Biodiversity and phylogeography of Northeast Atlantic and Mediterranean sponges
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SUMMARY

The Northeast Atlantic and Mediterranean region benefits from a long-standing tradition of sponge taxonomy which provides a wealth of information on species biology, ecology, and distribution. However, the scattered nature of the available information has kept sponge biodiversity and biogeographic patterns of this area concealed. The primary goal of this thesis is to uncover those patterns and to unveil how ecological and historical processes have shaped them.

A growing body of literature has yielded compelling evidence that current large-scale diversity patterns in both terrestrial and aquatic biota have been shaped by the Quaternary glaciations, particularly by the climatic changes observed during the Last Glacial Maximum (LGM; 30-19 kyr BP). In CHAPTER 2, I assess diversity patterns and zoogeography of the shallow-water demosponge assemblages of the Atlanto-Mediterranean at a metacommunity scale. By means of statistical analysis I compare the taxonomic diversity and zoogeographical relationships of the sponge assemblages of 28 areas. I show that this region constitutes a sponge diversity hotspot harbouring approximately 11% (745 species) of the currently known global demosponge species, with the Mediterranean being significantly richer (by about 12%) than the Northeast Atlantic. I found an Atlantic N-S and a Mediterranean NW-SE gradient of increasing taxonomic diversity which is strongly correlated to both contemporary and historical values (at the LGM) of sea surface temperatures. Based on their faunal similarities, these areas grouped into three biogeographical provinces,
namely the Northern European Seas, the Lusitanian, and the Mediterranean. Moreover these similarities were shown to be related to the distance between areas (isolation by distance) and to the oceanographic currents that connect them (connectivity leading to more similarity). A particularly important outcome of this study was the realization that the vast majority of the species exhibit an extremely restricted geographical range as single-area or narrow-range (2-3 areas) endemics.

Despite the extensive investigations in this region, there are still several areas (e.g. Madeira archipelago, southern Mediterranean) and ecosystems (caves, deep-sea, seamounts) for which the sponge fauna remains ill-known and underwater surveys will likely yield new records and new species for science. Seamounts, which are abundant topographical features in this region particularly between the Portuguese coast and Madeira Island, are one of such barely explored ecosystems. Thus in CHAPTER 3 I studied the demosponge assemblages associated to the Gettysburg and Ormonde seamounts (Gorringe Bank) that are part of the Horseshoe seamount chain. The collected material was identified and assigned to 23 species, all of which constitute new records for this area, adding to the 13 species previously recorded. I found the Gorringe Bank to possess a diverse demosponge fauna which is mainly composed of species with a wide Atlanto-Mediterranean distribution but also with a significant proportion of species (28% of the total) that are endemic to this bank or have a restricted geographical distribution. Some specimens could not be confidently ascribed to a particular species due to some morphological differences relative to described (mainland) species. The taxonomic status of these species/populations requires further investigation and uncovering their phylogenetic/phylogeographic relationships, with the aid of molecular markers, will provide important insights on the role of these ecosystems as stepping-stones or speciation centres for marine species (in progress).

In Porifera, the delimitation of species boundaries based solely on morphological characters is often difficult because morphological variation or the lack thereof may represent intraspecific phenotypic plasticity or interspecific morphological stasis, respectively. The Cliona aff. celata species complex uncovered in CHAPTER 4 is a good example of the latter. From the phylogenetic reconstructions of two mitochondrial (COI, Atp8) and one nuclear (28S) gene fragments, I unveiled the cryptic diversity of this ecologically important and allegedly cosmopolitan excavating species. Intraclide levels of diversity and
interclade levels of divergence, only compatible with interspecific relationships, demonstrated that at least four morphologically similar but genetically divergent species occur in the study area. I further showed that boring and massive growth forms constitute ecologically adapted phenotypes or growth stages of the same species, and that these occur in two of the species. I additionally provide an overview of the cases of cryptic speciation which have been reported to date within the Porifera. These cases, which are particularly prevalent in the simplest groups, suggest that both overconservative systematics and morphological stasis have led to an underestimation of sponge diversity. Furthermore, undetected cryptic species may compromise scientific and biotechnological advancement in areas for which sponges have been an increasing target group such as medical biology or pharmaceutics.

To further deepen our knowledge on the ecological and historical processes responsible for the geographic distribution of species and their populations I examined the genetic structure and phylogeographic history of two Atlanto-Mediterranean species. The genetic structure of the poecilosclerid sponge *Phorbas fictitius* (CHAPTER 5) was assessed from sequence data of the mitochondrial COI gene at two spatial scales: a regional scale comparing mainland (Iberian) and insular (Macaronesian) populations, and a local (Archipelagic) scale focusing on different island populations of the Azores archipelago. I found highly structured populations at both scales and a separation between island and mainland populations. In CHAPTER 6 I studied the genetic structure and elucidated the phylogeographic history of a haplosclerid sponge - *Petrosia ficiformis* - throughout its Atlanto-Mediterranean distribution range based on molecular data of two mitochondrial (COI and Atp8) and one newly developed nuclear ribosomal (28S-IGS) gene fragments. Phylogenetic and phylogeographic analyses revealed highly structured populations as a result of restricted gene flow with isolation by distance within each basin as well as allopatric fragmentation between Mediterranean (mainland) and Atlantic (island) populations. A contiguous range expansion across the geographical range of the species was inferred. The reduced genetic diversity that was encountered in the northwestern Mediterranean populations is likely a consequence of the climatic conditions of the LGM. I hypothesize that during this period the decrease of sea surface temperatures have caused a disruption of the reproductive cycle of this species and therefore a severe reduction in *P. ficiformis* populations or even its local extinction. One of the most striking results of this study was the discovery of a presumed deep-sea
affinity of some shallow-water populations in the northwest Mediterranean and the Azores archipelago. Whether specimens of these populations are the result of interspecific hybridization remains hypothetical and requires confirmation with additional markers.

In both *P. fictitius* and *P. ficiformis*, the pattern of higher genetic diversity in island (southern) populations, conforms to models of island refugia that have been observed in several other organisms in this area, thus highlighting the influence of the Macaronesian islands on the recent evolutionary history of the Northeast Atlantic marine biota. From these findings, along with previous studies for two other co-distributed species (*Crambe crambe* and *Scopalina lophyropoda*), the following phylogeographic pattern for the Atlanto-Mediterranean sponge fauna emerges: highly structured populations as a combined result of restricted gene flow and isolation by distance with, in some cases, signatures of allopatric fragmentation and refugia.