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Project acronym: LICHENOMICS

Project title: Lichen population genetics and genomics - Gene expression, neutral and adaptive genetic variation in natural populations of *Peltigera membranacea*

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One of the major questions pertaining to climate change is whether species can respond to rapid climate change, and avoid extinction. Many argue that contemporary climate change is a primary threat to biodiversity worldwide. In order to persist, populations must adapt to or tolerate the changed environmental conditions in situ, or migrate to sites with suitable conditions. To understand a species' response to climate change, it is thus essential to quantify the species' spread, its tolerance due to phenotypic plasticity, and its potential for adaptation through selection on adaptive phenotypes. The goal of this project is to assess the impacts of climate change on populations of the lichen fungus *Peltigera membranacea* by studying migration, adaptation and tolerance with landscape genetics, landscape genomics and experimental transcriptomics.

About one fifth of all fungi form lichen symbioses, and more than 15,000 species of lichen-forming fungi are known. Lichens are important components of terrestrial biota worldwide, contribute to important ecosystem functions such as nutrient cycling, food supply and habitat for invertebrates. Lichen-rich communities are known to host particularly high invertebrate diversity. Little is known about how environmental changes such as climate warming affect populations of lichen-forming fungi, but it is to be expected that mutualistic symbioses, fine-tuned associations of two or more partners interacting with each other to mutual benefit, might be strongly affected by climate change. Indeed, results from species distribution modelling based on bioclimatic envelopes predict major future range shifts for several species of lichen-forming fungi. Some lichen fungi show evidence of restricted gene flow or low dispersal ability. If unable to tolerate the conditions created by rapid climatic change, these species have an elevated extinction risk due to their limited ability to shift ranges. Thus, it is important to study gene flow patterns in lichen fungi and their potential for adaptation to a changing environment.

Peltigera membranacea (Ach.) Nyl. (lichenized Ascomycetes) is a terricolous lichen distributed in North America, Europe, Asia, and Africa. This species is one of the key players in carbon and nitrogen cycling in ecosystems at northern latitudes due to its symbiosis with cyanobacteria of the genus *Nostoc* and its high abundance in terrestrial, vegetated habitats. Substantial genomic resources were available for *P. membranacea* in the lab of the Icelandic host at the start of the project. We used this lichen-forming fungus as a study species to quantify various aspects of relevance to predict the species' performance in a changing climate. The main objectives of this project were the following: 1) To evaluate whether *P. membranacea* is able to migrate to new sites with favorable conditions. 2) To assess whether *P. membranacea* may tolerate changed environmental conditions in situ by changes in gene expression that would allow it to tolerate changed conditions. 3) To evaluate whether populations of *P. membranacea* are able to adapt to changed climatic conditions.

Objective 1. We quantified the species' dispersal potential by studying landscape-level patterns of genetic differentiation using microsatellite markers developed from available genomic resources. A low number of migrants per generation is sufficient to eliminate genetic differentiation among sites, implying that if genetic differentiation between populations is high, there is little ongoing and historical gene flow. Microsatellite markers were developed for the fungus *P. membranacea* to quantify population subdivision. Genetic differentiation among populations was studied with the microsatellite markers in two study landscapes in Iceland to assess whether *P. membranacea* is likely to spread to new sites with suitable conditions when the environment is changing. Our results showed that populations of the lichen-forming fungus *P. membranacea* are highly differentiated, implying low migration between sites within a landscape. These results imply that the fungus has a limited ability to spread to new sites, implying a low capacity for surviving environmental changes by long-distance colonization of new habitats with suitable conditions.

Objective 2. Based on existing genome data (host lab), we identified 119 genes involved in fungal environmental stress responses (ESR). We subjected individuals of *P. membranacea* with differing genetic backgrounds to temperature stress in a controlled laboratory environment, and quantified gene expression levels of ESR genes with a RNA sequencing approach. The experiment showed that gene expression differed significantly between high and low temperatures in several of the ESR loci, implying that the symbiosis has some potential to tolerate environmental stress in situ. We also quantified gene expression in lichen thalli physiologically adapted to the environment provided by coastal and inland sites in Iceland.

Objective 3. We quantified climatic correlations of microsatellite alleles after removing the effect of population structure, which reflects population history rather than climatic signal. Microsatellite alleles of *P. membranacea* showed significant associations with temperature-related bioclimatic variables. High-throughput sequencing of ESR genes based on RNA-sequencing data were used to identify SNPs with an association to environmental variables to infer the species' potential to adapt to the environment based on standing genetic variation within populations.

Overall, the results obtained during the course of the project have clarified the response of lichen fungi to climate change, in terms of the species' potential for adaptation, tolerance of changed conditions, and spread of individuals to new sites. This project has strengthened a unique discipline involving numerous fascinating biological phenomena yet to be explored.

Figure 1. The study species *Peltigera membranacea*, a ground-dwelling lichen which is a keyplayer in nitrogen and carbon fixation in northern ecosystems.