supplemented with Bold's basal medium (BBM; Starr and Zeikus 1993). Detected *Klebsormidium* filaments were transferred to Petri dishes with fresh BBM medium. After three transfers, the obtained cultures were observed to be unialgal by examination under a light microscope. Samples and unialgal stock cultures of *Klebsormidium* were maintained in BBM at 15°C under white fluorescent illumination of 30–50 $\mu$mol photons $m^{-2}$ $s^{-1}$ provided by 18 W cool tubes (Philips TLD 18W/33, the Netherlands), with a light:dark (L:D) cycle of 14:10 h. For the purpose of the population structure analysis, an additional 26 temperate strains belonging to the superclade B sensu (Rindi *et al.* 2011) were isolated from limestone and basalt rocks in the Czech Republic and Slovakia (Table S2, Supporting Information).

### Molecular analyses

A total of 32 *Klebsormidium* microcolonies (Table S2, Supporting Information) were used in subsequent molecular analyses. DNA was isolated according to the protocol published in Ryšánek, Hrčková and Škaloud (2015), and stored at –20°C. The sequences of the *rbc*L gene, which encodes the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase, were obtained using polymerase chain reaction (PCR) amplification with a Touchgene Gradient cycler (Techne, UK). The *rbc*L gene was amplified using the primers KF590 (5′-GAT GAA AAC GTA AAC TCT CAG C-3′) and *rbc*L-KR2 (5′-GGT TGC CTT CGC GAG CTA-3′; Škaloud and Rindi 2013). Both primers were designed specifically to amplify *Klebsormidium* species. Each 20 $\mu$L reaction for PCR was conducted as described in Ryšánek, Hrčková and Škaloud (2015). The PCR protocol followed that of Škaloud and Rindi (2013). Sequencing reads were assembled and edited by using SeqAssem (Hepperle 2004).

For phylogenetic analyses, the newly obtained *Klebsormidium* *rbc*L sequences were added to the sequences available in the GenBank database to produce an alignment. The final alignment was constructed using ClustalW (Thompson, Higgins and Gibson 1994) with MEGA 5.05 (Tamura *et al.* 2011). The aligned data set was analysed by using Bayesian analysis (BI) with MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001), maximum parsimony (MP) analysis with PAUP 4.0b10 (Swofford 2002), and maximum likelihood (ML) analysis with GARLI (Zwickl 2006). The evolutionary model was determined by using PAUP/MrModeltest 2.3 (Nylander 2004). The model selected under the Akaike Information Criterion was GTR + I + G. The BI analysis was performed using the prior set as the default in MrBayes; the robustness of the tree topologies was assessed by bootstrapping the data set as described by Škaloud and Rindi (2013).

### Population structure analyses

A total of 51 *Klebsormidium* strains belonging to the superclade B sensu (Rindi *et al.* 2011) were subjected to the analysis of population structure (Table S1, Supporting Information). Two molecular markers were selected based on the analysis of recently published plastid genomes (Civáň *et al.* 2014; Hori *et al.* 2014), including the plastid spacers atpE-trnM and ndhK-ndhC. The sequences were obtained by using PCR amplification with a Touchgene Gradient cycler (Techne, UK). The spacer atpE-trnM was amplified by using the newly designed primers atpE_F (5′-AGC ATT TCG TCG TGC CAA AGC A-3′) and trnM_R (5′-GGT TCA AAT CCA AGT GCG ACC-3′). The spacer ndhK-ndhC was amplified by the newly designed primers ndhK_F (5′-GTC CCA TAA AGC AAG GGC CA-3′) and ndhC_R (5′-TGG AAT TGA GCC TGT GGG AG-3′). Each 20 $\mu$L reaction for PCR was conducted as described in Ryšánek, Hrčková and Škaloud (2015). PCR amplification of the spacer atpE-trnM began with an initial denaturation at 95°C for 2 min, followed by 35 cycles of denaturing at 94°C for 1 min, annealing at 58°C for 1 min and elongation at 72°C for 1.5 min, with a final extension at 72°C for 8 min. The amplification of the spacer ndhK-ndhC began with an initial denaturation at 95°C for 2 min, followed by 35 cycles of denaturing at 94°C for 1 min, annealing at 56°C for 1 min and elongation at 72°C for 1.5 min, with a final extension at 72°C for 8 min. The PCR products were quantified on a 1% agarose gel stained with ethidium bromide. The purification and sequencing were performed as described in Škaloud and Rindi (2013). The sequencing reads were assembled and edited by using SeqAssem (Hepperle 2004).

For illustrating the genetic diversity within the superclade B, we constructed the haplotype networks on the basis of ML analyses of the available sequences. The haplotype network was made in Haplotype Viewer (G. Ewing; available at www.cibiv.at/~greg/haploviewer).

## RESULTS

### Analysis of molecular diversity

A total of 32 strains were isolated from the polar regions, including 26 Arctic and six Antarctic strains. The overall diversity was relatively low in comparison to the genetic diversity identified in the temperate zone (Rindi *et al.* 2011; Škaloud and Rindi 2013; Ryšánek, Hrčková and Škaloud 2015). In general, our molecular investigations revealed the presence of eight genotypes belonging to four distinct *Klebsormidium* lineages (Fig. 1), identified as clades B, E1, E2 and E4 sensu (Rindi *et al.* 2011). The great majority of strains (77%) were inferred within clade B, consisting of both Arctic and Antarctic isolates. The Arctic strain 818 inferred within clade E1 was related to strain K44, isolated from a peat bog in the Czech Republic (Škaloud and Rindi 2013). The three Arctic isolates belonging to clade E2 (ELS2, ELS3 and ELS4) were closely related to the members of lineage 4 sensu (Škaloud and Rindi 2013), consisting of aerophytic, synanthrophic strains isolated from Portugal, Germany, the Czech Republic and France. The remaining three strains inferred within clade E3 formed three separate genotypes. Whereas the two Antarctic strains LUC4 and LUC5 were related to the European aerophytic strains belonging to lineage 11 sensu (Škaloud and Rindi 2013), the Arctic strain 302 was inferred in the vicinity of the Australian terrestrial strain TR18. However, the relationship and exact phylogenetic position of the strains belonging to clade E2 remained unresolved by our analyses.

### Population differentiation of the superclade B strains

To evaluate the intercontinental dispersal capabilities of the polar *Klebsormidium* strains, we conducted a population-level investigation of all available strains belonging to superclade B i.e. 21 Arctic, 4 Antarctic,and 26 temperate strains. The superclade B represents a well delimited species-level lineage exhibiting a

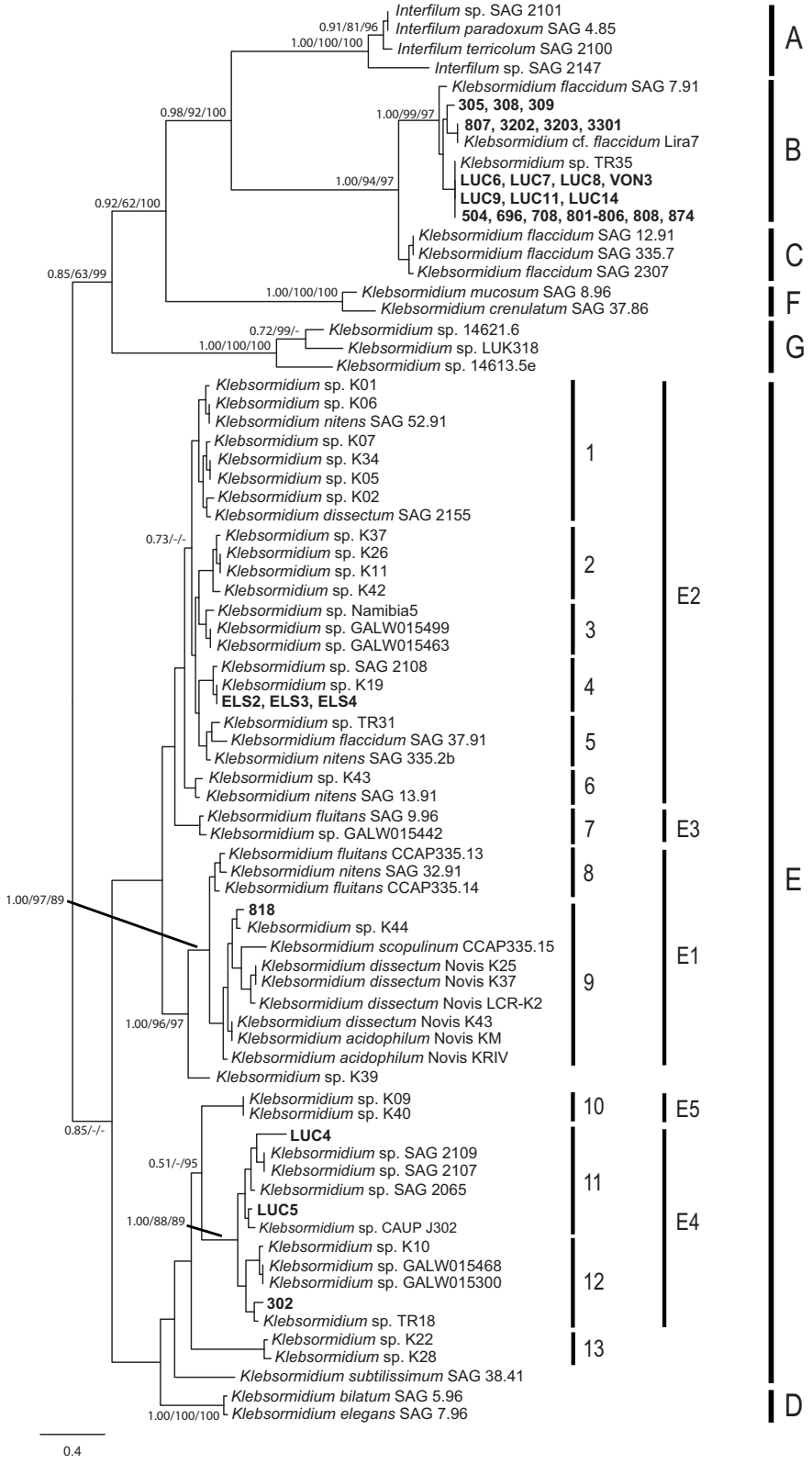
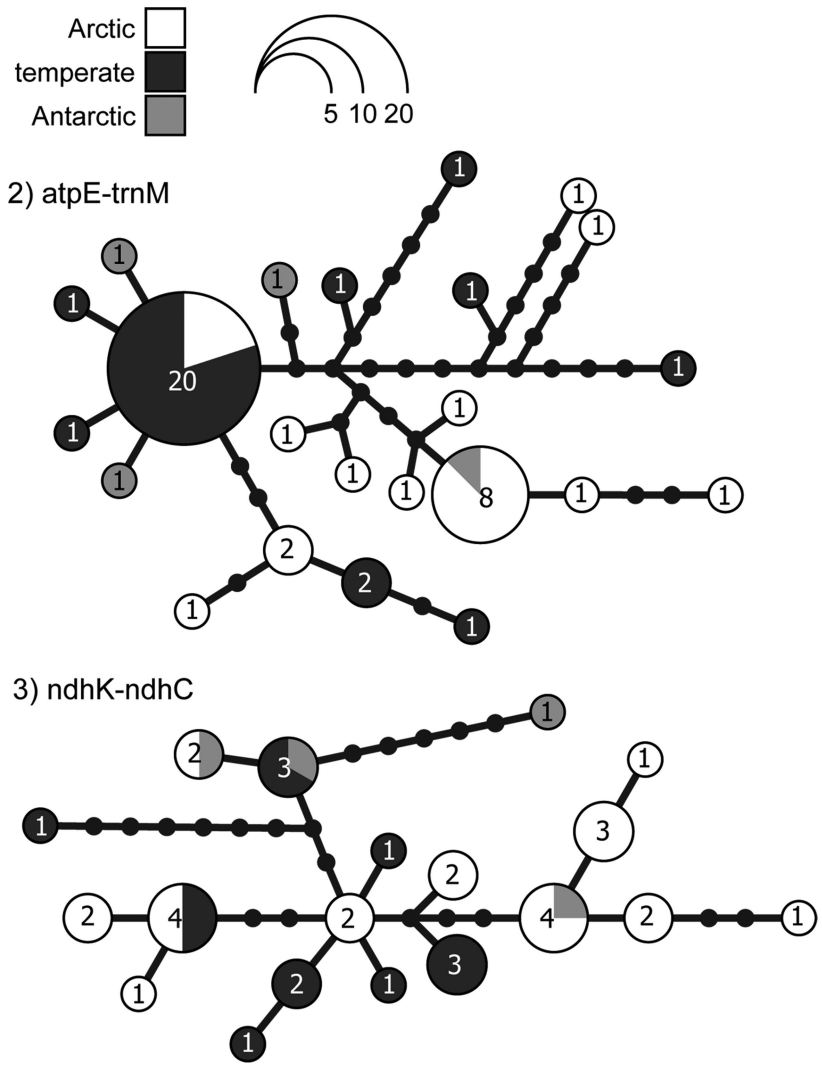



**Figure 1.** Phylogenetic tree obtained from BI based on an *rbc*L dataset, showing the position of the investigated *Klebsormidium* strains and their relatives. Values at the nodes indicate statistical support estimated by MrBayes posterior node probability (left), ML bootstrap (middle) and maximum parsimony bootstrap (right). The clade labelling (**A–G**, E1–E6) follows Rindi *et al.* (2011), the numbering of clades within the superclade E (1–13) follows Škaloud and Rindi (2013).




**Figures 2 and 3.** Haplotype genealogy from a ML tree of the spacer atpE-trnM (Fig. 2) and spacer ndhK-ndhC (Fig. 3), showing the relationship among haplotypes of the three regions. The circles represent the individual haplotypes. The scale shown on the upper left side of the figure indicates the relationship between circle sizes and the frequency of the haplotypes (numbers inside the circles specify the number of strains). Lines connecting the circles indicate a mutational step, and dots in the lines represent putative mutational steps between the haplotypes.

very low genetic diversity among the investigated strains (Rindi *et al.* 2011, Škaloud *et al.* 2014, Ryšánek, Hrčková and Škaloud 2015). Two highly variable, plastid-encoded spacers were used, including the 691 bp long spacer atpE-trnM (51 strains), and the 698 bp long spacer ndhK-ndhC (37 strains). Analyses of DNA variation in both sequenced spacers showed extensive sharing of haplotypes among the biomes, indicating the absence of geographical population structuring due to unlimited gene flow. A total of 23 different haplotypes were identified by analysis of the atpE-trnM sequences, of which 19 were represented by a single sequence only (Fig. 2). The most frequent haplotype had 20 records, containing 17 temperate and three Arctic strains. The second most common haplotype had eight records, including one Antarctic and seven Arctic strains.

The sequences of the spacer ndhK-ndhC were obtained for a total of 37 strains, including 20 Arctic,four Antarctic, and 13 temperate strains. A total of 19 different haplotypes were identified, of which eight were represented by a single sequence only (Fig. 3). Both of the two most common haplotypes (having four records each) were found in the two different biomes i.e. the Arctic-temperate and the Arctic-Antarctic regions. Haplotype sharing was detected in two additional cases (Fig. 3).

## DISCUSSION

### Diversity and abundance in polar regions

The genus *Klebsormidium* is one of the most abundant microautotrophs in various terrestrial and aerophytic habitats (Ettl and Gärtner 1995; Lokhorst 1996; John 2002, 2003). In fact, species of this genus are regularly listed as among the most abundant organisms found during diversity assessments of various habitat types worldwide (e.g. Lukešová and Hoffmann 1996; Neustupa 2001; Hoffmann, Ector and Kostikov 2007; Langhans, Storm and Schwabe 2009; Škaloud 2009; Schulz *et al.* 2015). Indeed, the recently published investigation of the *Klebsormidium* phylogeographic structure revealed its ubiquitous distribution on a global scale (Ryšánek, Hrčková and Škaloud 2015). All the above-mentioned studies thus imply the high global dispersal

and comparable diversity estimates of the genus *Klebsormidium* through the various regions.

However, our investigation of newly isolated *Klebsormidium* strains revealed a conspicuously low genetic diversity in the polar regions as compared to the recently published DNA-based diversity assessments. Based on the molecular investigations of a number of isolated strains, Rindi *et al.* (2011) and Škaloud and Rindi (2013) delimited a total of 22 well-supported clades belonging to the seven major superclades A–G. In their evaluation of *Klebsormidium* diversity in Northern temperate mixed forests, Ryšánek, Hrčková and Škaloud (2015) found a total of 44 unique *rbcL* genotypes, indicating a very high genotypic diversity in the dataset based on 15 sampling sites only. Most recently, Mikhailyuk *et al.* (2015) detected more than 25 ITS rDNA genotypes from 16 different localities in alpine soil crusts.

In contrast to the previously mentioned investigations, we recovered a total of onlyeight *rbc*L genotypes. Such low genetic diversity could be partly explained by a relatively small number of investigated strains. However, the abundance of *Klebsormidium* in polar regions is obviously very low, which makes very hard to obtain a considerably greater amount of isolated strains. In fact, despite our extensive sampling effort in both the Arctic and Antarctica, only 32 strains were successfully isolated. Indeed, the total number of samples we investigated (over 500) greatly exceeded the number of sampling sites investigated by both Ryšánek, Hrčková and Škaloud (2015) and Mikhailyuk *et al.* (2015). We even failed to isolate a single *Klebsormidium* clone in several samples, despite repeated inoculation of the samples to Petri dishes (Table S1, Supporting Information). Instead, a high number of *Xanthonema* colonies were obtained, indicating the good preservation of algal communities but a very low, undetectable abundance of *Klebsormidium* species in these samples. This low abundance is in concordance with many studies which focused on terrestrial algal assemblages in both Antarctica (Mataloni, Tell and Wynn-Williams 2000; Cavacini 2001; Fermani, Mataloni and Van de Vijver 2007) and the Arctic (Kaštovská *et al.* 2005, 2007; Stibal, Šabacká and Kaštovská 2006; Matuła *et al.* 2007). In these studies, *Klebsormidium* was usually reported as a rare taxon, exceeded in abundance by other microautotrophs, such as *Leptolyngbya, Phormidium, Xanthonema* and *Chlorella*.

Despite the above-mentioned low global abundance of *Klebsormidium* in polar regions, we presume that the observed low genetic diversity can only partly be attributed to the effect of undersampling. Quite recently, Škaloud and Rindi (2013) investigated the ecological differentiation of *Klebsormidium* lineages based on the genetic characterization of a number of strains, including 27 newly isolated strains from the Czech Republic (central Europe). Although the area of the Czech Republic is incomparably smaller than that of polar regions, the genetic characterization of strains revealed the presence of 13 different genotypes belonging just into the single superclade E. Thus, using the comparable number of investigated strains (27 versus 32 strains), the diversity detected in a small temperate area significantly exceeds the total diversity found in both the Arctic and Antarctica (13 versus. 8 genotypes). We therefore suppose that the observed low genetic diversity might be rather attributable to the overall low abundance of *Klebsormidium* in polar regions (Vogt, Beisner and Prairie 2010).

Almost 80% of all polar *Klebsormidium* strains were inferred within the cosmopolitan superclade B sensu (Rindi *et al.* 2011). Interestingly, Mikhailyuk *et al.* (2015) reported this clade to grow in higher altitudes, near and above the pine-forest line in alpine regions. Such a distribution pattern, together with the resistance to both freezing and desiccation stresses reported for several superclade B strains (Elster *et al.* 2008), suggest either a strong adaptation of this lineage to polar environments or a preadaptation that developed in some strains, enabling them to participate in long-distance dispersal events, including to the poles.

## Understanding the dispersal capacities

Considering its cosmopolitan distribution and predominance in the polar regions, superclade B represents an ideal model for testing the dispersal capabilities of microorganisms on a global scale. To differentiate the particular populations, we sequenced highly variable spacers between the chloroplast genes, a method frequently used in population structure assessment of higher plants (Doorduin *et al.* 2011; Hollingsworth, Graham and Little 2011). The most common haplotypes were shared across the arctic and temperate regions, indicating intensive gene flow and global dispersal. Such a high dispersal capacity explains the lack of differences in eco-physiological performance of seven superclade B strains isolated from the Arctic (LUC9, LUC11 and LUC14), Antarctica (LUC6, LUC7 and LUC8) and the temperate zone (LUC2), as reported by Elster *et al.* (2008). Seemingly, the intensive gene flow at a global scale may prevent adaptation of populations to the local environment (Kawecki and Ebert 2004; Whitaker 2006). However, our knowledge about local adaptation mechanisms of protists is severely limited and needs further investigations (Weisse 2008; Weisse *et al.* 2011; Rengefors *et al.* 2015).

While this population genetic investigation shows clear evidence of a high dispersal capability of superclade B, the absence of several genotypes in the polar regions points to the restricted distribution of the majority of *Klebsormidium* lineages. Such a pattern supports the moderate endemicity model proposed by the contemporary protistologist (Foissner 1999, 2006; Gast 2015). Consequently, unlimited dispersal should be considerably limited in the majority of the lineages. Although filamentous, the great majority of *Klebsormidium* species easily disintegrate into fragments containing a few cells (Škaloud 2006). These can then spread because of random events, such as hurricanes or wind currents. Indeed, viable *Klebsormidium* cells have been detected in lower troposphere air samples (Overeem 1937; Sharma *et al.* 2007). Factors limiting dispersal should be then connected to airborne survival, which is mainly affected by UV radiation and desiccation (Isard and Gage 2001; Figuerola and Green 2002; Sharma *et al.* 2007).

Various physiological studies demonstrated that terrestrial algae have several mechanisms to provide protection and adaptation to high UV radiation, in particular by the accumulation of mycosporine-like amino acids (MAAs; Holzinger and Lütz 2006; Hughes 2006; Karsten, Lembcke and Schumann 2007; Pichrtová *et al.* 2013; Karsten and Holzinger 2014). However, strains belonging to superclade B had a lower content of MAAs in comparison to the other *Klebsormidium* lineages (Kitzing and Karsten 2015), excluding UV radiation as a crucial factor affecting the dispersal capabilities. On the other hand, desiccation intolerance seems to offer a promising explanation of the restricted distribution of several *Klebsormidium* lineages, in particular those of superclade E. This clade has been recognized as the most common worldwide, containing at least 14 distinct, mainly ubiquitous lineages (Škaloud and Rindi 2013; Mikhailyuk *et al.* 2015; Ryšánek, Hrčková and Škaloud 2015). However, the great majority of these lineages are absent in the polar regions. Evaluation of their distribution patterns and ecology indicated that these lineages are mainly restricted to humid and shaded habitats, or even to fresh

waters (Škaloud and Rindi 2013; Mikhailyuk *et al.* 2015). Consequently, ecophysiological experiments did not reveal a high sensitivity to desiccation stress in several strains belonging to superclade E (Karsten and Rindi 2010; Karsten and Holzinger 2012). We therefore hypothesize that dispersal capacities of particular *Klebsormidium* strains are mainly shaped by different adaptations to desiccation stress during their airborne transport.

Our investigation revealed that one of the most common members of terrestrial algal communities in temperate regions, the Streptophyte green algal genus *Klebsormidium*, exhibits two different distribution patterns common to both macroorganisms and protists. On the one hand, we demonstrated unlimited dispersal and intensive gene flow proposed to characterize the ubiquitous distribution of protists (Montresor *et al.* 2003; Petz *et al.* 2007). On the other hand, we showed a significant decrease of species richness towards the poles i.e. the distribution pattern typical for macroorganisms, such as higher plants and vertebrates (Huston 1994). Therefore, the proposed distinction between the distribution patterns of protists and macroorganisms (Hillebrand and Azovsky 2001; Fenchel and Finlay 2004) cannot be generalized to all organisms. In fact, even the species within a single genus may exhibit contrasting distribution patterns, based on their dispersal capacities, which are shaped by both intrinsic (e.g. adaptations to desiccation and UV) and extrinsic factors (e.g. the availability of suitable habitats).

## SUPPLEMENTARY DATA

Supplementary data are available at FEMSEC online.

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