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## Nowhere safe? Exploring the influence of urbanization across mainland and insular seashores in continental Portugal and the Azorean Archipelago

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## ABSTRACT

Differences in the structure and functioning of intensively urbanized vs. less human-affected systems are reported, but such evidence is available for a much larger extent in terrestrial than in marine systems. We examined the hypotheses that (i) urbanization was associated to different patterns of variation of intertidal assemblages between urban and extra-urban environments; (ii) such patterns were consistent across mainland and insular systems, spatial scales from 10s cm to 100s km, and a three months period. Several trends emerged: (i) a more homogeneous distribution of most algal groups in the urban compared to the extra-urban condition and the opposite pattern of most invertebrates; (ii) smaller/larger variances of most organisms where these were, respectively, less/more abundant; (iii) largest variability of most response variables at small scale; (iv) no facilitation of invasive species by urbanization and larger cover of canopy-forming algae in the insular extra-urban condition. Present findings confirm the acknowledged notion that future management strategies will require to include representative assemblages and their relevant scales of variation associated to urbanization gradients on both the mainland and the islands.

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### 1. Introduction

The evidence that patterns of distribution, abundance and diversity of species and assemblages vary across biogeographic scales has been gathered for decades by ecologists, although progressively developing from the qualitative appreciation to the design of descriptive and manipulative experiments (Maurer, 1999). Several abiotic and biological factors vary across large scales, such as along latitudinal gradients, and can modulate the strength and nature of biological interactions (Menge et al., 2003) and the biological responses to anthropogenic perturbations, including climate change (Parmesan and Yohe, 2003).

Despite an increasing interest in assessing the generality vs. context-dependency of ecological processes (Chamberlain et al., 2014) and the development of approaches to indirectly test for the effects of large-scale drivers and overcome the logistic difficulty of manipulating them in the field (Menge et al., 2002), experimental analyses allowing

comparisons across broad spatial scales are still scarce (but see, for example, Pennings and Silliman, 2005).

Among anthropogenic disturbances, urban coastal sprawl is one of the strongest, most widespread and rising (Barragán and de Andrés, 2015). Urban development can be associated to habitat destruction (Dugan et al., 2011), introduction of alien species (Airoidi et al., 2015), pollution (Lotze et al., 2006) and contamination by marine debris (Leite et al., 2014). The separate and/or combined impacts of such stressors may be responsible for the decline, up to the extinction, of native species, landscape modifications, and biotic homogenization at local to regional, or even global, scales (McKinney and Lockwood, 1999; Knop, 2016) and across all levels of biological organization (Lotze et al., 2006; Halpern et al., 2008; Aronson et al., 2014). Recent progress of research in urban ecology has indicated differences in the structure and functioning of intensively urbanized vs. less human-affected systems, but such evidence was provided for a much larger extent in terrestrial than in marine systems (Bulleri, 2006).

Moreover, previous studies on the impacts of human pressure provided inconsistent evidence. An overall reduction of species diversity and evenness, through the replacement of numerous, relatively low abundant, sensitive species by a few, but very abundant, ones has

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been widely hypothesized and documented in marine and terrestrial systems (Olden and Rooney, 2006; Magura et al., 2009; Tamburello et al., 2011). Such ecological change may also lead to a homogenization of biodiversity among sites, i.e. a reduced beta diversity (e.g. Balata et al., 2007; Bevilacqua et al., 2012). However, it has been reported that such outcome may occur more frequently under extremely harsh conditions (McKinney, 2008). Moderate disturbances, in contrast, may increase heterogeneity, such as where native species are lost at slower rates than exotic species are added (McKinney, 2006), or where disturbance generates a mosaic of resources in otherwise more homogeneous habitats and assemblages (Sousa, 2001). Under such circumstances, testing whether anthropogenic activities are associated to a homogenization or an increased heterogeneity of organisms is crucial to detect their realized impacts and to guide effective mitigation strategies (Elmqvist et al., 2003). Hierarchical sampling designs provide a tool to unambiguously identify an actual environmental impact over the scale at which it actually occurs (Underwood, 1993; Bishop et al., 2002).

In the context of testing hypotheses on large-scale ecological processes, islands provide convenient systems, especially when compared with analogous processes on the mainland (Benedetti-Cecchi et al., 2003; González-Castro et al., 2012; Bertocci et al., 2014). Compared with less isolated systems, oceanic archipelagos are generally poorer of species, richer in endemism and more sensitive to human disturbance (Whittaker and Fernández-Palacios, 2007). Variable patterns of dispersal ability, immigration, speciation and extinction, dependent on factors such as the distance from sources of colonists and the size of islands, have been considered responsible, under pre-human contact conditions, for the unique biota observed in some islands, according to the classical Island Biogeography Theory (MacArthur and Wilson, 1967; Whittaker et al., 2008). Human contact has then determined events of anthropogenic immigration of species, habitat transformation and declines or extinction of populations, which, together with other historical traits, physical processes and biological interactions may have contributed to maintain insular environments different than mainland ones (Lomolino, 2005; Whittaker et al., 2008). However, biogeographic theory has been historically based on analyses of species-diversity patterns of islands, while functional traits of organisms and assemblages have been largely overlooked. In fact, variation in patterns of distribution and abundance of species with contrasting life-traits, regardless of their richness and endemic, native or exotic nature, could differentiate island and mainland systems not only in terms of functional diversity, but also of their relative ability to respond to anthropogenic perturbations, such as those related to urbanization (Whittaker et al., 2014).

The present study took advantage of biogeographic discontinuities existing along the Portuguese mainland coast and in the Azorean Archipelago, to examine the influence of urbanization on algal and invertebrate assemblages of rocky seashores. A latitudinal gradient in environmental variables (sea surface and air temperature, irradiation) is described along the Portuguese continental coast, with a 'cooler' northern region and a 'warmer' central and southern region (e.g. Tuya et al., 2012). This is associated to the overlapped distribution of boreal and Lusitanian species (Lima et al., 2007), the occurrence of southern and northern ranges of distribution of species with affinity for, respectively, cold and warm water (Lima et al., 2007), and clines in the abundance of several species (Boaventura et al., 2002).

The Azorean Archipelago includes nine major islands organized into three spatial groups (eastern, central and western). Clear latitudinal and climatic gradients do not occur in the Azores. This feature, adding to younger age, lower topographic heterogeneity and reduced climatic oscillations over evolutionary scales, was invoked as a possible explanation for the traditionally described lower number of single-island endemics in the Azores compared to other oceanic islands, such as the Canary Archipelago (Cardoso et al., 2010; Carine and Schaefer, 2010; Triantis et al., 2012). However, such apparent distinctive trait of the Azores has been questioned by recent molecular investigations, which suggested that, in particular, the diversity and degree of local endemism

of the Azorean flora would be much larger than it was assessed so far due to inadequate taxonomic tools, making this archipelago more similar, in terms of biogeographic discontinuities, to other island systems than it was previously assumed (Schaefer et al., 2011). Moreover, by coupling model projections of ocean circulation patterns and empirical data on oceanographic variables, it has been demonstrated that the western, central and eastern group of the Azores differ significantly for their respective ability to capture and retain drifting particles and organisms (Sala et al., 2016). Such differential capacity may directly affect the delivery of biomass originating outside the region and, consequently, the patterns of recruitment and distribution of organisms on islands belonging to each group (Morato et al., 2009) and their responses to environmental fluctuations (Santos et al., 1995).

Here, for the first time in a single empirical study, the variability in the structure of rocky intertidal assemblages and in the abundance of groups of algal and invertebrate organisms characterized by different life-history traits and functions was quantified and compared between urban (close to coastal cities, in densely populated and/or industrial or commercial areas) and reference ('extra-urban': far from coastal cities, in less anthropogenically disturbed areas) locations in mainland and insular systems, over multiple spatial scales ranging from 10s cm to 100s km and a temporal scale of three months. The main tested hypotheses were that (i) urbanization was associated to different patterns of variation of whole assemblages and individual morpho-functional groups at different scales, and (ii) responses were consistent independently of the mainland or insular trait. The lack of previous similar studies and the contrasting evidence provided by the literature on the effects of urbanization-related stress, and of human disturbances in general, on coastal populations and assemblages prevented to anticipate the more likely direction of responses towards a reduced or increased homogenization.

## 2. Materials and methods

### 2.1. Study systems

The studied mainland system comprised two regions (northern and southern) spanning ~400 km and ~4° of latitude along the continental coast of Portugal (Fig. 1). This almost rectilinear coastline is oriented from north to south and greatly exposed to prevailing westerly and north-westerly winds and waves. Such prevailing winds are responsible, during the summer, for nearshore upwelling of nutrient-rich water and consequent promotion of primary productivity (Lima et al., 2007). Along the coast, rocky stretches (limestone, sandstone, shale or granitic, typically 100s m long) are interspersed within extensive beaches entirely sandy or with sand and boulders mixed.

The insular system included the islands of São Miguel and Terceira, belonging, respectively, to the eastern and the central group (~130 km apart, corresponding to the 'regional' scale of the present study) of the Azorean Archipelago. These are the two most populated islands of the archipelago, collectively hosting about 80% of the total population and the two main cities (the capital Ponta Delgada and Angra do Heroísmo, respectively), where most port, commercial, touristic and even military activities also occur. The coastline is topographically complex, with steep cliffs alternating with rocky (mainly basaltic) beaches, and, analogously to the Portuguese continental shores, exposed to high levels of wave action. Based on the local input of nutrients only, the Azorean waters are normally designated as oligotrophic, but some upwelling hotspots may be possible due to particular topographic conditions affecting the circulation of water (Sala et al., 2016).

At both study systems, the tidal regime is semi-diurnal, with maximum spring tides reaching 3.5–4 m and ~2 m above Chart Datum (CD) on the mainland and in the archipelago, respectively. However, the range of distribution of several intertidal organisms in the Azores can extend much higher due to favourable conditions maintained by the large and frequent wave splash and swell (Martins et al., 2008).

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