

GENERAL INTRODUCTION

NICHE

Biogeography, systematics, population biology and other associated research areas become increasingly integrated into a cross-disciplinary framework for understanding the distribution of life on Earth (Diniz-Filho *et al.*, 2008). Theories and methods are getting shared, and some of these blends have yet been discussed (Richards *et al.*, 2007; Kozak *et al.*, 2008; Pearman *et al.*, 2008). A central concept underpinning this cross-disciplinary framework is the 'species niche'.

Despite its long standing history in ecological research, the niche concept has revived in recent years (Soberon & Nakamura, 2009). Many definitions to explain the term 'niche' have been suggested during the last century. Joseph Grinnell was the first to propose a concept of an ecological niche (Grinnell, 1917). The so-called Grinnellian niche can be defined by fundamentally non-interacting habitat variables and abiotic environmental conditions on broad scales (so-called "scenopoetic" variables), relevant to understanding coarse-scale ecological and geographic properties of species (Soberon, 2007). Later investigators focused niche concepts increasingly on the role of a species in an ecological community. This gave rise to the Eltonian niche, which focuses on biotic interactions and resource-consumer dynamics essentially acting at local scales (so-called "bionomic" variables) (Soberon, 2007).

For the purposes of this dissertation the ideas established by Hutchinson (1957) serve adequately. In his now famous “concluding remarks”, Hutchinson defined two correlated aspects of the niche which capture the relative pressures of both biotic and abiotic environments on a species’ range. The ‘fundamental niche’ describes the abiotic conditions in which a species is able to persist, whereas the ‘realized niche’ describes the conditions in which a species persists given the presence of other species as well as by spatial accessibility (Wiens & Graham, 2005) (Figure 1A). An interesting rephrasing of Hutchinson’s niche concept is to characterize it as the mapping of population dynamics onto a multidimensional abstract space, defined by environmental axes that affect an organism’s fitness (Holt, 2009). This allows us to represent the niche as a multidimensional, dynamic space, within which movement can occur along the different axes. Selective pressure along the niche axes can result in evolutionary responses to the environment. As such the niche represents the interface between ecological and evolutionary processes acting to shape a species’ geographical range (Powell, 2012). This concept serves as a common premise throughout this thesis.

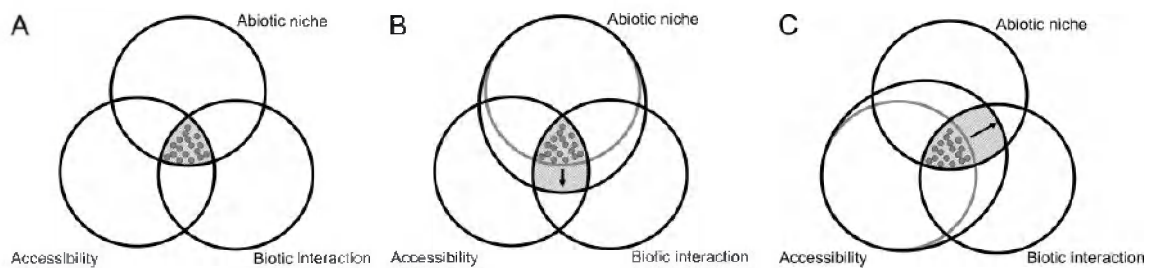


Figure 1: A) Diagram illustrating the three interacting factors that determine a species’ geographic distribution: the fundamental (abiotic) niche, biotic interaction and accessibility; B) Fundamental niche shift; C) better exploitation of the fundamental niche after access into new areas. The gray shaded area represents the realized niche. (Rodder *et al.*, 2009; after Soberon & Peterson, 2005)

NICHE modeling

The differentiation between fundamental and realized niches provides a conceptual framework in the context of ecological niche modeling practices (Pulliam, 2000). Some niche models use direct measures of species' physiological response to environmental conditions, as such estimating the fundamental niche of a species (see Kearney & Porter, 2009). This so-called mechanistic approach can additionally incorporate biotic interactions to predict a species' realized niche (Soberon & Peterson, 2005). However, the most common way of ecological niche modeling (also referred to as species distribution modeling) establishes the macroecological preferences of a given species based on observed distribution records and a set of macroecological variables (e.g. temperature, precipitation, soil conditions, nutrients) that are likely to influence the suitability of the environment for that species (Guisan & Zimmermann, 2000). These preferences can subsequently be used to predict geographical areas with suitable habitat for the species. There exist a whole range of different algorithms for such correlative modeling approaches (see (Elith *et al.*, 2006; Wisz *et al.*, 2008) for comparison). Results from ecological niche modeling studies have provided insight into a variety of questions relevant to ecology and evolutionary biology (Rissler & Apodaca, 2007). These include: the importance of niche conservatism to speciation (Kozak & Wiens, 2006); the geographic spread of invasive species (e.g. Broennimann *et al.*, 2007; Rodder & Lotters, 2009; see below); distributions of undiscovered species (Raxworthy *et al.*, 2003); inferences of historical and future distributions (e.g. Yesson & Culham, 2006; Peterson *et al.*, 2002) and historical biogeography (Smith & Donoghue, 2010).

ENVIRONMENTAL DATA

Environmental data is becoming more and more accessible (Kozak *et al.*, 2008). Such data include digital maps that quantify spatial variation and temporal variation in a series of environmental parameters (e.g. temperature, nutrients and salinity). Environmental data can be extracted as point data and subsequently used in combination with phylogenetic information for evolutionary studies (see below) or serve as gridded GIS maps for ecological niche modeling applications. Global environmental data for some predictor variables are easily accessible for terrestrial climates via the online data repositories WorldClim (<http://www.worldclim.org/>) and CLIMOND (<https://www.climond.org/>). Until recently, no comparable marine counterpart was available (Robinson *et al.*, 2011). However, chapter 1 in this thesis presents a marine dataset that attempts to boost marine ecological niche modeling.

NICHE dynamics

NICHE CONSERVATISM – NICHE DIVERGENCE

The evolution of niche features among species can provide important insights into ecological differentiation and species evolution (Ackerly *et al.*, 2006). A species' ecological niche changes, expands or contracts over time in response to natural selection acting on variations in fitness due to mutations, genetic drift and selection (Colwell & Rangel, 2009). Its corresponding geographical distribution can change dramatically or not change at all (Colwell & Rangel, 2009). For example, when climatic conditions change, a species can respond by moving, adapting or going extinct (Holt, 1990). In this context, the stability of the niche is of fundamental importance: it influences the need for species to track climate change via dispersal, or its potential to adapt to novel conditions. This is the principle of two non-exclusive scenarios of niche evolution. If species adapt, they consequently shift their niche. However, another possibility to respond to environmental change is by the colonization of new habitats. This scenario has been supported by studies on several species (e.g. Losos *et al.*, 2003; Graham *et al.*, 2004). In the opposed scenario, where species fail to adapt to new ecological conditions, species keep their niche characteristics (Wiens, 2004). This tendency to retain similar niches over time is known as niche conservatism (Wiens *et al.*, 2010).

NICHE MODELING OF INVASIVE SPECIES

Alien invasive species are a concern in nature conservation as they may have a negative impact on native biodiversity. Understanding the factors that make non-native species successful invaders is a crucial step to managing geographic spread (Medley, 2010). Invasive species may provide valuable insights for ecology and evolutionary biology (Sax *et al.*, 2007). Ecological niche models are currently the most commonly used tool for predicting the geography of species invasions (Thuiller *et al.*, 2005). However, when calculating niche models, it is assumed that the range of the target species is in equilibrium with environmental parameters (Araujo & Pearson, 2005) and that the niche of the studied species is conservative across space and time (Wiens & Graham, 2005). Niche conservatism may determine which species can invade which regions and where they will spread within those regions (Peterson *et al.*, 2003; Wiens & Graham, 2005). If a species fundamental niche is conserved, then this species will only be able to invade regions that have environmental circumstances similar to that of its native range (Wiens & Graham, 2005). Under this assumption, invasion ranges can be predicted with models fitted with data from the native range (Peterson & Vieglais, 2001). Some authors have however found a mismatch between species native and invasive ranges in terms of climatic niches (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Lauzeral *et al.*, 2011). Such mismatch could represent a shift either in the fundamental (Figure 1B) or realized niches (Figure 1C). Since invasive species enter areas where they were absent before, it is most likely that the 'new' climate envelope represents a better exploitation of the existing fundamental niche (Rodder *et al.*, 2009).

NICHE EVOLUTION MODELING

Niches are described for single species in the present time but many intriguing questions emerge when expanding this view to a comparative evolutionary framework: How and how fast does the multidimensional niche evolve? What are the outcomes of niche conservatism on the evolution of the species involved (Wiens & Graham, 2005) and what are the implications of niche shifts? Studies on niche dynamics disclose implications for several central questions at the intersection of ecology and evolution, including species richness patterns (Buckley *et al.*, 2010), community structure (Ackerly, 2009), invasive species potential (Broennimann *et al.*, 2007) and evolutionary responses to climate change (Evans *et al.*, 2009).

Comparative studies of biological diversification rely on a phylogenetic framework for interpretation. Such framework, in combination with information on species traits, contains the imprint of historical evolutionary processes. These processes include correlated evolutionary change and trajectories of trait evolution, convergent and parallel evolution, differential rates of evolution, speciation and extinction, the order and direction of change in characters, and the nature of the evolutionary process itself (Pagel, 1997). Hence, identification of changes in trait evolution rates along a phylogeny can reveal the mechanisms underlying the differences in the temporal, geographic and taxonomic distribution of biological diversity over large spatial and temporal scales (Thomas & Freckleton, 2012).

NICHE DYNAMICS AND DIVERSIFICATION

Even though phylogenetic comparative methods have lead to measures of diversification rates and how these vary across taxa (Ricklefs, 2007), there is still the question whether niche dynamics influence evolutionary processes and diversity patterns. Such diversity patterns must be ultimately dependent on mechanisms (speciation, extinction and dispersal) that directly change the number of species. These mechanisms rely on intrinsic characteristics of the species but also depend on the extrinsic characteristics like the environment and biotic interactions. Hence, it is most likely that a species niche influences its chances of undergoing speciation and suffering extinction. Furthermore, it is perfectly conceivable that not the characteristics of the niche on their own but the ability to change niches could impact diversification. This theorem has been confirmed as rapid shifts in climatic niches among tropical fauna cause higher diversification rates (Moritz *et al.*, 2000; Kozak & Wiens, 2007). Species in which climatic tolerances can evolve rapidly may be less susceptible to extinction from climatic change (Holt, 1990). Such species may diversify more rapidly by spreading into many different environments, thereby reducing competition and creating additional opportunities for speciation (Moritz *et al.*, 2000; Kozak & Wiens, 2010). In contrast, niche conservatism and the inability of populations to adapt to new environmental conditions play a crucial role in geographical isolation (Wiens, 2004; Kozak & Wiens, 2006) and may promote allopatric speciation. Niche breadth and evolvability of the ecological niche are relevant in discussions on species versus organismic selection (Rabosky & Mccune, 2010). Although regarded as aggregate, rather than emergent traits, these features clearly influence rates of speciation and extinction. Studying niche dynamics in a comparative context is therefore interesting.

SEaweEDS

Seaweeds appear to be good candidates for studying evolutionary dynamics of the macroecological niches among coastal marine organisms. Individual specimens are fixed in one location, yielding a direct link to georeferenced macroecological data. Seaweeds occur in a wide range of coastal habitats and many genera have a world-wide distribution, resulting in sufficient variability in macroecological dimensions and biogeographical patterns. In addition, seaweeds are straightforward to collect and process, making them suitable targets for this kind of research. The species and genera used in this thesis are carefully chosen because they meet specific criteria. The three species-rich genera *Halimeda*, *Codium* and *Dictyota* are selected as model systems because they have been studied extensively by our research group during the last decade (De Clerck, 2003; Verbruggen, 2005; Verbruggen *et al.*, 2007). Important is the availability of sufficient georeferenced localities, a nearly complete taxon sampling and trustworthy identifications. In addition, an elaborate knowledge about their phylogeny, ecology, morphology and anatomical characteristics is available for these genera. The availability of *Halimeda* fossils makes it possible to calibrate phylogenies in geological time in order to provide a temporal framework of green algal diversification. Both the highly invasive species *Caulerpa racemosa* var. *cylindracea* and *Codium fragile* subsp. *fragile* were selected because of their social and scientific relevance in addition to well known distributions (Verlaque *et al.*, 2004; Provan *et al.*, 2005).

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OBJECTIVES AND THESIS OUTLINE

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 explore how niches evolved, how niche dynamics can lead to diversification and how this results in observed distribution patterns. This research integrates phylogenetic and macroecological data in a GIS framework.

We specifically aim to:

- develop a global marine environmental data set for ecological niche modeling
- explore evolutionary dynamics of macroecological niches
- evaluate the relations between evolutionary niche dynamics and species diversification

In **chapter 1** we present a compilation of global marine environmental data. 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. We demonstrate global applicability through a case study of the invasive green alga *Codium fragile* subsp. *fragile*, predicting its potential spread.

Chapter 2 aims at improving the transferability of modeling introduced species. The presented framework is analyzed by forecasting the spread of a highly invasive seaweed: *Caulerpa cylindracea*.

In **chapter 3**, we integrate ecological niche models, macroecological data and high quality phylogenetic information of the green algal genus *Halimeda* to gain knowledge on macroecological niche dynamics, to get insights in the evolution of environmental preferences across a calibrated phylogenetic tree and to delineate areas for potential discoveries of sister species.

Chapter 4 aims at understanding the biogeography and niche evolution within a *Codium* species complex distributed across warm-temperate regions. Ecological niche models in combination with a molecular timeframe are used to elucidate the biogeographical pattern of these closely related sister species.

In **chapter 5** we investigate the evolution of thermal niches through time in relation to species diversity patterns within the brown algal genus *Dictyota*.

Notes to the reader:

Chapters 1, 4 and 5 are presented as manuscripts with LT as first author; chapter 2 is a co-authored paper with HV; chapter 3 represents a shared first co-authorship with HV and KP. Specific contributions are mentioned at the end of each chapter. Gene sequences used to reconstruct genealogical relationships in the various chapters were generated by Sofie D'Hondt and Tine Verstraete of the phycology research group.

All chapters have been printed, are submitted, or are in preparation to be submitted to SCI journals. Therefore some overlap in the content of the chapters does occur.