

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

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Lichens are a hyperdiverse symbiotic group spread across the globe in widely different niches 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 [1] while the fungus protects the photobiont from desiccation, leading to the coevolution of both species and adaptive radiation into new environments [2]. Lichenization is an evolutionarily and ecologically successful strategy (>20% of fungi are lichenized), resulting in approximately 14,000 lichen species known to date [1, 3]. 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 [4, 3].

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 the photobiont and have thus to find a compatible algae and/or cyanobacteria in order to reconstitute the lichen thallus (*relichenization*). This mechanism leads to the horizontal transmission of a new photobiont from a neighboring lichen or from a free-living photobiont, genetically different from the photobiont associated with the lichen from which the fungal spores come from.

This peculiar mode of reproduction strongly influences the genetic structure of lichen populations [5, 6], affecting dispersal and evolutionary rates. Though it has been recently shown, through the study of *L. pulmonaria* [5], 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 strategy for genetic recombination, allowing lichens to explore wider ecological niche by sharing photobiont between different lichens already adapted to diverse local conditions. It has been hypothesized [7] that

this 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. These loosely integrated functional units, where different species can exchange resources and genetics materials, are good candidates to explain the evolutionary success of lichens. They allow its different sub-components to evolve more or less independently, at different rates and under different ecological niche, thus making the whole community more responsive to environmental changes and able to adapt to a wider range of environmental conditions.

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 levels. This makes fields studies delicate and costly as they have to include lot of material from different places and different temporal scales. Experimental work is also difficult as lichens are fragile biological entities extremely dependent to their local environment, conditions complex and hard to reproduce in the laboratory.

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 [8, 9]. 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 [10]; 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 simulations' results with empirical evidences. We first show the ability of our model to reproduce simple dynamics already well studied and understood. Then, we demonstrate that this ability can be scaled through a 'bottom-up' approach to different levels of increasing complexity; before generalising to encompass all

the level of interaction, from simple well-known biological processes to broad interspecies co-evolutionary dynamics.

At the empirical level, we have first used a dataset from [5] to understand the very local process of dispersion and reproduction of the lichen *L. pulmonaria*. Using tools borrowed from 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 approach, we have studied a dataset from [11]. In this case, some key features of the interactions between different species of lichens, thus coming from wider populations, 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 push further our simulations to see if the emergence of more complex entities is possible, and if it is the case, under which conditions. We expect our results to help testing the solidity of the photobiont-mediated guilds hypothesis, thus unveiling the important factors driving the evolutionary dynamics of the lichen symbiosis, and through that, shed new light on how species can co-evolve to form complex ecological communities.

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