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Reproductive and dispersal strategies shape the diversity of mycobiontphotobiont association in *Cladonia* lichens



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ABSTRACT

Ecological preferences, partner compatibility, or partner availability are known to be important factors shaping obligate and intimate lichen symbioses. We considered a complex of *Cladonia* species, traditionally differentiated by the extent of sexual reproduction and the type of vegetative propagules, to assess if the reproductive and dispersal strategies affect mycobiont-photobiont association patterns. In total 85 lichen thalli from 72 European localities were studied, two genetic markers for both *Cladonia* mycobionts and *Asterochloris* photobionts were analyzed. Variance partitioning analysis by multiple regression on distance matrices was performed to describe and partition variance in photobionts genetic diversity. Asexually reproducing *Cladonia* in our study were found to be strongly specific to their photobionts, associated with seven unrelated *Asterochloris* lineages, thus being photobiont generalists. The reproductive mode had the largest explanatory power, explaining 44% of the total photobiont variability. Reproductive and dispersal strategies are the key factors shaping photobiont diversity in this group of *Cladonia* lichens. A strict photobiont specialisation observed in two studied species may steer both evolutionary flexibility and responses to ecological changes of these organisms, and considerably limit their distribution ranges.

1. Introduction

Lichens, as one of the most spectacular examples of mutualistic symbiotic associations, result from interdependent relationships between heterotrophic fungi, the mycobionts, and one or more population (s) of photosynthetic partners, the photobionts, these being either green or blue-green algae or both (Hawksworth and Honegger, 1994). The obligate and intimate associations between mycobionts and photobionts can lead to the co-evolution of both partners and to concerted diversification (del Campo et al., 2013; Rambold et al., 1998). These processes are in many cases conditioned by the ecological preferences for one or both partners and by the degree of partner specificity (defined as the potential range of compatible partners for a given symbiont; Rambold et al., 1998), with possibilities ranging from generalist associations for both partners, to strong reciprocal specificity, or any of a range of intermediate outcomes including local ecological specialization (Belinchón et al., 2015; Otálora et al., 2010; Yahr et al., 2004). In

lichens, species distribution and ecological adaptations to a certain niche depend on abiotic conditions, such as substrate, availability and different requirements of light, habitat quality and climate (Bannister et al., 2004; Giordani and Incerti, 2007); however, lichen distributions have also been hypothesized to strongly correlate with the ecological specialization and the physiological responses of the photobionts (e.g., Casano et al., 2011; Peksa and Škaloud, 2011; Yahr et al., 2006).

The degree of partner specificity is usually considered as that of the mycobiont towards the photobiont, and it has been correlated with the distributional range of the mycobionts (e.g., Blaha et al., 2006; Fernández-Mendoza et al., 2011; Muggia et al., 2014). In cosmopolitan lichen species-complexes with wide ecological amplitude, low photobiont specificity apparently allows the mycobiont to establish successful symbioses with locally adapted photobionts in a wide range of habitats (Muggia et al., 2014). Alternatively, a widely distributed, but ecologically more restricted mycobiont species was reported to have a narrower photobiont range, likely explained by habitat-scale factors

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Fig. 1. Schematic representation of *Cladonia* reproductive and dispersal modes. (a) The mycobionts *C. deformis* and *C. pleurota* reproduces mainly asexually and codisperse together with the photobiont vegetative by soredia, which size is up to 90 μm. (b) The mycobionts *C. coccifera* and *C. diversa* reproduce and disperse predominantly sexually by ascospores, therefore they need to find *de novo* a compatible photobiont; granules, plates and microsquamules are corticated thallus structures of 150–200 μm size.

(Domaschke et al., 2012; Fernández-Mendoza et al., 2011). Similarly, diverse reproductive strategies can result in varying patterns in fungalalgal specificity (Cao et al., 2015; Fedrowitz et al., 2011). On the other hand, interactions between symbionts at the local scale are responsible for observed patterns of selectivity (defined as the locally-observed patterns of association), and these can be influenced by interaction regimes between lichen species and interactions of mycobionts with the available photobionts in particular ecological settings (Belinchón et al., 2015; Yahr, et al., 2006).

While algal cells reproduce clonally by cell division inside the thallus, the different reproductive and dispersal modes which the mycobionts employ account for varying evolutionary advantages and drawbacks of the symbioses. Asexual propagules (in some species even thallus fragments), represent clonal diaspores in which the mycobiont and its compatible algal partner are co-dispersed. Soredia are tiny, abundant, powdery propagules of fungal hyphae wrapped around photobiont cells that detach easily from the thallus. Isidia, granules, plates and microsquamules are outgrowths of the thallus in which photobiont cells are enclosed by a cortex of fungal hyphae. Soredia are lighter and smaller in size than the corticate propagules (see Fig. 1), and potentially allow greater dispersal distances from the parent thallus (Büdel and Scheidegger, 2008). Asexual reproduction circumvents problems of low symbiont availability (Wornik and Grube, 2009), but it reduces the opportunities for adaptive evolution (Eckert, 2002). It is hypothesized that clonal dispersion can lead to high co-evolutionary rate of the two symbionts and their specialization to certain niches but it might decrease the genetic diversity of both partners (Otálora et al., 2012; Wornik and Grube, 2009). Alternatively, a sexually reproducing lichen mycobiont disperses independently by spores and must re-synthesize the thallus with a suitable photobiont. The thallus re-synthesis requires the presence of compatible algae in the environment where the spore germinates and is triggered by the degree of preference by the fungi towards the available photobionts (e.g., Beck et al., 1998; Honegger, 2008, 1993; Ott, 1987). Though sexually reproducing lichen fungi have to re-establish the symbiosis *de novo* every time, this type of reproduction increases the genotypic diversity and the successful dissemination by long range dispersal (e.g., Bailey, 1976; Belinchón et al., 2015; Pyatt, 1973; Werth et al., 2006). In addition, many closely related lichen species present either sexual or asexual reproductive structures, or both, and they proved to be, therefore, ideal subjects to investigate the dispersal patterns and the genetic diversity of the symbionts (Bannister et al., 2004; Cao et al., 2015; Otálora et al., 2012; Wornik and Grube, 2009).

The genus *Cladonia* is a group of lichenized fungi for which asexually and sexually reproducing taxa are known, and in some species both vegetative propagules and apothecia producing ascospores are present on the same thallus. *Cladonia* is distributed world-wide and is one of the species-richest and morphologically most distinctive genera of lichenized fungi (over 400 described species; Ahti, 2000; Stenroos et al., 2002). *Cladonia* species are also known for their high specificity towards the green algal photobiont genus *Asterochloris* (Trebouxiophyceae; Bačkor et al., 2010; Beiggi and Piercey-Normore, 2007; Nelsen and Gargas, 2006; Piercey-Normore et al., 2010; Škaloud et al., 2015; Yahr et al., 2004, 2006). In the same way, the genus *Asterochloris* has been found to associate only with a limited number of lichenized fungal genera which share similar ecological conditions, and these are correlated with the environmental factors preferred by *Asterochloris* photobionts (Peksa and Škaloud, 2011).

Recent phylogenetic analyses coupled with microscopic observations disentangled 20 phylogenetic lineages within the genus *Asterochloris*, and seven new species were described and characterized by genetic diversity, morphological and anatomical traits (Moya et al., 2015; Škaloud et al., 2015). The species diversity of *Asterochloris* was recorded across multiple, ecologically diverse lichen species (Škaloud et al., 2015; Škaloud and Peksa, 2010) but has never been investigated within a group of closely related lichens so far.

In the *Cladonia-Asterochloris* symbioses different patterns of specificity of the mycobionts towards the photobiont have already been

documented (Piercey-Normore and DePriest, 2001; Yahr et al., 2004, 2006). The role of different factors possibly shaping the algal-fungal association in *Cladonia* symbiosis was evaluated on *Cladonia* subtenuis by Yahr et al. (2006). The authors demonstrated that geographic position and habitat are the best predictors of algal genotype distribution. However, the relation of the photobiont diversity and the dispersal mode(s) of the mycobionts has not been studied so far in this group of lichens.

Here we considered a complex of four red-fruited Cladonia species (C. deformis (L.) Hoffm., C. pleurota (Flörke) Schaer, C. coccifera (L.) Willd. and C. diversa Asperges ex S. Stenroos) which are characterized by sharing chemical patterns (presence of usnic acid derivates and zeorin occasionally accompanied by porphyrilic acid) but are traditionally differentiated by the type of vegetative propagules (soredia, granules, plates or microsquamules) and by the incidence of producing sexually reproductive structures (apothecia with ascospores; Fig. 1). Because esorediate species (C. coccifera and C. diversa) present heavy, corticated, vegetative propagules (Fig. 1; plates, granules or microsquamules) which are produced in small amounts and are firmly attached to the potential surface, and regularly build sexual reproductive structures (apothecia, producing spores in large amounts), they have been considered here to reproduce mainly sexually. In contrast, sorediate species (C. pleurota and C. deformis) are seldom recovered with apothecia (Ahti et al., 2013) and therefore their primary dispersal mode has been hypothesized to be asexual and to depend on the small, light and ecorticate soredia produced in large amounts. Indeed, Molina et al., (2013) demonstrated that the viability of spores of the mixed lichen species Physconia grisea is much lower compared to its related sexual species (P. distorta). The four species treated here occur in habitats with low rate of competition by vascular plants, e.g., on sandy and rocky acidic soils, on soil in rock crevices; they are seldom found on bark or rotten wood on siliceous bedrock. In Europe the sorediate species C. deformis and C. pleurota are common in the Northern Scandinavian countries and in Central Europe. In British Isles, Western and Southern Europe they are usually restricted to mountains. On the other hand the esorediate taxa C. coccifera and C. diversa have broader distributions, and they dominate in areas where sorediate species are very rare (e.g., British Isles, Western Europe). C. coccifera is widespread in Europe growing from arctic to warm temperate areas (Ahti et al., 2013). C. diversa shows oceanic tendencies, is rather rare in the area of Fennoscandia and avoids high altitudes (Ahti and Steinová, personal observation). These four species as traditionally circumscribed have been previously shown not to be supported by molecular data (Steinová, et al., 2013), and therefore in this study, we focus on their reproductive traits as specimens, rather than at the species level for all statistical tests.

In this context, we aimed to test whether the type of reproductive strategy is the key factor shaping photobiont diversity in a complex of *Cladonia* lichen species across a broad geographical scale. In particular, we tested two main hypotheses: (i) the shared dispersal strategy of mycobiont and photobiont via soredia correlates with a higher specificity of mycobionts towards their photobionts (compared to esorediate lichens which reproduce mainly sexually); (ii) the photobiont diversity of esorediate lichens is determined by the mycobiont sexual reproduction and not by the vegetative dispersal of their propagules (plates, granules or microsquamules). To strengthen these hypotheses, the recovered photobiont diversity was tested against the genetic distance of the mycobionts, the geographic, the climatic and the reproductive variances.

2. Material and methods

2.1. Taxon sampling

collected or retrieved from herbarium collections (BG, C, CBFS, GZU, H, MACB, NMW, PL, PRA). The starting dataset for the mycobionts was the one published by Steinová et al. (2013) and it was here complemented with additional 44 new samples. A total of 43 specimens traditionally ascribed to the two sorediate species, *C. deformis* and *C. pleurota*, and 42 specimens ascribed to the esorediate species, *C. coccifera* and *C. diversa*, were used for molecular analyses. At five localities in the Czech Republic and in Germany we collected both sorediate and esorediate specimens growing up to 10 m from each other (Table 2). The specimens were determined using morphological and chemical characters. The presence of zeorin, as key trait of this lichen species complex, was confirmed by thin-layer chromatography (TLC) according to Orange et al. (2001).

2.2. DNA extraction, PCR and sequencing

Dry lichen material was ground to powder and was used for DNA extraction following either the CTAB protocol (Cubero et al., 1999) or the DNA extraction kit InstaGene Matrix (Bio-Rad). Genetic loci were analyzed for both the mycobionts and the photobionts. The fungal ITS region and an intron-containing portion of the β-tubulin gene were amplified as described in Steinová et al. (2013). The algal ITS rRNA gene was amplified using the algal-specific amplification primers ITS1T and ITS4T (Kroken and Taylor, 2000). The actin type I locus was amplified with primers actin_F and actin_R (Cocquyt et al., 2010). PCR conditions were applied as in Steinová et al. (2013) and Muggia et al. (2014). The PCR products were visualized on a 1% agarose gel stained with ethidium bromide and subsequently cleaned using the QIAquick PCR Purification Kit (Genomed) according to manufacturer's instructions. PCR products were sequenced with the same forward and reverse primers used for the PCR amplifications at Macrogen Corp. (Amsterdam, The Netherlands).

2.3. Sequence alignment and phylogenetic analyses

The new obtained sequences were assembled using the software SeqAssem (Hepperle, 2004) and checked for their identity in the Gen-Bank database by blast similarity search (Altschul et al., 1990). The sequences were aligned using MAFFT v.6 software (Katoh et al., 2002) under the QINS-I strategy. Ambiguous SNPs and aligned regions were estimated using the program Gblocks v.0.91b (Castresana, 2000) and were excluded from the alignment. Beginning and ending parts of the sequences containing missing data were also removed from the alignment. For a number of specimens we were unable to generate sequences for all of the selected loci. Additional mycobiont and photobiont sequences were retrieved from the previous study by Steinová et al. (2013) and from GenBank and included in the dataset (Table 1). Identical sequences were removed to speed-up the analyses.

Two different multilocus alignments were prepared for the phylogenetic analyses: (i) the fungal ITS rRNA concatenated with β -tubulin genes alignment, (ii) the algal ITS rRNA gene concatenated with actin alignment. Photobiont sequences were selected to encompass all known lineages of *Asterochloris* (Bačkor et al., 2010; Škaloud et al., 2015) for which data of both loci were available.

The phylogenetic network analyses of *Cladonia* mycobionts was conducted with the program SplitsTree 4 (Huson and Bryant, 2006) as in our previous study (Steinová et al., 2013), because the β -tubulin gene tree was incongruent with the ITS-based phylogeny. The consensus network based on the combined dataset of ITS rRNA and β -tubulin genes sequences was reconstructed using NeighborNet analysis option.

We used single locus trees analyses to detect possible phylogenetic conflicts between the *Asterochloris* photobiont ITS rRNA and the actin genes. As both phylogenies resulted in congruent topologies we used the concatenated dataset for the final analysis.

The phylogenetic analyses were performed with Bayesian inference (BI), Maximum Likelihood (ML) and weighted Maximum Parsimony

Table 1

List of the environmental samples used in the molecular analyses. DNA extraction numbers, voucher numbers, geographic origin and NCBI accessions for the new sequences (bold) obtained for both the mycobionts and the photobionts are reported.

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Cl.43Steinord 32 (PK)Cacch Rep., Karlonz, condanc, EsternabedNT99999NK-0191P.101117P.11CL.75Steinord 33 (PK)Huland, Heinola, Pritigirvi lakeNT99991NCNU30201NKCL37Steinord 53 (PK)March Steirische RandQbrigeNT99991NCNU30201NKCL375Steinord 52 (PK)Wacks, Pry, Steinord 52 (PK)NCNU30201NKCL376Steinord 52 (PK)Wacks, Davids HandNT99997NCNU30201NKCL376Steinord 52 (PK)Cacch Rep., Jöreld hort, Včari dalu)NT99997NCNU30201NKCL377Steinord 62 (PK)Cacch Rep., Jöreld hort, Včari dalu)NT99997NCNU30201NKCL378Steinord 63 (PK)Cacch Rep., Afondos, SnéžaNT99997NCNU30204NKCL383Steinord 63 (PK)Cacch Rep., Afondos, SnéžaNT99997NCNU30204NKCL384Steinord 63 (PK)Cacch Rep., Afondos, SnéžaNT99997NCNU30204NKCL385Steinord 63 (PK)Cacch Rep., Afondos, SnéžaNT99997NCNU30204NKCL386Steinord 63 (PK)Cacch Rep., Afondos, SnéžaNT99999 <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>HE61121</td>								HE61121
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CL79Steinov 337 (PRC)Finland, Hending, Pirtigin'i lake(F1989)29MIC0419(BI:11/2HICL347Steinov 537 (PRC)Norvay, Hordaland, BergenKT98905-KU05302MKCL375Steinov 536 (PRC)Cach Rep., Jizenski hary, Vžini kålyKT98905-KU05302MKCL376Steinov 536 (PRC)Cach Rep., Jizenski hary, Vžini kålyKT98905-KU05302MKCL377Steinov 536 (PRC)Cach Rep., Jizenski hary, Vžini kålyKT98905-KU05301MKCL381Ornage 2040 (MW)Malca Rep., JeitälKT98905-KU05301MKCL381Steinovi 630 (PRC)Cach Rep., Kkonole, StefalaKT99905-KU05301MKCL394Steinovi 630 (PRC)Cach Rep., Kkonole, StefalaKT99905-KU05301MKCL394Steinovi 640 (PRC)Cach Rep., Kkonole, StefalaKT99905-KU05301MKCL396Steinovi 640 (PRC)Cach Rep., Kkonole, StefalaKT99905-KU05302MKCL396Steinovi 640 (PRC)Cach Rep., Kkonole, StefalaKT99905-KU05302MKCL397Steinovi 320 (PRC)Cach Rep., Kkonole, StefalaKT99905-KU05302MKCL398Steinovi 320 (PRC)Cach Rep., Katonole, StefalaKT99905-KU05302MKCL396Steinovi 320 (PRC)Cach Rep., Katonole, StefalaKT99905-KU05302MKCL396Steinovi 320 (PRC)Cach Rep., Katono				-				MK0492
Cl347Steinov 537 (PRC)Austria, Steinzkiehe EndgebrigeKT98901-KU03002KKCl375Steinov 552 (PRC)Waler, Yr CanolKT98910-KU05302KKCl376Steinov 552 (PRC)Waler, Yr CanolKT98910-KU05302KKCl377Steinov 552 (PRC)Waler, St. Davids HeadKT98910-KU05302KKCl379Steinov 652 (PRC)Crech Rep., Jefeshé hory, Vélni skillKT98910-KU05302KKCl381Orage 2046 (NMW)Waler, Anglesey, Holyhend MountainKT98910-KU05301KKCl381Steinov 610 (PRC)Crech Rep., Katonolo, StežkaKT98910-KU05301KKCl394Steinov 610 (PRC)Crech Rep., Katonolo, Stežka-KU05101KKCl395Steinov 610 (PRC)Crech Rep., Katonolo, Stežka-KU05101KKCl396Steinov 610 (PRC)Crech Rep., Katonolo, StežkaNT98913-KU05101KKCl306Steinov 400 (PRC)Crech Rep., Katonolo, StežkaNT98913-KU05101KKCl307Vondrik 6242 (CRS)Belgum, Kalmtonu, Van GanzenvenKT98929-HE51116HECl308Steinov 400 (PRC)Crech Rep., Katonolo, StežkaNT98913-KU05101KKCl307Steinov 300 (FRC)Grech Rep., Katonolo, StežkaNT98913Cl308Steinov 300 (FRC)Grech Rep., Katonolo, StežkaNT98913 <td></td> <td></td> <td></td> <td>-</td> <td></td> <td></td> <td></td> <td>HE61122</td>				-				HE61122
C1374Steinov 320 (PRC)Norvay, Hordanda, BergenKT98990-KU03302MKC1375Steinov 535 (PRC)Cacch Rep., Jenski hory, Věria Isály-KU03308MKC1374Steinov 535 (PRC)Cacch Rep., Jenski hory, Věria Isály-KU03308MKC1379Steinov 526 (PRC)Cacch Rep., JesíndKT98990-KU05301MKC1381Ornarge 2406 (NMW)Valex, Anglesy, Holyheind MountainKT98990NEM04172KU03304MKC1381Steinovi 620 (PRC)Cacch Rep., JesíndKT99901-KU03304MKC1396Steinovi 640 (PRC)Cacch Rep., Katonole, SněžkaKT99903-KU03304MKC1396Steinovi 640 (PRC)Cacch Rep., Katonole, SněžkaKT99903-KU03304MKC1396Steinovi 640 (PRC)Cacch Rep., Katonole, SněžkaKT99903-KU05302MKC1396Steinovi 640 (PRC)Cach Rep., Katonole, SněžkaKT99903-KU05302MKC1396Steinovi 640 (PRC)Pentugh, Reira Ali, Argury Natural de Sera deKT98903-KU05303MKC1307Steinovi 630 (PRC)Steinovi 630 (PRC)Steinovi 630 (PRC)Steinovi 630 (PRC)Steinovi 630 (PRC)Steinovi 630 (PRC)KU08004MK-KU08010MKC1307Steinovi 630 (PRC)Steinovi 630 (PRC)Steinovi 630 (PRC)Steinovi 630 (PRC)Steinovi 630 (PRC)KU08004MK-KU08010MKC1307Steinovi 630 (PRC)<						MK049194		HE61122
C1375 Steinovis 529 (PRC) Wales, "Y Canol KT989999 - KU053037 MK C1376 Steinovis 528 (PRC) Wales, St. Davids Hend KT989999 - KU053022 MK C1379 Steinovis 528 (PRC) Wales, Anglesey, Holyhead Mountain KT989998 - KU053021 MK C1381 Orange 20406 (NMW) Wales, Anglesey, Holyhead Mountain KT989991 - KU053011 MK C1394 Steinovis 60 (PRC) Carch Rep., Khonols, Sněžka KT999933 - KU053014 MK C1396 Steinovis 60 (PRC) Carch Rep., Khonols, Sněžka KT99933 - KU053016 MK C1396 Steinovis 60 (PRC) Carch Rep., Khonols, Sněžka KT99933 - KU053016 MK C1396 Steinovis 400 (PRC) Carch Rep., Khonols, Sněžka KT99933 - KU054181 HE511166 HE C1306 Steinovis 351 (PRC) Betram, Karnhotu, Van Ganzenven KT989593 - HE511166 HE C1373 Steinovis 635 (PRC) Steinovi				Austria, Steierische Randgebirge		-		MK0492
Cl.376Steinová S56 (PRC)Cacch Rép., Jacnské hory, VEM si skůVT989914-KU050302KUCl.377Steinová S26 (PRC)Niela, S. Davidh HandVT989950-KU05010KUCl.381Orrange 2046 (PRC)Cacch Rep., JekinosVT989960-KU05010KUCl.381Steinová 639 (PRC)Cacch Rep., JekinosVT989916-KU05010KUCl.394Steinová 650 (PRC)Cacch Rep., Jekinos, SněžkaVT989917-KU050304KUCl.395Steinová 650 (PRC)Cacch Rep., Jekinos, SněžkaVT989918-KU050304KUCl.396Steinová 640 (PRC)Cacch Rep., Jekinos, SněžkaVT989918-KU050304KUCl.396Steinová 400 (PRC)Partagal, Béria Alla, Partaga Natural Berna-Hibi1165HibCl.154Boula 777 (PRC)Partagal, Béria Alla, Partaga Natural Berna-Hibi1165HibCl.137Steinová 400 (PRC)Partagal, Béria Alla, Partaga Natural Berna-Hibi1165HibCl.137Steinová 353 (PRC)Belgiun, Kalmhnut, Vin GanzarvenKT98997-<			• •			-		MK0492
Cl.377 Steinová 528 (PRC) Wales, St. Davids Head TY 1989897 - KU05302 MK Cl.381 Orange 20406 (NKW) Wales, Anglesy, Holyhead Muuntain KT989898 - KU05301 MK Cl.381 Orange 20406 (NKW) Wales, Anglesy, Holyhead Muuntain KT989898 - KU05301 MK Cl.394 Steinová 650 (PRC) Cacch Rep., Krkonošc, Sněžka KT989931 - KU053014 MK Cl.395 Steinová 650 (PRC) Cacch Rep., Krkonošc, Sněžka KT989939 - HE611164 HE Cl.396 Steinová 400 (PRC) Cacch Rep., Krkonošc, Sněžka KT989891 - HE611164 HE Cl.160 Steinová 400 (PRC) Cacch Rep., Krkonošc, Sněžka KT989891 - HE611166 HE Cl.172 Steinová 350 (PRC) Cach Rep., Krkonošc, Marcia Astana Ast		CL375	Steinová 529 (PRC)	Wales, Ty Canol	KT989896	-	KU053037	MK0492
Cl.379Steinová 634 (PRC)Finland, SondbyFY89993-KU05301KUCl.381Ornage 2406 (NNW)Wales, Angleser, Holyberd Mountal,KT989968-KU05301KUCl.394Steinová 650 (PRC)Cacch Rep., Jekino 65, SněžaKT989918-KU05301KUCl.395Steinová 650 (PRC)Cacch Rep., Jekino 65, SněžaKT989918-KU05302KUCl.396Steinová 640 (PRC)Cacch Rep., Kutonoš, SněžaKT98998-KU05302KUCl.396Steinová 640 (PRC)Peck Rep., Kutonoš, SněžaKT98989-KU05302KUCl.106Steinová 400 (PRC)Peckala, Angrues Marula de SternaKT98989-KU05302KUCl.105Steinová 400 (PRC)Peckala, Sněža, Angrues Marula de SternaKT98989-KU05303KUCl.130Vondrák C424 (CRIS)Demará, ScantolaKT98989-KU05304KUCl.132Steinová 53 (PRC)Gelgium, Kalinthout, Van GanzenvenKT98987-KU05304KUCl.364Steinová 65 (PRC)Genava, Saxov, Oterlansitzer HeideKT98987-KU05304KUCl.364Steinová 65 (PRC)Spain, Asturias, Parque Natural de RedesKT98998-<		CL376	Steinová 586 (PRC)	Czech Rep., Jizerské hory, Věžní skály	KT989914	-	KU053038	MK0492
Cl.379Steinori 624 (PRC)Finland, SondbyTY399930-K U05301KKCl.381Orange 2046 (NMWWiles, Angleser, Mchonok, SnežkaKT989905KU05171KU05304KKCl.394Steinori 650 (PRC)Cacch Rep., JeKionok, SnežkaKT989913-KU05301KKCl.395Steinori 640 (PRC)Cacch Rep., JeKionok, SnežkaKT989933-KU05303KKCl.396Steinori 640 (PRC)Cacch Rep., JeKionok, SnežkaKT98983-KU05303KKCl.396Steinori 640 (PRC)Portagl, Aleri Alar Parque Natural de SeradoKT98988-KI051161HECl.106Steinori 400 (PRC)Portagl, Aleri Alar Parque Natural de SeradoKT98988-KI051161HECl.130Vondrak 6242 (CBPS)Demark, GranholmKT98989KK04918HE011166HECl.132Steinori 450 (PRC)Gemark, Saron/Dorhanister HeideKT989893-KU05303KKCl.364Steinori 450 (PRC)Belgium, Kalmthout, Yan GanzernenKT98989-KU05303KKCl.364Steinori 450 (PRC)Spin, Asturias, Parque Natural de RedesKT98989-KU05303KKCl.364Steinori 450 (PRC)Cacch Rep., Listrict Tabor, MjryKT98989-KU05303KKCl.364Steinori 450 (PRC)Cacch Rep., Listrict Tabor, MjryKT98989-KU05303KKCl.364Steinori 450 (PRC)Cacch Rep., Listrict Tabor, MjryKT98996-KU05303KK<		CL377	Steinová 528 (PRC)	Wales, St. Davids Head	KT989897	-	KU053022	MK0492
Cl.381Orange 20406 (NMWWales, Angless, Holyhead MountainPT399898-KU05301MKCl.393Steinovi 630 (PRC)Cacch Rep., Koknost, SněžaKT989917-KU05304MKCl.394Steinovi 640 (PRC)Cacch Rep., Koknost, Ohř adloKT989918-KU05304MKCl.395Steinovi 640 (PRC)Cacch Rep., Koknost, SněžaKT98993-KU05301MKdiveraaCl.54Bouda 777 (PRC)Cacch Rep., Časkoaské Švýcarsko, BabylonRT98988MK09108HE611166HECl.160Yondrik 6242 (2BFS)Denmark, Zealand, Melby OvedereKT989898MK09181HE611166HECl.172Steinovi 351 (PRC)Belgium, Kalmithout, Van GanzenvenKT989898NK09181HE611166HECl.363Ahtr 72006 (PRC)Germany, Saxony, Oberlausitzer HeideKT989997-KU05303MKCl.364Steinovi 356 (PRC)Germany, Saxony, Oberlausitzer HeideKT989991-KU05303MKCl.367Steinovi 636 (PRC)Germany, Saxony, Oberlausitzer HeideKT989996-KU05303MKCl.370Steinovi 636 (PRC)Germany, Saxony, Oberlausitzer HeideKT989996-KU05303MKCl.370Steinovi 636 (PRC)Cach Rep., HradikåKT989969-KU05303MKCl.370Steinovi 630 (PRC)Germany, Saxony, Oterlausitzer HeideKT989969-KU05303MKCl.370Steinovi 630 (PRC)Germany, Kauan, Arruita HegesKT989969- <td></td> <td></td> <td>Steinová 624 (PRC)</td> <td></td> <td>КТ989930</td> <td>-</td> <td></td> <td>MK0492</td>			Steinová 624 (PRC)		КТ989930	-		MK0492
Cl.381Steinovi 6.39 (PR.O)Cacch Rep., Jerkone's, SnéžlaKT99907MK049178KU030304MKCl.394Steinovi 650 (PR.O)Cacch Rep., Krkone's, Orbi selloKT99917-KU05304MKCl.396Steinovi 650 (PR.O)Cacch Rep., Krkone's, Orbi selloKT99918-KU05303MKCl.396Steinovi 640 (PR.O)Cacch Rep., Krkone's, Orbi selloKT99928-KU05302MKdiversaCL16Steinovi 600 (PR.O)Cacch Rep., Krkone's, Orbi selloKT99891-HE11116HECL16Steinovi 400 (PR.O)Portugal, Beira Alta, Parque Natural de Serra de EstrelaKT99892-HE511166HECL173Steinovi 351 (PR.O)Belgium, Kalinthout, Van GanzenvenKT99892-HE511166HECL364Steinovi 650 (PR.O)Germany, Saxony, Oberlausizer HeideKT99891-KU05303MKCl.364Steinovi 650 (PR.O)Germany, Saxony, Oberlausizer HeideKT99891-KU05303MKCl.364Steinovi 650 (PR.O)Germany, Saxony, Oberlausizer HeideKT99891-KU05303MKCl.364Steinovi 650 (PR.O)Germany, Saxony, Oberlausizer HeideKT99891-KU05303MKCl364Steinovi 610 (PR.O)Spain, Asturian, Parque Natural RedesKT99891-KU05303MKCl372Abti 68670 (PR.O)Cacch Rep., district Tabor, MiynKT99890-KU05304MKCl372Abti 68670 (PR.O)Cacch Rep., district Tabor, Mi						_		MK0492
C1.394Scienovi 642 (PR.O)Czech Rep., Krkonsé, Ohř sadiKT989918-KU05304MKC1.395Steinovi 649 (PR.O)Czech Rep., Krkonsé, SnřžhaKT989938-KU05303MKdiversaC1.54Boula 77 (PR.O)Czech Rep., Casbonské Švjcansko, BahylonKT989981-KU05103MKdiversaC1.54Boula 77 (PR.O)Czech Rep., Casbonské Švjcansko, BahylonKT989891-HE511116HEC1.130Vondrák (S424 (CBS)Demmark, BornholmKT989891MK09121HE11166HEC1.172Steinovi 351 (PR.O)Belgium, Kalmthout, Van GanzenvenKT989927-HE511166HEC1.363Ahti Z000 (H)Netherlands, Gelderland, GarderenKT989913-KU05303MKC1.364Steinovi 656 (PR.O)Gernamy, Saxony, Oberlausitzer HeideKT989914-KU05303MKC3.67Steinovi 636 (PR.O)Spin, Asturias, Parque Natural de RedesKT989914-KU05303MKC3.70Steinovi 616 (PR.O)Czech Rep., district Tálor, MjnyKT989894-KU053034MKC3.97Steinovi 616 (PR.O)Czech Rep., district Tálor, MjnyKT989894-KU05304MKC3.97Steinovi 616 (PR.O)Czech Rep., district Tálor, MjnyKT989894-KU05304MKC3.97Steinovi 616 (PR.O)Czech Rep., district Tálor, MjnyKT989894-KU05304MKC3.97Steinovi 616 (PR.O)Demmark, Zataland, Isrotich HeginKT989894<								MK0492
Cl.395Steinová 650 (PRC)Czech Rep., Knonoté, SnéžkaKT98991-KU05303KUCl.396Steinová 640 (PRC)Czech Rep., Knonoté, SnéžkaKT98993-KU05302MKdiversaCL54Steinová 00 (PRC)Czech Rep., Časkoaská Švjcarsko, BabylonKT98987-KU05402MKCL106Steinová 400 (PRC)Portugal, Leira Alta, Parque Natural de Serara de StreiaKT989891AH511164HECL130Vondriá Co242 (CBRS)Demanzk, ZennholmKT989892-H5611167HECL173Steinová 351 (PRC)Belgium, Kalmthout, Van GanzenvenKT989891-H5611167HECL364Steinová 553 (PRC)Spain, Asturás, Parque Natural de RedesKT989912-H501106HECL364Steinová 654 (PRC)Spain, Asturás, Parque Natural de RedesKT989913-KU053005MKCL370Steinová 654 (PRC)Spain, Asturás, Parque Natural de RedesKT989914-KU053004MKCL370Steinová 654 (PRC)Cacch Rep., dirafite?KT989914-KU053004MKCL370Steinová 616 (PRC)Cacch Rep., dirafite?KT989914-KU053004MKCL370Steinová 616 (PRC)Cacch Rep., dirafite?KT989914-KU053004MKCL370Steinová 616 (PRC)Cacch Rep., dirafite?KT989914-KU053044MKCL370Steinová 50 (PRC)Demark, Zealand, fivride? HangKT98994-KU053044MK <td></td> <td>-</td> <td></td> <td>-</td> <td></td> <td></td> <td></td> <td>MK0492</td>		-		-				MK0492
Cl396 Steinovi 649 (PK) Czech Re, S. Kokonés, Sněžka FT989903 - NU05303 MU diversa Cl54 Boudin 717 (PKC) Czech Re, Čakosaké Švjcarko, Balylon KT989801 - HEI1110 HE Cl1030 Vondrák C242 (CBK) Cennark, Bornholm KT989801 KT989802 - HEI1110 HE Cl172 Steinovi 400 (PKC) Belgium, Kalmthout, Van Ganzenven KT989802 - HEI1110 HE Cl173 Steinovi 351 (PKC) Belgium, Kalmthout, Van Ganzenven KT989803 - HEI31110 HE Cl363 Ahti 72006 (H) Netherlands, Celderland, Garderen KT989903 - HE031103 HK Cl364 Steinovi 634 (PKC) Spain, Atturias, Parque Natural de Redes KT989904 KK09179 KU05303 HK Cl370 Steinovi 634 (PKC) Spain, Atturias, Parque Natural de Redes KT989904 - KU05303 HK Cl370 Steinovi 634 (PKC) Cache Re, Hradish KT989904 KK09197 KU05304 HK Cl370 Steinovi 634 (PKC) Cache Re, Hradish KT989964 KK09190 - - Cl370 Steinovi 304 (PKC) Cache Re, Justand, Bredvandshaker KT989964 KK09190 - <td></td> <td></td> <td></td> <td>-</td> <td></td> <td></td> <td></td> <td>MK0492</td>				-				MK0492
Cl.398Seching 2125 (C)Demank, Zealand, Melly OvedrevKT99999, NU05302KUdiversaCL306Secion's 400 (PRC) Secion's 400 (PRC)Cacch Rep., Českosakć Švjcarsko, Balyn Portugal, Beira Halp, Parque Natural de SeriaKT999989, HE91116HEL1300Vondrák 6242 (CBFS)Belgium, Kalmthout, Van GanzenvenKT999992, HE91116HECL172Steinová 351 (PRC)Belgium, Kalmthout, Van GanzenvenKT999923, CHE51116HECL364Steinová 352 (PRC)Belgium, Kalmthout, Van GanzenvenKT999912, CKU05303MKCL364Steinová 635 (PRC)Germany, Saxony, Obelasitz/FeldedKT999913, CKU05303MKCL364Steinová 635 (PRC)Spain, Asturias, Parque Natural de RedesKT99995, CKU05303MKCL370Steinová 637 (PRC)Cacch Rep., HradiskKT999905, CKU05304MKCL372Steinová 637 (PRC)Cacch Rep., diristif Tábor, MjnynKT999905, CKU05304MKCL400Seching 28.X. 2013 (C)Demaraf, zatland, BredevandshakkerKT999905, CKU05304MKCL400Seching 21.54 (C)Demaraf, Steinderi AghlonKT999995, CKU05304MKCL400Seching 21.54 (C)Demaraf, Steinderi AghlonKT999995, C, C, CCL400Seching 20.54 (C)Steinová 30 (PRC)Filada, Sumosalmi, KT999956, C, C, CCL400Seching 20.54 (C)Filada, Sumosalmi <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>MK0492 MK0492</td>								MK0492 MK0492
diversa CL54 Bouda 777 (PRC) Czech Rep., Českosaké Švýcarsko, Babylon KT989889 - HE511164 HE CL106 Steinová 400 (PRC) Fortugal, Beira Alta, Parque Natural de Serra de Extrela K7318671 MK049182 HE511166 HE CL120 Vondrík 6242 (CBFS) Demmark, Bornholm K7398992 - HE511166 HE CL173 Steinová 352 (PRC) Belgium, Kalmthout, Van Ganzenven K7989992 - KU05303 MK CL364 Steinová 356 (PRC) Belgium, Kalmthout, Van Ganzenven K7989991 - KU05303 MK CL364 Steinová 636 (PRC) Spain, Asturias, Parque Natural de Redes K7989996 - KU05303 MK CL367 Steinová 637 (PRC) Czech Rep., Hradište K7989996 - KU05303 MK CL370 Steinová 616 (PRC) Czech Rep., district Tábor, Miýny K7989990 - KU05304 MK CL397 Scheinog 28.X. 2013 (C) Czech Rep., district Tábor, Miýny K7989904 - - - - -								MK0492 MK0492
Cl.06Steinovi 400 (PRC) EstrelaPertugal, Beira Ala, Parque Natural de Serra de IstrelaKP31867MK 04918IEE01116IEE IEE01116IEE IEE01116IEECl.130Vondråk 6242 (DRC) Steinovi 352 (PRC)Denmark, BornholmKT989892-HE51116IEECl.173Steinovi 552 (PRC) Steinovi 552 (PRC)Belgium, Kalmithout, Van GanzenvenKT989929-HE51116IEECl.364Steinovi 6356 (PRC) 	1		-					
Cl.30Vondrák 6242 (CBFS)Denmark, BornholmKT989891MK04918HE611169HECl.172Steinová 351 (PRC)Belgium, Kalmthout, Van GanzenvenKT989927-HE611169HECl.363Ahti 72006 (H)Netherlands, Gelderland, GarderenKT989927-KU053017MKCl.364*Steinová 556 (PRC)Spain, Asturias, Parque Natural de RedesKT989949-KU053018MKCl.366Steinová 634 (PRC)Spain, Asturias, Parque Natural de RedesKT989969-KU053018MKCl.370Steinová 616 (PRC)Cecch Rep., HradištéKT989997-KU053014MKCl.372Steinová 616 (PRC)Cecch Rep., district Tábor, MlýnyKT989999-KU053014MKCl.392Steinová 616 (PRC)Denmark, Jutland, BredevandsbakkerKT989909-KU053014MKCl.404MACB 97615Denmark, Jutland, BredevandsbakkerKT989909-KU053014MKCl.404MACB 97615Spain, Riofró de Riza, sierra de AyllónKT989908-KU053019MKCl.175Steinová 330 (PRC)Finland, VarkausKT98994Cl.354Petis 12154 (CP)Finland, VarkausKT98994KU053019MKCl.355Steinová 603 (PRC)Germary, Saxony, Oberlausizer HeideKT98996-KU053020MKCl.355Steinová 627 (PRC)Cech Rep., Jésrict Tábor, MlýnyKT98996-KU053020MKCl.35	C. alversa			Portugal, Beira Alta, Parque Natural de Serra de				HE6112 HE6112
C1.173 Steinová 332 (PRC) Belgrum, Kalmthout, Van Ganzenen KT98992 - HE61116 HE7 C1.364 Steinová 596 (PRC) Germany, Saxony, Oberlausitzer Heide KT989913 - KU053003 MK C1.364 Steinová 635 (PRC) Spain, Asturias, Parque Natural de Redes KT989913 - KU053003 MK C1.367 Steinová 633 (PRC) Spain, Asturias, Parque Natural de Redes KT989904 - KU053003 MK C1.370 Steinová 616 (PRC) Czech Rep., Hradišté KT989905 - KU053004 MK C1.397 Steinová 616 (PRC) Czech Rep., district Tábor, Mlýny KT989900 - KU053004 MK C1.400 Sching 12.154 (C) Denmark, Jutand, Bredevandsbaker KT989900 - KU053004 MK C1.404 MCB 97615 Spain, Riofró de Riaz, sierra de Ayllón KT989904 - KU053029 MK C1.176 Steinová 330 (PRC) Finland, Suomeslami KT989926 MK049199 HE611180 HE C1.357 Steinová 603 (PRC) Finland, Suomeslami KT989961 - KU053020 MK <td>CL130</td> <td>Vondrák 6242 (CBFS)</td> <td></td> <td>KT989891</td> <td>MK049181</td> <td>HE611166</td> <td>HE6112</td>		CL130	Vondrák 6242 (CBFS)		KT989891	MK049181	HE611166	HE6112
Cl.363 Ahri 72006 (H) Ne.Tberlands, Gelderland, Garcen KT989913		CL172	Steinová 351 (PRC)	Belgium, Kalmthout, Van Ganzenven	KT989892	-	HE611167	HE6112
Cl.363 Ahri 72006 (H) Ne.Tberlands, Gelderland, Garcen KT989913				-		_		HE6112
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Cl.367Steinová 635 (PRC)Spain, Ásturias, Parque Natural de RedesKT989913-KU053036MKCl.368Steinová 637 (PRC)Czech Rep., HradištéKT999906MK04107KU053046MKCl.372Ahti 68670 (H)Norway, Hordaland, BergenKT989999AU053046MKCl.392Steinová 616 (PRC)Czech Rep., districit Tábor, MlýnyKT989990AU053046MKCl.397Sechting 28. X. 2013 (C)Denmark, Jutland, Bergen andshakkerKT989900-KU053046MKCl.400Sochting 12154 (C)Denmark, Jutland, Bergen andshakkerKT989903deformisCLAD 08Peksa 918 (PL)Czech Rep., districit Asa, sierra de AyllónKT989903HE611106HECl.175Steinová 330 (PRC)Finland, SuomeslininaKT989904MK04919HE611106HECl.175Steinová 330 (PRC)Finland, SuomeslininaKT989904KK04919HE611106HECl.354Pentti Alanko 150786 (H)Finland, SuomeslininaKT989964-KU053028MKCl.355Steinová 637 (PRC)Czech Rep., district fabor, MlýnyKT989964-KU053028MKCl.356Steinová 637 (PRC)Czech Rep., JisravaKT989964-KU053028MKCl.357Steinová 637 (PRC)Czech Rep., JisravaKT989964-KU053028MKCl.356Steinová 637 (PRC)Czech Rep., JisravaKT989964-KU053028MKCl.								MK0492
R1.368Steinová 634 (PRC)Spain, Asturias, Parque Natural de RedesKT989984MKU053003MKC1.370Steinová 637 (PRC)Czech Rep., HradištěKT989985-KU053004MKC1.392-5Steinová 616 (PRC)Czech Rep., district Tábor, MlynyKT989989-KU053004MKC1.392-5Steinová 616 (PRC)Czech Rep., district Tábor, MlynyKT989900-KU053004MKC1.400Sochting 12154 (C)Denmark, Jutanda, BeredevandshakkerKT989900C1.401MCB 97015Spain, Riofrió de Rizaz, sierra de AyllónKT989070C1.76Steinová 330 (PRC)Finland, SuconosaliniKT989916MK049199HE611190HE611190HE6C1.75Steinová 330 (PRC)Finland, SuconosaliniKT989964MK049199HE611190HE6C1.354Steinová 6317 (PRC)Czech Rep., district Tábor, MlýnyKT989964-KU053002MKC1.355Steinová 6317 (PRC)Czech Rep., sknonös, VýrovkaKT989963-KU053020MKC1.356Steinová 657 (PRC)Czech Rep., Sknonös, VýrovkaKT989964-KU053020MKC1.350Steinová 657 (PRC)Czech Rep., Sknonös, VýrovkaKT989965-KU053020MKC1.401Steinová 658 (PRC)Czech Rep., Sknonös, VýrovkaKT989964KU053020MKC1.402Palce 11305 (PRA)Czech Rep., Sknonös, VýrovkaKT989954- <td< td=""><td></td><td></td><td></td><td></td><td></td><td></td><td>MK0492</td></td<>								MK0492
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Cl.372Ahti 68670 (H)Norway, Hordaland, BergenKT989895-KU05303MKCl.392Steinová 616 (PC)Czech Rep., district Tábor, MlýnyKT989809-KU05304MKCl.302Sochting 28. X. 2013 (C)Demmark, Jutand, BredevandsbakkerKT989900-KU05304MKCl.400Sochting 12154 (C)Demmark, Jutand, BredevandsbakkerKT989903deformisCLAD 08Peksa 918 (PL)Czech Rep., ChvaleticeFM94537-HE511186HE6Cl.175Steinová 330 (PRC)Finland, SuomossalmiKT989904MK049108HE611186HE6Cl.354Petriá Janko 16076 (H)Finland, SuomossalmiKT989967-KU05302MKCl.355Steinová 617 (PRC)Czech Rep., district Tábor, MlýnyKT989961-KU05302MKCl.355Steinová 603 (PRC)Finland, SondhyKT989963-KU05302MKCl.356Steinová 603 (PRC)Gzech Rep., SimanyaKT989963-KU05302MKCl.357Steinová 637 (PRC)Finland, SondhyKT989963-KU05302MKCl.359Steinová 637 (PRC)Czech Rep., SimanyaKT989963-KU05303MKCl.401Sochting 10. X.2013 (C)Czech Rep., SimanyaKT989963pleurotaBackor 18Peksa 580 (PL)Czech Rep., Dialtide Kite, Site, S								
CL392 ⁵ Steinová 616 (PRC) Czech Rep., district Tábor, Mlýny KT989899 - KU053014 MK CL397 Sochting 28, X.2013 (C) Demmark, Jutland, Bredevnadsbakker KT989900 - KU053040 MK CL400 Sochting 2154 (C) Demmark, Jutland, Bredevnadsbakker KT989903 - - - deformis CLA0 Peksa 918 (PL) Czech Rep., Chvaletice FM945357 - HE611205 HE CL175 Steinová 330 (PRC) Finland, Suomosalmi KT989928 MK049193 HE611180 HE CL354 Pentti Alanko 150786 (H) Finland, Suomenlinna KT989967 - KU053029 MK CL355 ⁵ Steinová 617 (PRC) Czech Rep., district Tábor, Mlýny KT989963 - KU053029 MK CL357 Steinová 627 (PRC) Finland, Sondby KT989963 - KU053020 MK CL350 Steinová 627 (PRC) Czech Rep., Krkonoše, Výrovka KT989963 - KU053020 MK CL350 Palice 16632 (PRA) Czech				-				MK0492
Cl.397Søchting 28. X. 2013 (C) Søchting 12154 (C)Denmark, Zealand, Tisvilde HegnKT989900-KU05304MKCL404MACB 97615Denmark, Zealand, Tisvilde HegnKT989902deformisCLA0 08Peksa 918 (PL)Czech Rep., ChvaleticeFM945357-HE611205HE611		-						MK0492
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CL354Pentti Alanko 150786 (H)Finland, SuomenlinnaKT98997-KU053019MKCL355Steinová 617 (PRC)Czech Rep., district Tábor, MlýnyKT989961-KU053020MKCL356Steinová 603 (PRC)Germany, Savany, Oberlauitzer HeideKT989962-KU053020MKCL357Steinová 627 (PRC)Finland, SondbyKT989964-KU053020MKCL359Steinová 587 (PRC)Czech Rep., Krkonoše, VýrovkaKT989964-KU053020MKCL360Palice 16632 (PRA)Czech Rep., JeštédKT989964-KU053020MKCL393Steinová 644 (PRC)Czech Rep., JeštédKT989964-KU053020MKCL401Søchting 10. IX. 2013 (D)Denmark Harrild HedeKT989964pleurotaBackor 18Peksa 820 (PL)Slovakia, Veľká Fatra, HarmanecKT989961CL400Palice 11305 (PRA)Czech Rep., ChvaleticeFM945331-HE611191HE6CL26Palice 11305 (PRA)Czech Rep., Brdy, HrébenecKT989961MK04905HE611181HE6CL37Haffelner 65635 (GZU)Austria, Stubalpe, LahnhofenKT989954MK04905HE611182HE6CL36Haffelner 65635 (GZU)Austria, Stubalpe, LahnhofenKT989954MK04905HE611182HE6CL37Hefs 6563 (GZU)Austria, Stubalpe, LahnhofenKT989954MK049020HE611182HE6CL47Peksa 564 (PL)Czech				-				HE6112
CL355 ⁵ Steinová 617 (PRC) Czech Rep., district Tábor, Mlýny KT989961 - KU053029 MK CL356 ⁴ Steinová 603 (PRC) Germany, Saxony, Oberlausitzer Heide KT989962 - KU053026 MK CL357 Steinová 637 (PRC) Finland, Sondby KT989964 - KU053020 MK CL350 Steinová 587 (PRC) Czech Rep., Krkonöe, Výrovka KT989964 - KU053002 MK CL360 Palice 16632 (PRA) Czech Rep., Ještěd KT989948 - KU053028 MK CL393 ³ Steinová 644 (PRC) Czech Rep., Ještěd KT989948 - KU053031 MK CL401 Sochting 10. IX. 2013 (C) Denmark, Harrild Hede KT989940 -						MK049193		HE6112
CL356 ⁴ Steinová 603 (PRC) Germany, Saxony, Oberlausitzer Heide KT989962 - KU053026 MK CL357 Steinová 627 (PRC) Finland, Sondby KT989963 - KU053027 MK CL359 Steinová 627 (PRC) Czech Rep., Krkonös, Výrovka KT989964 - KU053020 MK CL360 Palice 16632 (PRA) Czech Rep., Ještéd KT989982 - KU053028 MK CL393 ³ Steinová 644 (PRC) Czech Rep., Ještéd KT989966 - KU053028 MK CL401 Søchting 10. IX. 2013 (C) Denmark, Harrild Hede KT989966 - <td>-</td> <td></td> <td></td> <td></td> <td>-</td> <td></td> <td>MK0492</td>		-				-		MK0492
CL357 Steinová 627 (PRC) Finland, Sondby KT989963 - KU053027 MK CL359 Steinová 587 (PRC) Czech Rep., Krkonoše, Výrovka KT989964 - KU053020 MK CL360 Palice 16632 (PRA) Czech Rep., Šumava KT989948 - KU053003 MK CL393 ³ Steinová 644 (PRC) Czech Rep., Ještěd KT989966 - KU053028 MK CL401 Sochting 10. IX. 2013 (C) Denmark, Harril Hede KT989966 -			• •					MK0492
CL359Steinová 587 (PRC)Czech Rep., Krkonoše, VýrovkaKT989964-KU053020MKCL360Palice 16632 (PRA)Czech Rep., ŠumavaKT989948-KU053030MKCL393 ³ Steinová 644 (PRC)Czech Rep., JeštédKT989963-KU053028MKCL401Søchting 10.I.X. 2013 (C)Denmark, Harrild HedeKT989966-KU053030MKCL405MACB 97100SpainKT989967pleurotaBackor 18Peksa 820 (PL)Slovakia, Veľká Fatra, HarmanecFM945351-HE611191HE6CL40Peksa 588 (PL)Czech Rep., Dolní LoučkyKT989964CL36Palice 11305 (PRA)Czech Rep., Dolní LoučkyKT989951MK049200HE611193HE6CL37Haffelner 65635 (GZU)Austria, Stubalpe, LahnhofenKT989952-KU163444MKCL43Peksa 563 (PL)Czech Rep., Brdy, HřebenecKT989953MK049201HE611183HE6CL44Peksa 563 (PL)Czech Rep., Brdy, HřebenecKT989953MK049201HE611183HE6CL44Peksa 563 (PL)Czech Rep., Brdy, HřebenecKT989953MK049203HE611183HE6CL64Vondrák 3631 (CBFS)Romania, Retezat, Cheile ButiiKT989954MK049203HE611183HE6CL67Vondrák 2686 (RE)SCzech Rep., Křivoklátksko, Na AnděluKT989955-HE611173HE6CL67Vondrák 3631 (CBFS)Czech			Steinová 603 (PRC)			-	KU053026	MK0492
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CL74 Peksa 575 (PL) Czech Rep., Radvanice KT989944 - KU053025 -				-				
				-				HE6122
CL85 Steinova 103 (PRC) Czech Rep., Brdy, Zdár K1989935 – HE611196 HE6				· · ·				
		CL85	Steinova 103 (PRC)	czech kep., Bray, Zdar	к 1989935	-	HE011196	HE6112

(continued on next page)

Table 1 (continued)

Taxon name	DNA extraction	Collection No.	Locality	GenBank No.			
	No.	(herbarium)		Photobiont		Mycobiont	
				ITS	actin	ITS	β-tubulin
	CL98	Steinová 45 (PRC)	Czech Rep., Krkonoše, Kotel	KT989957	-	HE611188	HE611240
	CL99	Steinová 99 (PRC)	Czech Rep., Brdy, Žďár	KT989958	-	HE611202	HE611254
	CL100	Steinová 65 (PRC)	Czech Rep., Slavkovský Les, Křížky	KT989967	MK049199	HE611176	HE611228
	CL101	Steinová 108 (PRC)	Czech Rep., Brdy, Žďár	KT989923	MK049189	HE611203	HE611255
	CL104	Steinová 126 (PRC)	Czech Rep., Brdy, Hřebenec	KT989924	MK049190	HE611185	HE611237
	CL125	Steinová 161 (PRC)	Czech Rep., Sedlčansko, Husova kazatelna	KT989959	-	KU053032	-
	CL128 ²	Steinová 164 (PRC)	Czech Rep., Sedlčansko, Drbákov-Albertovy skály	KT989960	MK049204	HE611180	HE611232
	CL136	Steinová 215 (PRC)	Finland, Helsinki, Rastila	KT989925	MK049191	HE611200	HE611252
	CL148	Steinová 241 (PRC)	Austria, Gurktaler Alpen, Nassbodensee	KT989945	MK049197	HE611189	HE611241
	CL150	Steinová 187 (PRC)	Finland, Vantaa, Fagersta	KT989926	MK049192	HE611204	HE611256
	CL350	GZU 000303377	Monte Negro, Prokletije Mountain Range, Krš Bogićevica	KT989937	-	KU053018	MK049240
	CL385	Peksa 1722 (PL)	Czech Rep., Ledce, Krkavec	KT989965	-	-	-
	CL386	Steinová 551 (PRC)	Austria, Gurktaler Alpen, Hochrindl	KT989938	-	KU053033	MK049241
	CL388	Steinová 176 (PRC)	Austria, Koralpe, Weinebene	КТ989949	-	KU053045	MK049242
	CL389	Steinová 312 (PRC)	Czech Rep., Slavkovský les, Dominova skalka	KT989950	-	-	MK049243
	CL390	Steinová 339 (PRC)	Norway, Rondane, Einsethøe	КТ989939	-	-	-
	CL391	Steinová 341 (PRC)	Norway, Rondane	КТ989931	-	_	-
	CL403	Tønsberg 42460 (BG)	Norway, Oppland, Lom, Breidsæterdalen	КТ989934	-	-	MK049244

(wMP) approaches. Models of molecular evolution were selected independently for the two photobiont loci, ITS rRNA and actin genes, according to the Bayesian information criterion (BIC) as implemented in jModelTest 2.1.4 (Darriba et al., 2012). The models applied were the TIM2ef+G for the photobiont ITS rRNA gene partition, and the TrNef + G for the actin partition. A Bayesian analysis was implemented using MrBayes version 3.2.1 (Ronquist et al., 2012) and was used for the phylogenetic tree construction. Two parallel MCMC runs were carried out for five million generations, each with four chains. Trees and parameters were sampled every 100 generations. The convergence of the chains was assessed during the run by calculating the average standard deviation of split frequencies (SDSF). Further, the log-likelihood scores were plotted against generation time using Tracer 1.4 (Rambaut and Drummond, 2007) to determine when the stationarity of likelihood values have been reached (e.g., the burn-in stage; Ronquist et al., 2012). Burn-in was set at one million generations and the majority rule consensus trees were calculated from the posterior samples of 40,000 trees. The SDSF value between simultaneous runs was 0.006174 in the concatenated dataset. ML and MP phylograms were used for bootstrapping and they were obtained using Garli version 2.0, and PAUP version 4.0b10 (Swofford, 2002), respectively. ML analyses consisted of rapid heuristic searches (100 pseudo-replicates) by using automatic termination (the genthreshfortopoterm command set to 100,000). The weighted parsimony (wMP) bootstrapping (1000 replications) was performed using heuristic searches with 100 random sequence addition replicates, tree bisection reconnection swapping, random addition of sequences (the number limited to 10,000 for each replicate), and gap characters treated as a fifth character state. The weight to the characters was assigned using the rescaled consistency index on a scale of 0-1000. New weights were based on the mean of the fit values or each character over all of the trees in memory. The phylogenetic trees were visualized in TreeView (Page, 1996).

2.4. Variance partitioning

We performed variance partitioning by multiple regression on distance matrices (MRM; (Legendre et al., 1994; Lichstein, 2006; Manly, 1986; Smouse et al., 1986) to describe and to partition variance in photobiont genetic diversity. This method computes adjusted R^2 for the complete model, estimating how much of the total variability is defined by explanatory variables. It also allows estimating R^2 for each of the explanatory variables as well as their shared components. The photobiont genetic distance matrix was used as response matrix, whereas genetic distance of the mycobionts as well as geographic, climatic and reproductive distances were used as explanatory matrices. Pairwise genetic distances of photobionts was obtained from the alignment of ITS rDNA using JC69 model of evolution (Jukes and Cantor, 1969). The JC69 model was also used for the concatenated fungal ITS rRNA and β-tubulin genes alignment. Geographic distances were calculated from longitudinal and latitudinal data of the sampling localities. Climatic variation was modelled using climatic database WorldClim (Hijmans et al., 2005) at resolution of 2.5 arc minutes. Principal component analysis of 19 bioclimatic variables was used to reduce dimensionality (for list of bioclimatic variables and PCA biplot see Supplementary material Fig. S1 and Table S1). Similarity in reproductive strategy (asexually vs. sexually) was defined as Jaccard distance (Jaccard, 1912). All the analyses of the variance partitioning were performed using R (ver. 3.0.3; R Development Core Team).

3. Results

The final dataset contained 271 sequences, 187 of which were newly obtained in this study: 80 algal ITS rRNA sequences, 28 algal actin sequences, 38 fungal ITS rRNA sequences and 41 fungal β -tubulin sequences (Table 1). Additional 84 sequences (of both fungi and algae) were retrieved from our previous datasets (Bačkor et al., 2010; Škaloud et al., 2015; Steinová et al., 2013) and from GenBank. Sequence data were unambiguous, suggesting that only single genotypes of both mycobionts and photobionts were present in the thallus. Fungal ITS rRNA and β -tubulin sequences were 547 and 673 base pairs in length, respectively, with 69 and 79 variable and 52 and 47 informative characters, respectively. For algal loci, ITS rRNA sequences were 509 base pairs long, with 76 variable characters of which 58 were parsimonyinformative. Algal actin sequences were 576 base pairs long with 392 variable sites and 342 parsimony-informative sites.

3.1. Network analyses of Cladonia mycobionts

The consensus network of ITS rRNA and β -tubulin sequences (see Fig. 3) resulted in conflicting relationships among species, already found in our previous results (Steinová et al., 2013). The broad edges at the core of the network and the absence of long branches (except one subgroup of *Cladonia pleurota* containing specimens C6, CL67, CL73, CL100 and CL128) suggested incomplete lineage sorting or ongoing



Fig. 2. Geographic maps of the collection sites across Europe with expanded maps of the Central Europe. The distribution of the *Cladonia* mycobionts (a) and the *Asterochloris* photobionts species (b) is colour coded. (a) Sorediate species with asexual reproduction and vegetative dispersion (green), esorediate species with sexual reproduction and dispersion (red). (b) Distribution of the *Asterochloris* photobionts: the eight lineages and the single *Asterochloris* sequences correspond to those recognized in the phylogenetic analysis of Fig. 4; the two *Asterochloris* lineages associated with the asexually reproducing *Cladonia* species are labelled in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Comparison of Asterochloris diversit	v recovered in five localities in whic	h multiple samples have been collected	I. Samples in grey represent sorediate collections.

Locality ID	Geographic origin	Cladonia lichen species	sample ID	Asterochloris photobiont
1	Czech Rep., Brdy, Žďár	C. coccifera	CL86	A. lobophora
	Czech Rep., Brdy, Žďár	C. pleurota	CL85	A. irregularis
	Czech Rep., Brdy, Žďár	C. pleurota	CL99	A. glomerata
	Czech Rep., Brdy, Žďár	C. pleurota	CL101	A. irregularis
2	Czech Rep., district Tábor, Mlýny	C. diversa	CL392	A. italiana
	Czech Rep., district Tábor, Mlýny	C. deformis	CL355	A. glomerata
3	Czech Rep., Ještěd	C. coccifera	CL394	clade 8
	Czech Rep., Ještěd	C. deformis	CL393	A. irregularis
4	Czech Rep., Sedlčansko, Drbákov-Albertovy skály	C. coccifera	CL124	A. italiana
	Czech Rep., Sedlčansko, Drbákov-Albertovy skály	C. pleurota	CL128	A. glomerata
5	Germany, Saxony, Oberlausitzer Heide	C. diversa	CL364	A. italiana
	Germany, Saxony, Oberlausitzer Heide	C. deformis	CL356	A. glomerata



Fig. 3. Neighbor-net analysis of *Cladonia* mycobionts based on the combined fungal loci ITS and β-tubulin. Sorediate and esorediate species segregate in two defined groups joined by broad splits.

speciation among the four studied taxa, and corroborate the results previously shown by Steinová et al. (2013). Four samples of *C. coccifera* (CL178, CL179, CL379 and CL396) were inferred on isolated splits and remained separated from both the sorediate and esorediate groups.

3.2. Phylogenetic analyses of the Asterochloris photobionts

The Bayesian, MP and ML phylogenies resulted in similar topologies and were congruent with the phylogenetic inference of Škaloud et al. (2015). Bayesian analysis of the concatenated ITS rDNA and actin dataset resulted in 19 well-resolved *Asterochloris* lineages (see Fig. 4). Thirteen clades represented already described *Asterochloris* species, the remaining six have not been assigned a name yet (two of which were preliminary identified by the names "clade 8" and "clade A9"). The species *A. excentrica* was represented by a single sequence and was on its own single branch. The clades were fully resolved and the majority of them were highly supported. A total of eight *Asterochloris* lineages plus two *Asterochloris* sequences, which were recovered on individual branches and did not correspond to any currently recognized lineage, were found to associate with the sampled *Cladonia* taxa. *Asterochloris glomerata*, *A. italiana* and *A. irregularis* were the most common photobionts and were recovered in 31, 24 and 18 samples, respectively.

All studied sorediate *Cladonia* specimens associated only with *A.* glomerata and *A. irregularis.* However, *A. irregularis* was also the photobiont of the esorediate mycobionts, whereas *A. glomerata* associated exclusively with the sorediate mycobionts. The esorediate *Cladonia* specimens, on the other hand, exhibited a much lower level of specificity towards the associated photobionts: seven *Asterochloris* lineages and those two *Asterochloris* sequences recovered on individual branches were found to associate with them. *C. coccifera* was found to associate with six *Asterochloris* lineages (*A. irregularis, A. woessiae, A. italiana, A. lobophora, Asterochloris* clade 8 and clade A9) and the two unique

Asterochloris sequences. C. diversa was found to associate with four Asterochloris species (A. irregularis, A. echinata, A. italiana and A. lobophora).

Asterochloris italiana was the most frequent photobiont associated with the esorediate *Cladonia* specimens (24 samples), and two subclades were recognized: the first containing samples from Belgium, Denmark, Netherlands, Spain, Wales and from lower altitudes from Czech Republic, the second comprising samples from higher elevation in Czech Republic, Austria, Germany and Spain. Specimens of sorediate (CL85, CL99, CL101, CL128, CL355, CL356, and CL393) and esorediate (CL86, CL142, CL364, CL392, and CL394) samples which were collected in the same localities were always found to associate with different photobionts.

Clear differences of photobiont distribution across Europe and in Cladonia thalli could be recognized (Fig. 2b). A. italiana was mostly recovered from localities spread in the North-Western oceanic part of Europe, including Great Britain, Denmark, Belgium, The Netherlands and the Norwegian coast, but also from Central Europe (Austria, Czech Republic and Germany), Portugal and Spain (Table 1). In the North-Eastern Fennoscandia we detected only A. glomerata and A. irregularis (associated both with sorediate and esorediate fungal species). Cladonia samples collected in Central and Southern Europe associated with a considerably higher number of Asterochloris lineages. Although we included only six Cladonia samples from the Iberian Peninsula, we found four Asterochloris lineages associated with the mycobionts in this region (A. echinata, A. irregularis, A. italiana and A. woessiae). Samples collected in Central Europe contained seven Asterochloris lineages and the two unique Asterochloris sequences. The Austrian Alps and the Krkonoše Mts. in the Czech Republic were the regions with the richest Asterochloris diversity detected in Central Europe.



Fig. 4. Multigene phylogenetic inference of *Asterochloris* photobionts: Bayesian hypothesis based on the combined dataset of ITS and actin I loci. Bootstrap support for the ML and MP analyses and the Bayesian posterior probability are reported at the corresponding branches. Branches have been collapsed to report multiple samples represented by the same sequence data. Upper case numbers (1–5) correspond to specimens of sorediate and esorediate species collected at the same locality, as reported in Table 2. Samples are colour coded according to the reproductive and dispersal mode of the lichens: sorediate asexual species in green and esorediate sexual species in red. *Asterochloris* lineages recovered in the studied *Cladonia* are in bold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 5. Variance partitioning analysis showing the percentage of explained photobiont diversity based on the four explanatory variables of (i) the mycobiont genetic diversity, (ii) the geographic, (iii) the climatic and (iv) the reproductive distances. Values in bold show pure effects of the explanatory variables.

3.3. Variance partitioning

The PCA of bioclimatic variables revealed two main gradients. The first PC axis explained 40.39% of photobiont variability and was mainly following a precipitation gradient. The second axis corresponded to the temperature range and seasonality gradient and explained 31.52% of variability in the climatic data set (see PCA biplot in Supplementary material Fig. S1). In downstream analyses, we use scores of sites for PC1 and PC2 to represent climatic conditions.

Our linear regression model including reproductive strategies, geographical distance, climatic similarity and genetic distance of mycobiont significantly explained altogether 46.16% of variability in the genetic distance of photobionts (Fig. 5). Of these, the reproductive mode had the largest explanatory power, with 43.90% of variability explained, though a large portion was also represented by the covariance with the mycobiont genetic distance. The isolated effect of reproduction mode, when accounted for covariance with all other explanatory matrices, was associated with 16.7% of variability in genetic distance of photobiont (Fig. 5). The other explanatory variables accounted only for minor percentages of variability, although they were selected as significant for the complete linear model. A substantial percentage of variability remained unexplained by our model (53.8%) and might account for some unmeasured environmental heterogeneity, or alternatively, a degree of stochasticity in associations.

4. Discussion

4.1. Species delimitation in Cladonia lichens

In our study we tested whether reproductive mode might shape the diversity of mycobiont-photobiont association in *Cladonia* lichens. For this purpose we analyzed specimens that differed by the type of the vegetative propagules present on the podetium, which is at the same time an important morphological character used for the taxonomic assignment in this group of lichens.

As found previously, the phylogenetic analysis of the mycobionts

did not support the current delimitation of the studied taxa which is based on morphological characters, in particular the type and size of vegetative propagules. Such a discrepancy between the traditional morphologically based species delimitation and the results of phylogenetic analyses is, however, not uncommon in *Cladonia* lichens (e.g., Pino-Bodas et al., 2010, 2011, 2012) and suggests that a critical revision of characters used for species delimitation in this group of lichens is needed. Our previous study (Steinová et al., 2013) showed that some of the lineages can be characterized by subtle chemical differences.

4.2. Symbiotic diversity is shaped by host reproductive strategies

Mutualistic interactions offer suitable examples to study co-evolution, partner specificity, evolutionary responses and ecological adaptations to symbiotic lifestyles (Bronstein et al., 2004). So far only few studies have evaluated the influence of reproductive strategies of mycobionts on the specificity of photobiont associations (Cao et al., 2015; Fedrowitz et al., 2011; Otálora et al., 2010; Wornik and Grube, 2009). The selected complex of the four Cladonia taxa is well suited to test multiple hypotheses in this context. Because the mycobionts of sorediate species rarely build sexual reproductive structures, they have been hypothesized to reproduce and disperse asexually. The prevailing asexual dispersal mode would logically justify specific mycobiontphotobiont associations, because fungi and algae are co-dispersed. Alternatively the esorediate taxa, in which mycobionts abundantly produce apothecia, are hypothesized to reproduce mainly sexually by ascospores. By reproducing sexually, these mycobionts could show different levels of specificity towards their photobiont.

Within the broad spectrum of their geographic distribution in Europe, our results show that the two sexually reproducing *Cladonia* species adopted a generalist strategy by associating with numerous *Asterochloris* lineages. In contrast, the asexually reproducing species were associated exclusively with *A. glomerata* or *A. irregularis* even in localities where other *Asterochloris* species were detected in the sexually reproducing species (Table 2). The strict maintenance of these two *Asterochloris* lineages over large geographic distances indicates high

specificity towards its photobionts (Fedrowitz et al., 2012). A similar pattern of high mycobiont specificity towards its symbionts in asexually reproducing lichens, coupled with a low level of specificity in sexually reproducing lichens, was observed also previously in other *Cladonia* species (Yahr et al., 2004, 2006) and in *Nostoc*-associating *Nephroma* and *Degelia* species by Fedrowitz et al. (2011) and Otálora et al. (2012).

All Cladonia species studied here produce some kind of vegetative propagules. We hypothesize that the different specificity of the mycobiont toward its photobiont can be attributed to the differences in size and amount of vegetative propagules built on the podetium, and the ability to produce viable ascospores. The role of the relatively large vegetative propagules of esorediate *Cladonia* species in lichen dispersal is likely very limited, and the mycobiont dispersion is ensured by the ascospores produced in the always- abundant ascomata. Therefore, the low specificity towards the algal partner is advantageous for the esorediate Cladonia fungi, which have to find a suitable algal partner shortly after their germination. On the contrary, soredia represent abundant and light vegetative propagules that detach easily and can replace ascospores as the main dispersal propagules with all pros and cons of this strategy. Interestingly, it has been reported that ascospores of sorediate lichens can have a strongly reduced reproductive function (Molina et al., 2013). The authors compared the spore viability between the mixed species Physconia grisea and the related sexual species P. distorta and showed that mature apothecia from both species discharged meiospores capable of germination, but spores from P. grisea rarely (0.43%) developed, whereas those from P. distorta developed and germinated successfully.

The algal genetic diversity in populations of lichenized fungi having distinct propagation strategies is, however, not always necessarily different. This can be explained by the process denoted as "algal switching" (Piercey-Normore and DePriest, 2001), where a successful horizontal photobiont transmission is commonly observed in sexually reproducing lichen fungi, but it seldom takes place in asexual species. *Physconia* species, though reproducing vegetatively by soredia, presented an unexpected high photobiont diversity (Wornik and Grube, 2009). It was suggested that depending on the viability of the soredial algae, the soredial fungi could choose between establishing the new thallus with the co-propagated alga or with another photobiont, likely better adapted to the local conditions. The main role of the original photobiont would be to prolong the survival of the co-propagated fungal hyphae (Wornik and Grube, 2009).

Photobiont switching is now understood as a rather common phenomenon in lichen symbiosis (e.g., Nelsen and Gargas, 2009; Piercey-Normore, 2006) allowing the mycobiont to adapt to local environmental conditions (Werth and Sork, 2010) or to extend its geographical range or ecological niche (Fernández-Mendoza et al., 2011). The asexual Cladonia fungi, by having the possibility to switch algae, would be guaranteed the option of either maintaining their algal partner, or replacing it if a better-adapted one is available. Other symbiotic systems, such as corals, are well known for their in situ adaptation and capacity to regulate their fitness according changing ecological conditions. Studies on Anthopleura-Symbiodinium/Elliptochloris symbioses have shown how the presence and the identity of the photobionts in different environmental conditions balance the life and the reproductive strategies of the anemone host (Bingham et al., 2014). In lichens the maintenance of the symbiotic association would, therefore, be an option but not a strict consequence of the joint, vegetative symbiont propagation (Wornik and Grube, 2009).

Our results show that the studied asexual *Cladonia* species do not switch photobionts, and we suggest that this may result in severe consequences for their survival in a changing environment. The ability to switch photobionts allows a fine-tuned symbiosis to be flexible and resilient over geographic and environmental gradients in space and time, while a very specific mutualism may lead to its termination (Nelsen and Gargas, 2009). This is particularly true for asexually reproducing lichens in which a substantial proportion of the evolutionary flexibility has already been lost by the absence of sexual reproduction, thought to be beneficial to the longevity of a species (Muller, 1932). Clonal reproduction via vegetative propagules helps to overcome the problem of limited availability of symbiotic partners. However, such a tight and rigid relationship between symbiotic partners together with the loss of adaptability by strictly asexual reproduction may become an evolutionary trap in the long term.

In corals, the adaptive bleaching hypothesis (Buddemeier and Fautin, 1993) explains that process by which the animal hosts reshuffle their photosynthetic symbiont to overcome environmental changes and survive (Baker, 2003; Parkinson and Baums, 2014). The studied *Cladonia* species are found in diverse ecological conditions, and we demonstrate that the photobionts are significantly structured by both climate and geography, although the explanatory power of these is smaller compared to the mode of reproduction. In the future, however, they might face severe environmental changes. If they will not evolve the ability to switch to locally adapted photobionts, they may become rare or even go extinct (Domaschke et al., 2012), as it has already been shown in other systems (LaJeunesse et al., 2003).

4.3. Can symbionts substantially control the distribution of the hosts?

We observed two main patterns of Asterochloris diversity across Europe: (i) high Asterochloris diversity within relatively small geographic regions, and (ii) wide geographic areas dominated by only one or two Asterochloris species. The first group was represented in Czech Krkonoše Mts. and the Austrian Alps, where we found five named Asterochloris lineages plus a single Asterochloris type, belonging to a still unnamed taxon: these were associated with seven (from Krkonoše Mts.) and ten (from Austrian Alps) Cladonia specimens respectively. The Central European mountains seem therefore to represent hotspots of Asterochloris species richness. In contrast, the North-Western oceanic parts of Europe were dominated by A. italiana. In Nordic countries (Norway and Finland), Cladonia species were found to associate mostly with A. glomerata and A. irregularis. This can be explained either by the preference of the Cladonia species to associate with those Asterochloris lineages adapted to the local environmental conditions or by a very low Asterochloris diversity in these areas. The low Asterochloris diversity in the area of Fennoscandia may be caused by environmental filtering (Dal Grande et al., 2017) or, alternatively, can possibly be the consequence of the recolonization history after the last glacial maximum (e.g., Hoarau et al., 2007). This finding would contradict the hypothesis of ubiquitous distributions of microorganisms caused by their high dispersal rates (Fenchel and Finlay, 2004; Finlay, 2002; Ryšánek et al., 2015; but see Lowe et al., 2012). However, patterns similar to those observed here have already been reported for other symbiotic protists (Domaschke et al., 2012; LaJeunesse et al., 2010) and might well be explained by the co-propagation of both symbiotic partners constraining their distributional ranges. Further study of other potential Asterochloris hosts in Fennoscandia could help to test this hypothesis.

There is strong evidence that symbiotic organisms associate preferentially with locally adapted partners, both in lichens (e.g., Dal Grande et al., 2017, 2012; Muggia et al., 2014) and other mutualistic associations (e.g., Finney et al., 2010; Pánková et al., 2014; Sampavo et al., 2007; Ulstrup and Van Oppen, 2003). This implies that low specificity of the host towards its symbiotic partner(s) helps the host to take advantage of the locally adapted symbiotic partners and colonize larger geographic areas. In contrast, hosts which strictly associate with a limited number of symbiotic partners are expected to show narrower ecological width, resulting in more restricted geographical and/or ecological distribution. In symbiotic associations the generalist pattern is far more common and has been reported from coral-algae symbioses (Pochon and Pawlowski, 2006; Rowan et al., 1997), fungus-farming insects (Schlick-Steiner et al., 2008), mycorrhizae (Porras-Alfaro and Bayman, 2007), as well as lichens (Rikkinen et al., 2002). In contrast the specialist pattern is much rarer and has been reported for rare

orchid species associating with a limited number of fungal species (Graham and Dearnaley, 2011; Swarts et al., 2010) or for Nostoc-associating lichen fungi (Otálora et al., 2010). In our study, the sexually reproducing Cladonia lichens were shown to be generalists, whereas asexual Cladonia can be considered specialists. Also, there are clear differentiations in the geographical distributions in Europe which correlate with the degree of mycobiont specificity of the studied Cladonia species. The asexually reproducing Cladonia deformis and C. pleurota are common in boreal zone and in mountain regions all over Europe but are rare in North-Western oceanic part of Europe (Belgium, Denmark, Great Britain, Ireland, Netherlands). This is, at the same time, an area in which the photobiont A. italiana has been shown to dominate in this lichen group and where the sexually reproducing lichens showing lower level of specificity (C. coccifera and C. diversa) are common (Fig. 2). It is possible that the distribution of sorediate Cladonia species in this part of Europe may be limited by the local environmental conditions not suitable for the physiological optimum of their preferred photobionts A. glomerata and A. irregularis. Another possible explanation is that the performance of both interacting partners as one unit (holobiont) can be negatively affected by the local conditions (Dal Grande et al., 2017), although A. glomerata and A. irregularis may be present in the same geographical area associated with other mycobionts. This could be confirmed or ruled out by a more extensive sampling of other Cladonia species potentially harbouring A. glomerata and A. irregularis in W Europe. These observations would then support the hypothesis that photobiont availability and its ability to cope with local environmental conditions may play key roles in shaping the distribution of lichens which present high specificity towards their algal partner.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2019.02.014.

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