



Cryptic diversity and symbiont interactions in rock-psy lichens



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ABSTRACT

Identifying factors that influence species interactions is central to research in symbiotic systems. While lichens represent iconic models of symbiosis and play important roles in understanding the biology of symbiotic interactions, patterns of interactions in lichen symbionts and mechanisms governing these relationships are not well characterized. This is due, in part to the fact that current taxonomic approaches for recognizing diversity in lichen symbionts commonly fail to accurately reflect actual species diversity. In this study, we employed DNA-based approaches to circumscribed candidate species-level lineages in rock-psy lichen symbionts (mycobiont = *Rhizoplaca* s. lat. species; photobiont = *Trebouxia* species). Our results revealed a high degree of cryptic diversity in both the myco- and photobionts in these lichens. Using the candidate species circumscribed here, we investigated the specificity of the symbionts toward their partners and inferred the relative importance of various factors influencing symbiont interactions. Distinct mycobiont species complexes, ecozones, and biomes are significantly correlated with the occurrence of photobiont OTUs, indicating that complex interactions among mycobiont lineages, ecogeography, and microhabitat determine interactions between photobionts and their mycobionts in lichen symbiosis. One-to-one specificity between mycobiont and photobiont species was not found, with the exception of *R. maheui* that associated with a single *Trebouxia* OTU that was not found with other *Rhizoplaca* s. lat. species. We estimated the most recent common ancestor of the core *Rhizoplaca* group at c. 62.5 Ma, similar in age to the diverse parmelioid core group in the well-studied family Parmeliaceae. However, in contrast to Parmeliaceae, species in *Rhizoplaca* were found to associate with a narrow range of photobionts. Our study provides important perspectives into species diversity and interactions in iconic lichen symbiotic systems and establishes a valuable framework for continuing research into rock-psy lichens.

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1. Introduction

Symbiotic interactions are considered a fundamental feature of life (Gilbert et al., 2012; Margulis, 1970; McFall-Ngai, 2008). These intimate, and often obligate, interactions among organisms from evolutionarily distinct lineages play central roles in physiology, reproduction, evolution, and other fundamental biological processes (Godfrey-Smith, 2015; Oliver et al., 2009; Turnbaugh and Gordon, 2009). In spite of the overarching importance of symbioses, teasing apart specific mechanisms structuring interactions

among symbionts has historically been stymied due to a variety of factors, including an incomplete perspective of diversity and a general inability to accurately identify microbial partners. Recognition of species-level diversity in symbiotic systems has enabled an improved understanding of several fundamental aspects of symbiotic interactions (Darwell et al., 2014; Franklin et al., 2012; Gazis et al., 2011; Pinzón and LaJeunesse, 2011).

Lichens represent iconic examples of symbioses and consist of a filamentous fungus – the mycobiont – usually obligatorily associated with a photosynthesizing partner – the photobiont. Lichens are commonly referred to as dual or composite organisms, or even miniature ecosystems. The latter two terms may be more appropriate as lichen-forming fungi have been shown to associate with a

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broad range of other microorganisms in addition to their primary photobiont partners (Arnold et al., 2009; Aschenbrenner et al., 2014; Grube et al., 2009; Hodkinson and Lutzoni, 2009; Muggia et al., 2013). Cryptic, or previously unrecognized species-level lineages have been shown to be common in lichen symbionts (Leavitt et al., 2015; Lücking et al., 2014; Lumbsch and Leavitt, 2011; Muggia et al., 2014; Pérez-Ortega et al., 2012; Sadowska-Deś et al., 2014). The increasing ability to accurately delimit and recognize species-level lineages provides opportunities for better understanding symbiosis using these iconic symbiotic systems.

Interactions among potential lichen symbionts have been described in terms of selectivity, specificity, and availability; and each has been shown to have significant impacts on structuring lichen associations (Fernández-Mendoza et al., 2011; Muggia et al., 2013, 2014; Vargas Castillo and Beck, 2012; Werth and Sork, 2010; Wirtz et al., 2003; Yahr et al., 2006). From the perspective of the mycobiont, specificity can be defined as the range of compatible photobiont partners, while selectivity is used to describe the frequency of association with distinct photobiont lineages (Rambold et al., 1998). Distributions of lichen symbionts are known to play important roles in shaping lichen symbiotic interactions (Dal Grande et al., 2012; Fernández-Mendoza et al., 2011; Fernández-Mendoza and Printzen, 2013; Muggia et al., 2014; Peksa and Škaloud, 2011; Werth and Sork, 2014) and evolution in these symbiotic systems (Magain and Sérusiaux, 2014; Rambold et al., 1998; Rikkinen et al., 2002).

The algal genus *Trebouxia* Puymaly associates with half or more of all lichen-forming fungal species, and members of this genus are especially common as photobionts in extra-tropical regions (Ahmadjian, 1993). However, species-level diversity in *Trebouxia* remains poorly characterized. A number of recent studies highlight that the current taxonomy woefully underestimates the actual number of species-level lineages in this important genus of lichen photobionts and the pressing need for a provisional nomenclatural system (Casano et al., 2011; Kroken and Taylor, 2000; Leavitt et al., 2015; Muggia et al., 2014; Sadowska-Deś et al., 2014; Werth and Sork, 2014). Currently, four major clades are known within *Trebouxia*; the ‘*arboricola/gigantea*’, ‘*galapagensis/usneae*’, ‘*impressa/gelatinosa*’, and ‘*simplex/letharii/jamesii*’ clades (Beck et al., 2002; Helms, 2003). Within each clade, provisional species-level photobiont OTUs have been circumscribed using a barcode gap detection approach for photobionts associating with the diverse mycobiont family Parmeliaceae (Leavitt et al., 2015). Arguably, increasing our ability to recognize species-level lineages in *Trebouxia* and accurately identifying samples will help facilitate research improving our perspective of symbiotic interactions in lichens.

In this study we use rock-posy lichens (Fig. 1) as a model for exploring diversity and interactions among lichen myco- and photobionts. Rock-posy lichens comprise a mycobiont from the genus *Rhizoplaca* s. lat. (Lecanoraceae) – *Rhizoplaca* species and *Protoparmeliopsis peltata* (Ramond) Arup, Zhao Xin & Lumbsch (Zhao et al., 2016) – in association with photobionts from the genus *Trebouxia* (Arup and Grube, 2000). Rock-posies are commonly found in arid, exposed, continental habitats throughout the world. However, *Rhizoplaca* s. lat. species are almost completely absent from Africa, with the exception of Morocco and the Canary Islands, and appear to be completely absent from Australia. The mycobiont genus *Rhizoplaca* s. lat. is comprised of ca. 24 species, with the highest diversity in Central Asia and western North America. Some species are known to occur across broad ecological and intercontinental distributions, including *P. peltata*, *R. chrysoleuca* (Sm.) Zopf, *R. melanophthalma* (DC.) Leuckert & Poelt, and *R. subdiscrepans* (Nyl.) R. Sant. In contrast, other species are only found in geographically and ecologically restricted habitats. For example, *R. macleanii* (C.W. Dodge) Castello occurs strictly in

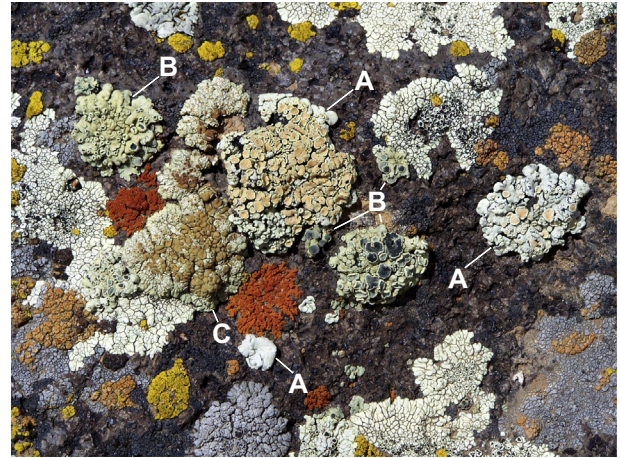


Fig. 1. Three common rock-posy lichens with broad, intercontinental distributions co-occurring on a basalt boulder in southern Utah, USA: A – “orange rock-posy” lichen (mycobiont = *Rhizoplaca chrysoleuca* s. lat.); B – “green rock-posy” lichen (mycobiont = *Rhizoplaca melanophthalma* s. lat.); and C – “scattered rock-posy” lichen (mycobiont = *Rhizoplaca subdiscrepans* s. lat.). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

continental Antarctica; *R. maheui* (Hue) Gómez-Bolea & M. Barbero is known exclusively from central Spain; and *R. marginalis* (Hasse) W.A. Weber occurs solely in the southern portion of the Sierra Nevada range in southern California, USA.

Previous studies have revealed cryptic diversity in both the nominal taxa *R. chrysoleuca* and *R. melanophthalma* (Leavitt et al., 2011; Zhou et al., 2006). The center of diversity for the *R. melanophthalma* group is the Great Basin region of western North America, where all known species within this complex occur (Leavitt et al., 2013b). A number of species in this group, including *R. melanophthalma* s. str. and *R. parilis*, occur in geographically disjunct populations worldwide, including documented populations in Central Asia, Europe, the southern Andes in South America, and western North America (Leavitt et al., 2013a). However, the remaining species – *R. haydenii*, *R. idahoensis*, *R. occulta*, *R. polymorpha*, *R. porteri*, and *R. shushanii* – are currently known only from western North America, although *R. haydenii* has been reported from China (Zheng et al., 2007).

In contrast to the *R. melanophthalma* group, the potential for cryptic species-level diversity and their associated distribution patterns are not well characterized for other nominal *Rhizoplaca* s. lat. species. Zhou et al. (2006) reported that samples of *R. chrysoleuca* from montane regions in China occur in two distinct phylogenetic clades with corresponding phenotypic variation. Similarly, DNA sequence data revealed the potential for cryptic species in the Antarctic endemic *R. macleanii* (Pérez-Ortega et al., 2012). However, phylogenetic inferences and species delimitation analyses for both *R. chrysoleuca* and *R. macleanii* were limited to a single genetic region, the internal transcribed spacer region (ITS). While a limited number of specimens representing other *Rhizoplaca* species have occasionally been included in phylogenetic studies (Arup and Grube, 2000; Cansaran et al., 2006; Kondratyuk et al., 2014; Zheng et al., 2007), the potential for cryptic species-level lineages within species complexes and evolutionary relationships among species remain largely untested. Furthermore, estimating the timing of diversification of cryptic species-level lineages can aid in identifying factors that give rise to commonly overlooked biodiversity.

The number of mycobiont species greatly exceeds the number of available photobiont partners, and reciprocal one-to-one specificity is generally not expected (Ahmadjian, 1960; Otálora et al., 2010). However, reciprocal symbiont specificity has been observed

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