

SUMMARY

Evolution, diversity en niche dynamics of seaweeds

Plants and animals are not randomly distributed on the face of the planet, but exhibit nearly always well defined ranges and meet universally recognizable patterns. During the past decades, studies of species diversity patterns were for the most part approached from an ecological perspective and focused largely on finding links between environmental parameters and species richness. Although this type of research confirmed the strong correlations between climate and species diversity, the fundamental question how climate affects the number of species in a particular community or region was not satisfactorily answered.

A number of recent studies approached questions relating to species diversity patterns by investigating species' ecological niches in an evolutionary framework. Each species is characterized by a particular ecological niche, a set of biotic and abiotic conditions in which they can thrive and can maintain stable populations. Statistical inference of ecological niches, known as niche modeling, is also used to determine whether variation in the macro-ecological environment affects diversification in space and time. In other words, what effect has niche evolution in a given group of species on its diversification?

Until recently, evolutionary niche dynamics were only studied for terrestrial organisms. Despite the fact that niche modeling was already successfully applied for marine organisms, an evolutionary approach of studying ecological niches and its relationship with diversity patterns was never attempted. To achieve this objective, seaweeds (marine macroalgae) are a well suited group of organisms. Previous knowledge of macroecological niches of seaweeds arises on the one hand from ecophysiological experiments that determined survival, growth and reproduction under different culture conditions, and on the other hand from studies correlating algal distribution patterns with isotherms. Evolutionary dynamics of macroalgal niches never received much attention. Important progress in the field of niche modeling and tools for analyzing evolutionary patterns in a phylogenetic context currently allow a more global approach to this issue.

In general, this thesis aims at characterizing macroecological niches and large-scale geographic diversity patterns of seaweeds from an evolutionary point of view. Our goal is to elucidate how niches evolved, how niche dynamics can lead to diversification and how this results in observed distribution patterns. For this purpose both a global marine environmental data set as well as new modeling tools is developed. This in combination with techniques from phylogenetic, ecological, evolutionary and geographical research helps us to clarify these patterns.

Chapter 1 presents Bio-ORACLE (Ocean Rasters for Analysis of CLimate and Environment). This data set aims to boost marine distribution and niche modeling applications by providing the first comprehensive standardized and uniform global marine environmental dataset, readily downloadable and usable for predictive studies.

Bio-ORACLE is constructed from a combination of satellite imagery and interpolations of in situ oceanographic measurements and currently contains 23 raster map layers containing different dimensions representative for the marine environment. We demonstrated global applicability through a case study of the invasive green alga *Codium fragile* subsp. *fragile*, predicting its potential spread.

The choices made during the ecological niche modeling process can affect the transferability and overall predictive performance of the resulting model. **Chapter 2** presents a framework designed to promote correlative modeling of invasive species. We introduce two methods that have the potential to increase the transferability of correlative species distribution models (SDMs), more specifically a tool that reduces geographical bias in occurrence records and one that identifies suitable sets of predictors. We apply these methods to the introduced and highly invasive seaweed species *Caulerpa cylindracea*, aiming to infer a solid niche model for this species that can assist in predicting areas with suitable habitat worldwide and assessing the risk of further spreading. Our results show that reducing the set of predictors to those anticipated to be of global significance yielded a strong improvement of SDM transferability, with occurrence thinning, model complexity and background choice having relatively minor effects. If both occurrences from the native and invaded regions are available, they should be combined, as this results in the best-performing models and reduces the sensitivity to choices made in the modeling process. The resulting SDM of the highly invasive species *Caulerpa cylindracea* achieves very high predictive power.

In **chapter 3**, we infer the evolutionary history of the green algal genus *Halimeda* using a time calibrated molecular phylogeny. We model distributions and reconstruct the ancestral niche of the current species within the genus. Results showed that the niche of *Halimeda* is conserved for tropical, nutrient depleted habitats, while one section of the genus invaded colder waters several times independently. Since known distribution ranges are considerably smaller than modeled potential ranges, we conclude that restricted geographical ranges are likely the result of dispersal limitation.

In **chapter 4**, we present an empirical approach to gain understanding in the biogeography and evolution of warm-temperate marine floras. The focus in this chapter lies on the marine green algal *Codium decorticatum* species complex. We use climatic niche modeling and divergence time estimation to explore the historical biogeography and evolution of thermal variables within the complex. The climatic models were projected to the Last Glacial Maximum and the Pliocene to examine whether the Indian Ocean served as a thermal barrier for dispersal. Our results suggest that during the late Miocene – early Pliocene species within the *C. decorticatum* complex dispersed via episodic dispersal events. After geographic isolation, species have adapted to local conditions and their thermal niches have diverged from their closely related species.

In **Chapter 5**, we examined the evolution of the thermal niche through time in relation to the diversity pattern of the brown alga genus *Dictyota*. The evolutionary history of this genus was characterized by means of a time calibrated molecular phylogeny in combination with thermal data. In addition, the relationship between the evolution of the thermal niches and the diversification rate was studied. Results show that species diversification within this genus is positively associated with the ability of clades to shift their thermal niche. This outcome might have implications for the interpretation of large scale marine diversity patterns.