

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 a fungus (also called the mycobiont) and a photobiont (cyanobacteria, algae or both) allows the fungus to obtain carbohydrate-rich resources directly from their photosynthetic partner [8] while the fungus protects the photobiont from desiccation, leading to the coevolution of both species and adaptive radiation into new environments [10]. Lichenization is an evolutionarily and ecologically successful strategy (>20% of fungi are lichenized), resulting in approximately 14,000 lichen species known to date [8, 7]. 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 [1, 7].

Lichens can reproduce sexually and asexually. In the asexual mode of reproduction, mycobionts and photobionts are co-dispersed via fragmentation of the main thallus body or via specialized asexual propagules, resulting into a genetically identical lichen where the photobiont is vertically transmitted from the initial thallus to the new lichen. In the sexual mode of reproduction, the fungal spores are spread without photobiont and have thus to find a compatible algae and/or cyanobacterium in order to reconstitute the lichen thallus (*relichenization*). This mechanism lead to the horizontal transmission of a new photobiont from a neighbouring lichen or from a free-living photobiont, genetically different than the photobiont associated with the mother lichen.

These peculiar mode of reproduction strongly influences the genetic structure of lichen populations [4, 2], affecting dispersal and evolutionary rates. Though it has been recently shown, through the study of *L. pulmonaria* [4], that asexual reproduction could be the main way of reproduction for lichen, sexual reproduction is suspected to play a central role at larger evolutionary scale. Relichenization process could be a successful strategies for genetic recombination, allowing

lichens to explore wider ecological niche by sharing photobiont between different lichens already adapted to different local conditions. It has been hypothesized [11] that those process could lead to the emergence of photobiont-mediated guilds, where different species of lichen interact and exchange similar photobionts within an evolutionary coherent structure. Those loosely integrated functional units, where different species can exchange chemical elements and genetics materials, are a good candidate to explain the evolutionary success of lichen. They allow its different sub-components to evolve more or less independently, at different rate and under different ecological niche, thus making the whole community more responsive to environmental change and able to adapt to wider range of environmental condition.

Nonetheless, studying the evolutionary dynamics of such assemblages is a difficult task. It involves a broad range of heterogeneous entities that co-evolve and interact ecologically at various spatial and temporal level. This makes fields study delicate and costly as they have to include lot of material from different place and different temporal scale. Experimental work is also difficult as lichen are fragile biological entities extremely dependent to they local environment that are complex and hard to reproduce in laboratories.

One solution to encompass such obstacles is the use of computer simulations. It allows the study of a wide range of parameters involving a massive number of heterogeneous entities. In order to do so and to unveil which are the potential factors driving the evolution of the lichen symbiosis and of broader ecological and evolutionary interactions, we constructed an agent-based model based on the widely used ECHO framework [5, 6]. 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 [9]; 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).

To legitimate the choice and the design of our model, we crossed the study of the result of the simulations with empirical evidences. Our idea is to first show the ability of our model to reproduce simple dynamics already well stud-

ied and understood and then demonstrate that this ability can be scaled from the “bottom up”, to different level of increasing complexity; before generalizing to encompass all the level of interaction, from simple well-known biological processes to broadest interspecies co-evolutionary dynamics.

In a first time, we used the data coming from [4]. The goal of that study is to understand the very local process of dispersion and reproduction of one kind of lichen *L. pulmonaria*, at the level of limited populations of the same lichen. Using tools borrowed to network theory, we show that our model can successfully reproduce the dynamics and the general properties exhibited by populations, implying that the implemented processes are consistent with the biological ones.

In a second time, we look at data from [3]. In that case, some key features of the interactions between different species of lichens, thus coming from wider population, are measured. We use our model to show that those key features can indeed emerge from the generalization and the expansion of the same process previously described, as far as certain particular conditions are met.

In the future, and given the ability of our model to reproduce those first level of dynamics, we want to expand our simulation to greater and see if the emergence of more complex entites is possible, and if yes under which condition. We expect that our results could help to measure the solidity of the photobiont-mediated guilds hypothesis and could give pist for biologist onton what they should expect to find.

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