

Modeling the Coevolutionary Dynamics of the *Lobaria pulmonaria* Lichen Symbiosis

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Abstract

Lichens are a hyperdiverse symbiotic group spread across the globe in widely different *niche* and climates. This partnership between fungi and a photobiont (cyanobacteria, algae or both) allows the fungi to obtain carbohydrate-rich resources directly from their photosynthetic partner[14] while the fungus protects the photobiont from desiccation, allowing for coevolution and adaptive radiation into new environments[17]. Lichenization is an evolutionarily and ecologically successful strategy (>20% of fungi are lichenized), resulting in approximately 14,000 lichen species known to date[14, 13]. Although the nature of the lichen symbiosis is still widely debated, many sources agree that the lichen system represents an ecologically obligate mutualistic interaction whereby the net fitness of all partners is maximized[5, 13].

Lichens can reproduce sexually via fungal spores (horizontal transmission) and asexually via vegetative propagules and thallus fragmentation (vertical transmission). In the sexual mode of reproduction, the fungal spores must interact with a compatible free-living algae and/or cyanobacterium in order to reconstitute the lichen thallus. In the asexual mode of reproduction, mycobionts and photobionts are co-dispersed via fragmentation of the main thallus body and specialized asexual propagules.

These peculiar mode of reproduction strongly influences the genetic structure of lichen populations[6, 7], affecting dispersal and evolutionary rates. This was evidenced by recent articles in the most studied lichen system: *L. pulmonaria*, where thalli from 62 populations in forests throughout Europe, North America, Asia, and Africa were genotyped at several hypervariable microsatellite loci[6]. These studies concluded that the *L. pulmonaria*-*S. reticulata* symbiosis showed significant within-population genetic structure due to restricted gene flow and vertical transmission (i.e. co-dispersal of vegetative propagules).

The lichen symbiosis is extremely interesting, as the nature of the system is different from the widely studied plant-animal mutualistic systems[19, 3, 2,

4, 18, 9]. Its different modes of reproduction, the fact that you find events of delichenization throughout evolution [15] and that non of the partners is mobile (only throughout spores), make of it a rather particular system. Moreover, it has been conjectured the asymmetry in the coevolution of the two species, due to a limited capacity of adaptation in the photobiont[10] as well as that the relationship between the two species cannot always be considered a mutualism but rather a comensalism or even parasitism (with the fungi taking advantage over the photobiont) [1].

In order to unveil which are the potential factors driving the evolution of the lichen symbiosis, as well as its population structure, we constructed an agent-based model based on the widely used ECHO framework[11, 12]. The ECHO model typically consists of a collection of entities living in a simplified spatial domain, which can move around and interact with one another and with their environment. The interactions among agents can be used to model different kinds of processes -such as mating-, and are driven by locality as well as agent-specific properties, namely the agents' genotypes. The ECHO model is also a continuous genetic algorithm[16]; upon reproduction old genotypes are copied with slight mutations, giving rise to quantifiable evolutionary dynamics.

In our case, we used the tag system of ECHO to model the molecular recognition (receptors and physical embedding) between algae and fungi necessary to create the lichen. We considered two different lichenization functions based on similarity, sigmoid (hill function with $n = 2$) and michaelis-menten (saturation dynamics). Additionally, other ecologically relevant features such as dispersal rates (introduced here as random walks) and the ratio between sexual and asexual reproduction were included in the model. Simulations were carried out assuming a wide range of ecological relations between the algae and fungi: competition (both algae and fungi are better off on their own than forming a lichen), parasitism (only one type of agent benefits from the partnership) and mutualism (both agents benefit).

On the other hand, we have studied two available data sets [6, 8]. The first consists of the fungal and algal symbionts of 1960 *L. pulmonaria* thalli from 62 populations in forests throughout Europe, America, Asia and Africa genotyped at eight and seven microsatellite loci, respectively. The sparseness of this dataset has only allowed us to find potential similarities at a sampling scale (for each region sample) with the population of lichens retrieved from the ECHO model. The second one, were seven alga-specific microsatellite of a particular algal species were genotyped for a total of 13 fungal species forming partnership, allowed us to compare the structure of the bipartite network arising from a higher level, where significant modular structure is found. Different measures from network theory have been used to unveil the structure of the studied bipartite networks, with different interesting results arising. Having the temporal scale in the ECHO model has allowed us to study the possible coevolution signatures that might be driving the evolution of the lichen symbiosis.

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References

1. Ahmadjian, V.: The lichen symbiosis. John Wiley & Sons (1993)
2. Bascompte, J., Jordano, P.: The structure of plant-animal mutualistic networks. Ecological networks: linking structure to dynamics in food webs. Oxford University Press, Oxford, UK pp. 143–159 (2006)
3. Bascompte, J., Jordano, P., Olesen, J.M.: Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312(5772), 431–433 (2006)
4. Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J.: The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458(7241), 1018–1020 (2009)
5. Bronstein, J.L.: Our current understanding of mutualism. *Quarterly Review of Biology* pp. 31–51 (1994)
6. Dal Grande, F., Widmer, I., Wagner, H., Scheidegger, C.: Vertical and horizontal photobiont transmission within populations of a lichen symbiosis. *Molecular ecology* 21(13), 3159–3172 (2012)
7. Dal Grande, F.: Phylogeny and co-phylogeography of a photobiont-mediated guild in the lichen family Lobariaceae. Ph.D. thesis (2011)
8. Dal Grande, F., Beck, A., Cornejo, C., Singh, G., Cheenacharoen, S., Nelsen, M.P., Scheidegger, C.: Molecular phylogeny and symbiotic selectivity of the green algal genus *dictyochloropsis* sl (trebouxiophyceae): a polyphyletic and widespread group forming photobiont-mediated guilds in the lichen family lobariaceae. *New Phytologist* 202(2), 455–470 (2014)
9. Guimaraes Jr, P.R., Jordano, P., Thompson, J.N.: Evolution and coevolution in mutualistic networks. *Ecology letters* 14(9), 877–885 (2011)
10. Hill, D.J.: Asymmetric co-evolution in the lichen symbiosis caused by a limited capacity for adaptation in the photobiont. *The Botanical Review* 75(3), 326–338 (2009)
11. Holland, J.H.: Echoing emergence: Objectives, rough definitions, and speculations for echo-class models. In: *Complexity*. pp. 309–342. Perseus Books (1999)
12. Holland, J.H.: Hidden order: How adaptation builds complexity. Basic Books (1995)
13. Honegger, R.: The lichen symbiosis—what is so spectacular about it? *The Lichenologist* 30(3), 193–212 (1998)
14. Lutzoni, F., Miadlikowska, J.: Lichens. *Current Biology* 19(13), R502–R503 (2009)
15. Lutzoni, F., Pagel, M., Reeb, V.: Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* 411(6840), 937–940 (2001)
16. Mitchell, M.: An introduction to genetic algorithms. MIT press (1998)

17. Nash, T.H.: Lichen biology. Cambridge University Press (1996)
18. Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P., Bascompte, J.: Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448(7156), 925–928 (2007)
19. Rohr, R.P., Saavedra, S., Bascompte, J.: On the structural stability of mutualistic systems. *Science* 345(6195), 1253497 (2014)