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Macroevolutionary dynamics of marine algae

Introduction

Systematic biologists aim to characterize and understand the diversity of life on earth. Their goals can be subdivided into three broad categories: (1) delimiting and describing species, (2) reconstructing the tree of life, and (3) characterizing and explaining patterns of diversification. Thanks to the availability of new data (mainly DNA sequences) and a suite of new statistical techniques, great progress has been made on the first two goals. As a consequence, it has become possible to proceed to the third goal.

Macroevolutionary studies aim to **characterize and explain large-scale patterns and processes in the history of life**. The patterns are situated above the species level and include the origins of novel organismal designs, speciation–extinction dynamics, and other evolutionary trends. Explanations are sought by **integrating systematics with other scientific disciplines** such as genetics, ecology, geography and paleontology, aiming to relate the data from these other disciplines to evolutionary trends in a phylogenetically explicit statistical framework. Although many advances have been made in studies of macroevolutionary dynamics, the interdisciplinary nature of the research and the need for custom-tailored analysis pipelines still hinders progress. Marine algae form ideal model systems for this line of research (see below) but very little research has been carried out on their macroevolutionary dynamics. This project focuses on three key evolutionary issues that can be addressed with marine algae: cytological diversification, evolutionary niche dynamics and historical biogeography.

Goals

The goal of this project is to advance our knowledge of the evolutionary diversification of seaweeds, focusing on three aspects of their macroevolution.

1. Genetic correlates of cytological diversification of the Ulvophyceae

Starting from unicellular ancestors, a diversification of organismal designs has taken place in the green algal class Ulvophyceae [1, 2]. One lineage still has remained unicellular (*Ignatius*) but other lineages have developed multicellular filamentous and membrane-like thalli (Ultrichales, Ulvales, Trentepohliales). In contrast to these groups, which have uninucleate cells, another lineage developed multinucleate cells (Cladophorales, Bryopsidales). The Cladophorales form branched filamentous thalli. The Bryopsidales and its sister order Dasycladales are essentially unicellular: they have large, branched, siphonous cells with complex patterns of cytoplasmic flow. This diversification of designs has been known for a long time but remains poorly understood. The molecular cell-biological characteristics that facilitate multicellularity and multinucleate and siphonous cells have, for the most part, remained unidentified. Large evolutionary changes often occur in association with gene or genome duplication events, after which redundant gene copies can evolve a new or more specialized function. The first goal of this project is to gain insight in the genetic correlates of the evolution of multicellularity, siphonous cell structure and multinucleate cells.

2. Evolutionary dynamics of the macroecological niche

The distribution patterns of seaweed species are far from random [3]. Their niche is determined by their physiological tolerances, which are in turn susceptible to evolutionary forces. As a consequence, niche characteristics can be interpreted as evolutionary phenomena. Very little is known about evolutionary niche dynamics in seaweeds [4] even though such insights are crucial to answering questions about biogeography, biodiversity patterns and conservation biology [5, 6]. The second goal of this project is to characterize the evolutionary dynamics of the macroecological niche in the seaweed genera *Halimeda* and *Codium*. A related goal is to infer whether and how niche dynamics affect rates of speciation.

3. Flexible framework for historical biogeographic inference

Seaweeds offer excellent model systems for marine biogeographic research. Having low natural dispersal potential [7], they feature high regional endemism and yield vast amounts of information that can be used to infer historical biogeographic processes. Formal biogeographic inference with

explicit spatial and phylogenetic components is relatively recent. The first, elementary methods such as dispersal-vicariance analysis [8] can be expected to be replaced with model-based techniques that allow more flexibility. A recent technique uses a spatially explicit model of cladogenesis (speciation), local extinction and dispersal [9]. This results in biologically interpretable parameter estimates, facilitates the identification of an optimal biogeographic scenario, and opens perspectives for formal tests of alternative biogeographic hypotheses. The third goal of this project is to improve the current models and use them to characterize the global biogeographic history of marine macroalgae.

General strategy

Integration of different sources of data and techniques from various disciplines is crucial to reach these goals. In order to identify the genetic correlates of cytological diversification, the evolution of protein families will be inferred from expressed sequence tag (EST) libraries. Evolutionary niche dynamics will be investigated by integrating methods from geographic research (GIS) with ecological niche modeling and evolutionary inference techniques. Macroecological data will be derived from satellite imagery, species occurrence data will be obtained from carefully identified collections, and phylogenetic trees will be inferred from multi-locus DNA datasets. The biogeographic element requires some technical developments and performance assessments with simulation studies. For the practical application, large geographic and phylogenetic datasets of marine macroalgae are available.

Summary of methods

Each of the goals requires its own set of techniques for data preparation, which will be detailed below. The shared methodological component is the way in which the evolutionary dynamics of the relevant features are inferred from the datasets. This is achieved by **modeling the evolution of the features** in question in a phylogenetically explicit framework. The phylogenetic trees that serve as the backbone for these studies will be inferred from DNA alignments using state of the art model-based techniques [10]. The evolutionary dynamics of relevant characters will be inferred by optimizing models of trait evolution that are variants or generalizations of Markov models for categorical (including binary) data and Brownian motion models for continuous data [11, 12]. The mode and tempo of evolution will be further investigated with the Pagel branch-length modifiers [12]. Associations between rates of diversification and trait evolution will be investigated by fitting character-state dependent models of cladogenesis [13, 14].

1. The genetic correlates of cytological diversification will be derived from genomic information and **expressed sequence tag (EST) libraries**. Complete genomes and/or EST libraries are available for various unicellular outgroups and representatives of the Ulvales and Dasycladales. Libraries for representatives of the Cladophorales and Bryopsidales are being generated and I will apply for funding to obtain ESTs for *Ignatius* and Trentepohliales. Analysis of the EST data will allow the **identification of expanding gene families** in the focal group. Partial information about functional diversification can be gleaned from in-silico analysis [15]. After a selection of apparently diversifying gene families has been made, targeted gene amplification in a broader set of taxa will complete the image of their diversification in association with the cytological diversification. The EST approach offers the advantage that even gene families that would not *a priori* be expected to be associated with the cytological diversification can be detected. A paper that my colleagues and I recently published in *BMC Evolutionary Biology* used a similar approach to model patterns of gain and loss of alternative elongation factor genes in green algal genomes [16].
2. The evolutionary niche dynamics of the seaweed genera *Halimeda* and *Codium* will be studied in collaboration with Lennert Tyberghein and Klaas Pauly, two PhD students that I am co-supervising. The **evolutionary history of niche affinities will be estimated** from the observed niche affinities of present species with evolutionary modeling techniques. The macroecological niche of extant species will be derived from **georeferenced species occurrence data** and global **macroecological datasets** derived from satellite imagery (NASA: oceancolor.gsfc.nasa.gov) and interpolated in-situ

measurements (NOAA: www.nodc.noaa.gov). Due to the taxonomic complications caused by cryptic diversity and convergent evolution, species boundaries will be inferred from DNA sequence data [17] and phylogenies will be inferred from multi-locus alignments. Parts of these data are already available from previous research. Evolutionary dynamics of the macroecological niche will be studied by model fitting approaches as mentioned above. This is illustrated in a recent paper my colleagues and I published in the journal *Global Ecology and Biogeography* [18].

3. For the **historical biogeographic** aspect, the most advanced technique that is currently available will be improved. The present technique uses a spatially explicit model of cladogenesis (speciation), local extinction and dispersal, which is optimized along a phylogenetic tree using maximum likelihood [9]. The limitation of this model is that all parameters are constant in time, which is unrealistic (e.g. by continental drift, changing ocean current intensities). I will adapt this model to **allow temporal variation in the parameters** [19]. In order not to unnecessarily inflate parameter space, model reduction approaches guided by clustering analyses of parameter estimates will be used [20]. The new theoretical developments will be thoroughly tested with **simulated datasets** for which the true biogeographic history and parameter values are known. The technique will be applied to infer global marine biogeographic patterns from **extensive datasets of marine macroalgae** generated in the Ghent lab and by various collaborators.

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