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NEWS AND VIEWS

PERSPECTIVE

Exploring symbiont management in lichens

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Lichens are unique among fungal symbioses in that their mycelial structures are compact and exposed to the light as thallus structures. The myriad intersections of unique fungal species with photosynthetic partner organisms (green algae in 90% of lichens) produce a wide variety of diverse shapes and colours of the fully synthesized lichen thallus when growing in nature. This characteristic complex morphology is, however, not achieved in the fungal axenic state. Even under ideal environmental conditions, the lichen life cycle faces considerable odds: first, meiotic spores are only produced on well-established thalli and often only after achieving considerable age in a stable environment, and second, even then *in vivo* resynthesis requires the presence of compatible algal strains where fungal spores germinate. Many lichen species have evolved a way around the resynthesis bottleneck by producing asexual propagules for joint propagation of symbionts. These different dispersal strategies ostensibly shape the population genetic structure of lichen symbioses, but the relative contributions of vertical (joint) and horizontal (independent) symbiont transmission have long eluded lichen evolutionary biologists. In this issue of *Molecular Ecology*, Dal Grande *et al.* (2012) close in on this question with the lung lichen, *Lobaria pulmonaria*, a flagship species in the conservation of old growth forests. By capitalizing on available microsatellite markers for both fungal and algal symbionts, they show that while vertical transmission is the predominant mode of reproduction, horizontal transmission is demonstrable and actively shapes population genetic structure. The resulting mixed propagation system is a highly successful balance of safe recruitment of symbiotic clones and endless possibilities for fungal recombination and symbiont shuffling.

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The study of lichens has been for many years the almost exclusive purview of enthusiastic systematists. Although the symbiotic nature of lichens became clear already in the second half of the 19th century, most researchers have continued to focus on the fungal structures and only rarely have paid closer attention to the algal symbionts. While it has always been possible to assess relationships among the fungal partners through microscopy of their complex structures, the same cannot be said for the algae, which are smaller and usually do not develop diagnostic characters in the symbiotic stage. Culturing of lichen photobionts has been the only possibility to distinguish and classify species of microalgae and cyanobacteria isolated from lichen symbioses, but such approaches are cumbersome and, therefore, limited in their use. Consequently, although more than 18 500 species of lichenized fungi are known, the algal partners of most lichen symbioses have yet to be identified (little more than 100 species have been reported; Lücking *et al.* 2009). The refinement of molecular methods and development of specific primers for algal gene loci has dramatically improved our baseline knowledge of the diversity and variability of photosynthetic partners. It furthermore has enabled lichen evolutionary biologists to posit an array of new questions and cleared the way for lichens to be tapped into as model systems in the context of microbial and molecular ecology.

Molecular studies of lichen photobionts have revealed different degrees of selectivity in entering into partnerships in the lichen symbiosis. Some lichenized fungi form symbioses with several algal lineages, while others are more restricted to a single species. In both cases, it has been

Fig. 1 The lung lichen, *Lobaria pulmonaria*, pursues two strategies of symbiont propagation. Production of sexual fungal spores in disc-shaped fruiting bodies (s) contributes to horizontal transmission of symbionts. The fungal spores must re-associate with algae of the environment to resynthesize the lichen. Locally, the lichen thallus also develops grain-like structures composed of both fungal and algal partners (v). These structures easily detach from the lichen and represent a way to vertically transmit successful symbiont combinations (Photograph by P. Bilovitz).

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found that the fungal partner commonly switches algal symbiont genotype, casting doubt on hypotheses of fungal–algal coevolution. Biont switching could instead be an important adaptive strategy that merits more detailed analysis. Most studies to date have relied on sequenced DNA markers of the lichen algae (mostly ITS). While such markers provide sufficient resolution for the detection of distinct lineages of algae, they are too conserved to assess lichen symbiont population structures and the effects of vertical and horizontal transmission at a population genetic level.

The lung lichen *Lobaria pulmonaria* forms large, leafy thalli in cool, humid forests with long-term habitat continuity. It is extremely sensitive to air pollution and, therefore, an esteemed bioindicator of first-class air quality. The species is widespread in the Northern Hemisphere and present also in mountain regions of the Tropics and in South America. Throughout Europe and in parts of North America, *L. pulmonaria* is declining because of habitat loss, air pollution and the effects of climate change. On account of the considerable interest that has been shown by conservation biologists, *L. pulmonaria* is perhaps the best studied lichen species at a worldwide scale from an ecological and population genetic point of view. *Lobaria pulmonaria* associates with a single species of green alga, *Dictyochloropsis reticulata*, throughout its entire geographic range. While *D. reticulata* provides the fungus with photosynthates, nitrogen supply is backed up by the inclusion of cyanobacterial (*Nostoc*) colonies embedded in the thallus. For both fungal and the algal partners, microsatellite loci developed in the laboratory of C. Scheidegger and co-workers have made it possible to gain detailed insight into the genetic structure of a model case of lichen symbiosis.

Lobaria pulmonaria has two possibilities for producing progeny: fungal ascospores spread from conspicuous, disc-shaped fruiting bodies, and vegetative propagules produced in small outgrowths (called isidia or soredia) in which the alga is packaged into bundles of compact fungal hyphae (Fig. 1). Until now, it has been unclear to what extent sexual propagation horizontally reshapes the genetic structure of the component bionts of *L. pulmonaria* by reshuffling fungal and algal genotypes otherwise transmitted vertically in pre-packed, joint vegetative propagules. In their study, Dal Grande *et al*. (2012) use eight fungal and seven algal microsatellite markers to parse the contribution of horizontal and vertical transmission to the genetic structure of *L. pulmonaria* populations. By restricting the analysis for one symbiont to pairs of lichen thalli with genetically identical symbiotic partners, they show that 77% of fungal and 70% of algal pairs are represented by clones. The analysis of variable microsatellite data also provides evidence for mutations in the algal partner, but without significant evidence for recombination. The fungal genetic structure by contrast is significantly shaped by recombination. The authors suggest that faster mutation rates could be responsible for comparable genetic variation in the asexual algal partners.

It has been previously shown that dispersal of vegetative propagules is spatially limited in *L. pulmonaria* (Walser 2004), and the present work of Dal Grande *et al*. (2012) shows that the signal for vertical transmission is cut in half over distances of 10 m. Vegetative propagules represent minute thallus initials that are larger, heavier and less aerodynamic than fungal spores. However, vertical transmission conveys clear advantages, including bypassing the bottleneck of biont resynthesis and, once established and producing sexual structures, opening the possibility for experimentation with new biont lineages under new microhabitat conditions. *Lobaria pulmonaria* is only one example of the advantages of a mixed propagation system. With their large number of species, body plans and biont combinations, lichens offer an evolutionary cornucopia for other insights into symbiont management. To adapt to local climatic conditions, lichens can adjust the ratio of algae as producers versus fungi as consumers in their thalli (Sun & Friedman 2005), and in other cases, lichenized fungi have been shown to select locally optimized strains or species for thallus formation (Blaha *et al*. 2006; Fernández-Mendoza *et al*. 2011), and recent studies demonstrate intrathalline coexistence of two closely related but physiologically differing algal partners (Casano *et al*. 2011). With these recent advances, we conclude that the ecological success of lichens may owe itself in no small part to their ability to calibrate biont associations across a wide range of environmental conditions.

References

Blaha J, Baloch E, Grube M (2006) High photobiont diversity in symbioses of the euryoecious lichen *Lecanora rupicola* (Lecanoraceae, Ascomycota). *Biological Journal of the Linnean Society*, **88**, 283–293.

Casano LM, del Campo EM, García-Breijo FJ *et al*. (2011) Two *Trebouxia* algae with different physiological performances are ever-present in lichen thalli of *Ramalina farinacea*. Coexistence versus competition? *Environmental Microbiology*, **13**, 806–818.

Dal Grande F, Widmer I, Wagner H, Scheidegger C (2012) Vertical and horizontal photobiont transmission within populations of a lichen symbiosis. *Molecular Ecology*, **21**, 3159–3172.

Fernández-Mendoza F, Domaschke S, García MA, Jordan P, Martín MP, Printzen C (2011) Population structure of mycobionts and photobionts of the widespread lichen *Cetraria aculeata*. *Molecular Ecology*, **20**, 1208–1232.

Lücking R, Lawrey JD, Sikaroodi M *et al*. (2009) Do lichens domesticate photobionts like farmers domesticate crops? Evidence from a previously unrecognized lineage of filamentous cyanobacteria. *American Journal of Botany*, **96**, 1409–1418.

Sun HJ, Friedman EI (2005) Communities adjust their temperature optima by shifting producer-to-consumer ratio, shown in lichens as models: II. Verification. *Microbial Ecology*, **49**, 528–535.

Walser JC (2004) Molecular evidence for limited dispersal of vegetative propagules in the epiphytic lichen *Lobaria pulmonaria*. *American Journal of Botany*, **91**, 1273–1276.

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