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NEWS AND VIEWS

PERSPECTIVE

Fungal farmers or algal escorts: lichen adaptation from the algal perspective

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Domestication of algae by lichen-forming fungi describes the symbiotic relationship between the photosynthetic (green alga or cyanobacterium; photobiont) and fungal (mycobiont) partnership in lichen associations (Goward 1992). The algal domestication implies that the mycobiont cultivates the alga as a monoculture within its thallus, analogous to a farmer cultivating a food crop. However, the initial photobiont 'selection' by the mycobiont may be predetermined by the habitat rather than by the farmer. When the mycobiont selects a photobiont from the available photobionts within a habitat, the mycobiont may influence photobiont growth and reproduction (Ahmadjian & Jacobs 1981) only after the interaction has been initiated. The theory of ecological guilds (Rikkinen *et al.* 2002) proposes that habitat limits the variety of photobionts available to the fungal partner. While some studies provide evidence to support the theory of ecological guilds in cyanobacterial lichens (Rikkinen *et al.* 2002), other studies propose models to explain variation in symbiont combinations in green algal lichens (Ohmura *et al.* 2006; Piercey-Normore 2006; Yahr *et al.* 2006) hypothesizing the existence of such guilds. In this issue of *Molecular Ecology*, Peksa & Škaloud (2011) test the theory of ecological guilds and suggest a relationship between algal habitat requirements and lichen adaptation in green algal lichens of the genus *Lepraria*. The environmental parameters examined in this study, exposure to rainfall, altitude and substratum type, are integral to lichen biology. Lichens have a poikilohydric nature, relying on the availability of atmospheric moisture for metabolic processes. Having no known active mechanism to preserve metabolic thallus moisture in times of drought, one would expect a strong influence of the environment on symbiont adaptation to specific habitats. Adaptation to changes in substrata and its properties would be expected with the intimate contact between crustose lichens in the genus *Lepraria*. Altitude has been suggested to influence species distributions in a wide range of taxonomic groups. This is one of the first studies to illustrate an ecological guild, mainly for exposure to rainfall (ombrophiles and ombrophobes), with green algal lichens.

Keywords: ecological guild, environmental effects, lichen adaptation, photobiont

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The elegance of this study is the test of the theory of ecological photobiont guilds (Rikkinen *et al.* 2002) using a sterile green algal lichen eliminating the possibility of algal switching (algal transfer among fungal partners) by ascospore dispersal and thallus re-establishment. Even though algal transfer between soredia and thalli of *Lepraria* has been previously hypothesized (Nelsen & Gargas 2008), and habitat specialization was shown for a sexually reproducing fruticose epiphyte (Werth & Sork 2010), this study links the algal transfer among *Lepraria* spp. with environmental parameters. The authors recorded ecological parameters, such as exposure to rain, altitude and substratum type, and removed the mode of reproduction as a confounding factor to test the theory of ecological guilds. They were able to show that the photobiont (*Asterochloris*), which associates with members of the genera *Lepraria* and *Stereocaulon*, exhibits environmental preferences, and the algal phylogenetic relationships were largely explained by these environmental influences. The objectives of the study were to test whether environmental preferences exist in *Asterochloris* implying they form ecological guilds. Nucleotide sequences of two algal loci, the internal transcribed spacer of ribosomal DNA (ITS rDNA) and the actin type I locus were compared among 46 algal cultures and 61 lichen thalli and were supplemented with sequences from GenBank accessions. The ecological variables were superimposed on the phylogenetic tree revealing three main ecological guilds for *Asterochloris*: ombrophobic acidophilous lichens, ombrophilic mountain lichens on siliceous rocks and ombrophilic lowland lichens on SiO_2 poor substrates.

The focus of this study is on a sterile genus *Lepraria*, but Peksa & Škaloud (2011) also examined members of a related but sexually reproducing genus *Stereocaulon* for comparison. The mode of reproduction is thought to influence the outcome of symbiont combinations in lichens because vegetative reproduction can be achieved by release of thallus propagules that contain both symbionts. However, ascospores are released from ascomata without the algal partner during sexual reproduction, which promotes new symbiont combinations at each dispersal event. Because most ascomycete lichen fungi form obligate associations with algal partners, a germinating ascospore is hypothesized to die if a photobiont is not encountered

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Fig. 1 The gray fruticose pseudopodetia of *Stereocaulon* sp. mask the photobionts but reveal tiny black fruit bodies from sexual reproduction by the fungal partner.

Fig. 2 The crustose thallus of *Lepraria* sp. is composed of a mass of vegetative propagules, soredia. (Photograph by T. Booth).

within a suitable habitat after ascospore germination. Most lichens have the ability to reproduce sexually such as *Stereocaulon* (Fig. 1), but few lichens are considered to be completely sterile. Members of the genus *Lepraria* are some of the few lichens that have no known sexual phase and reproduce vegetatively by producing large masses of soredia that contain both the algal and fungal partners (Fig. 2). This would eliminate the possibility that algae are transferred among fungal genotypes by sexual reproduction and would promote the same combinations of symbionts in all offspring. However, the hypothesized transfer of algal genotypes among fungal partners in *Lepraria* has been shown by Nelsen & Gargas (2008). Therefore, one of the limiting factors for algal association with the fungal partner would be the ecological preference of the algal partner, rather than algal availability through different reproductive modes. If ecologically available algal genotypes, free living or lichenized, are limited by the ecological conditions, then the fungal ascospores that disperse to those habitats can only associate with the algae that survive in the habitat and with those algae to which both fungal and algal partners are genetically compatible.

As with any key contribution, this study raised new questions for further research. An understanding of environmental influences on the photobiont alone, rather than the photobiont within the symbiosis, would contribute to our knowledge of the ecological requirements of the photobiont. A better understanding of environmental effects on the algal partner might be achieved with more detailed measurements of a larger breadth of ecological variables. For example, the substratum description of 'wood-bark' highlights the need to narrow the definition of substratum in further epiphytic photobiont research. The simple elegance of the study also reflects a limitation of the study in that only two genera of green algal lichens were examined. The limitation of testing the theory with only two genera leaves the question of ecological guilds unanswered for other crustose lichens. It also leaves the question unanswered for foliose and fruticose lichens that have less thallus contact with the substratum and more thallus exposed directly to atmospheric conditions. Further studies of fruticose lichens with a crustose primary thallus, such as *Stereocaulon*, might improve our understanding of environmental influence on developmental stages of lichen thalli. Habitat preference by the fungal partner has not been addressed within the scope of this study, prompting further investigation to incorporate fungal adaptation and shedding more light on its role in the symbiosis. Lastly, the presence of ecological guilds for photobionts of rare or endemic species could also have repercussions for species risk assessment and habitat preservation.

This study has significant implications for other symbioses in a changing environment. As an example, the relationship between phylogenetic lineages and moisture preferences of sterile lichens is similar to the relationship shown by colonies of *Montastraea* corals and light levels (Rowan 1998). That these findings extend to both aquatic and terrestrial symbioses highlight the sensitivity of environmental fluctuations to the photosynthetic partner in the symbiosis. Similar results between a terrestrial and aquatic symbiosis suggest that the habitat preferences of one partner are widely occurring in nature. Sexual reproduction of the fungal partner in lichens is analogous to egg production by some corals (van Oppen *et al.* 2001), in that the coral must find suitable symbiotic partners for every generation. The sensitivity to environmental conditions displayed by algal partners in the symbiosis provides plasticity to different environmental conditions in which the coral and the fungus can adapt by forming associations with native (optimal) algae. This adaptive plasticity is further strengthened by the coral's ability to associate with multiple partners at once and by the lichen's ability to select optimal algal partners for the habitat to which it has dispersed. The fungal farmer may cultivate the photobiont for optimal food production, but the photobiont is predetermined by the habitat and it escorts the fungal partner through various habitats in the establishment of the lichen association.

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