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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

Urban sprawl is a main anthropogenic disturbance in coastal areas. 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 centimetres to 100s kilometres, 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.

Keywords: Human impacts – Rocky intertidal – Algal and invertebrate assemblages – Spatio-temporal scales – Variance components

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

27 nature of biological interactions (Menge et al., 2003) and the biological responses to
28 anthropogenic perturbations, including climate change (Parmesan and Yohe, 2003).
29 Despite an increasing interest in assessing the generality *vs.* context-dependency of
30 ecological processes (Chamberlain et al., 2014) and the development of approaches to
31 indirectly test for the effects of large-scale drivers and overcome the logistic difficulty of
32 manipulating them in the field (Menge et al., 2002), experimental analyses allowing
33 comparisons across broad spatial scales are still scarce (but see, for example, Pennings and
34 Silliman, 2005).
35 Among anthropogenic disturbances, urban coastal sprawl is one of the strongest, most
36 widespread and rising (Barragán and de Andrés, 2015). Urban development can be associated
37 to habitat destruction (Dugan et al., 2011), introduction of alien species (Airoldi et al., 2015),
38 pollution (Lotze et al., 2006) and contamination by marine debris (Leite et al., 2014). The
39 separate and/or combined impacts of such stressors may be responsible for the decline, up to
40 the extinction, of native species, landscape modifications, and biotic homogenization at local to
41 regional, or even global, scales (McKinney and Lockwood, 1999; Knop, 2016) and across all
42 levels of biological organization (Lotze et al., 2006; Halpern et al., 2008; Aronson et al., 2014).
43 Recent progress of research in urban ecology has indicated differences in the structure and
44 functioning of intensively urbanized *vs.* less human-affected systems, but such evidence was
45 provided for a much larger extent in terrestrial than in marine systems (Bulleri, 2006).
46 Moreover, previous studies on the impacts of human pressure provided inconsistent
47 evidence. An overall reduction of species diversity and evenness, through the replacement of
48 numerous, relatively low abundant, sensitive species by a few, but very abundant, ones has
49 been widely hypothesized and documented in marine and terrestrial systems (Olden and
50 Rooney, 2006; Magura et al., 2009; Tamburello et al., 2011). Such ecological change may also
51 lead to a homogenization of biodiversity among sites, i.e. a reduced beta diversity (e.g. Balata
52 et al., 2007; Bevilacqua et al., 2012). However, it has been reported that such outcome may

53 occur more frequently under extremely harsh conditions (McKinney, 2008). Moderate
54 disturbances, in contrast, may increase heterogeneity, such as where native species are lost at
55 slower rates than exotic species are added (McKinney, 2006), or where disturbance generates a
56 mosaic of resources in otherwise more homogeneous habitats and assemblages (Sousa, 2001).
57 Under such circumstances, testing whether anthropogenic activities are associated to a
58 homogenization or an increased heterogeneity of organisms is crucial to detect their realized
59 impacts and to guide effective mitigation strategies (Elmqvist et al., 2003). Hierarchical
60 sampling designs provide a tool to unambiguously identify an actual environmental impact
61 over the scale at which it actually occurs (Underwood, 1993; Bishop et al., 2002).
62 In the context of testing hypotheses on large-scale ecological processes, islands provide
63 convenient systems, especially when compared with analogous processes on the mainland
64 (Benedetti-Cecchi et al., 2003; González-Castro et al., 2012; Bertocci et al., 2014). Compared
65 with less isolated systems, oceanic archipelagos are generally poorer of species, richer in
66 endemism and more sensitive to human disturbance (Whittaker and Fernández-Palacios, 2007).
67 Variable patterns of dispersal ability, immigration, speciation and extinction, dependent on
68 factors such as the distance from sources of colonists and the size of islands, have been
69 considered responsible, under pre-human contact conditions, for the unique biota observed in
70 some islands, according to the classical Island Biogeography Theory (Mac Arthur and Wilson,
71 1967; Whittaker et al., 2008). Human contact has then determined events of anthropogenic
72 immigration of species, habitat transformation and declines or extinction of populations,
73 which, together with other historical traits, physical processes and biological interactions may
74 have contributed to maintain insular environments different than mainland ones (Lomolino,
75 2005; Whittaker et al., 2008). However, biogeographic theory has been historically based on
76 analyses of species-diversity patterns of islands, while functional traits of organisms and
77 assemblages have been largely overlooked. In fact, variation in patterns of distribution and
78 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).

The study was done on macroalgal and invertebrate assemblages from the emergent rocky habitat located at low (0-0.5 m above CD) and mid (2-2.5 m and 1-1.5 m above CD on the mainland and the islands, respectively) intertidal heights. The dominant organisms at these shore heights and systems were described in detail elsewhere (Martins et al., 2008; Bertocci et al., 2014). In spite of some specific differences (for instance, mussels dominate midshore space on the mainland, especially in northern Portugal, but they are virtually absent in the Azores), the overall distribution of assemblages is comparable between the mainland and the islands,

157 with turf-forming algae dominating lower on the shore, barnacles dominating highshore and
158 gastropods (mostly limpets) representing the most common grazers throughout the tidal range.
159
160 *2.2. Sampling design and collection of data*
161 The study was done at four rocky locations (100s m long) interspersed within 10s km of
162 each mainland and insular region. Two locations are in highly urbanized areas. Such areas are
163 adjacent to coastal cities (on the mainland: Porto and Vila Nova de Gaia in the north, and Sines
164 and Vila Nova de Milfontes in the south; in the Azores: Ponta Delgada and Rabo de Peixe at
165 São Miguel, and Angra do Heroísmo and Praia da Vitória at Terceira) characterized by dense
166 population and/or commercial and industrial activities. The other two locations occur 10s km
167 far from them, in areas with small resident population and no large industrial and commercial
168 plants (Fig. 1). At all locations, the sampled shore is characterized by natural rock, high wave
169 exposure and easy access.
170 At both mainland and insular systems, two areas (~20 m long, 10s m apart) were
171 randomly selected within each urban and extra-urban location, with 15 quadrats (25 x 25 cm,
172 10 s cm apart) in each area. The same design was adopted at each of two times (June-July 2015
173 and September-October 2015, hereafter indicated as Time 1 and Time 2, respectively). New
174 sets of independent areas and quadrats were chosen at random at each sampling time.
175 At each time, organisms in each replicate quadrat were visually sampled by means of a
176 square frame divided into twenty-five 5 x 5 cm sub-quadrats. The abundance of most sessile
177 organisms was estimated as percentage cover (Dethier et al., 1993), while that of solitary
178 sessile and mobile animals was quantified as number of individuals per quadrat. When species
179 could not be identified in the field, they were lumped into broader taxonomic or morphological
180 groups (Steneck and Dethier, 1994).
181
182 *2.3. Statistical analyses*

183 Separately for the midshore and the lowshore habitat, patterns of spatial variability of the
184 structure of whole assemblages were quantified and compared between the urban and the extra-
185 urban condition by calculating independent estimates of pseudo-variance components (Terlizzi
186 et al., 2007) at each scale. As illustrated in Oliveira et al., (2014a), the procedure started with
187 randomly establishing three groups of five, out of the total 15, replicates sampled in each area
188 and location. For each time, condition (urban *vs.* extra-urban), system (mainland *vs.* island) and
189 randomly assembled group, this produced a three-way model including the random factors
190 (two levels each) Region, Location (nested in Region) and Area (nested in Location and
191 Region), with three replicates. Pseudo-variance components at each scale (including the
192 among-quadrats one) were then calculated with permutational multivariate analysis of variance
193 (PERMANOVA, Anderson, 2001) based on Bray-Curtis untransformed dissimilarities, by
194 equating observed and expected mean squares (Underwood, 1997). Obtained negative pseudo-
195 variance estimates were set to zero, following the logic illustrated by Underwood (1996). This
196 procedure originated three independent estimates of pseudo-variance components for each
197 combination of four spatial scales, two systems, two conditions and two times of sampling,
198 which were finally analysed with a four-way analysis of variance (ANOVA) including the
199 crossed factors: Time (2 levels, random), System (2 levels, fixed), Condition (2 levels, fixed)
200 and Scale (4 levels, fixed). The assumption of homogeneity of variance was checked with
201 Cochran's *C* test and data were transformed when necessary. When heterogeneous variances
202 could not be stabilised by transformation, untransformed data were analysed and results
203 considered robust if significant at $p<0.01$ (instead of $p<0.05$), to compensate for increased
204 probability of type I error. SNK tests were used for post-hoc comparisons of means. For the
205 present purposes, only within-condition comparisons for each combination of other factors
206 involved in significant interactions were considered relevant.
207 The same statistical procedures were used for variance components of the abundance of
208 individual morpho-functionally, and likely ecologically, similar groups of organisms

209 (Appendix A). These were established by *a posteriori* collapsing taxa (with the exclusion of
210 cyanobacteria and lichens) into five algal groups, i.e. articulated calcareous, foliose, corticated,
211 filamentous and encrusting (adapted from Steneck and Dethier, 1994), and five invertebrate
212 groups, i.e. grazers (typically herbivore), predators (typically carnivore), detritus-feeders,
213 solitary and gregarious sessile species (adapted from Knox, 2001). Basing on widespread
214 evidence that urbanization may facilitate biological invasions (Airoldi et al., 2015) and be
215 associated to a decline of habitat-forming macroalgae (e.g. Benedetti-Cecchi et al., 2001;
216 Airoldi and Beck, 2007; Mangialajo et al., 2008), two additional groups were isolated,
217 including invasive and canopy-forming algae, respectively (Appendix A). Groups that were too
218 low abundant and sparse to allow meaningful statistical tests were not formally analysed.
219
220 **3. Results**
221 A total of 147 taxa, including 103 algae, 39 invertebrates, 4 cyanobacteria and 1 fungi
222 (Appendix A), were identified over the course of the study and used in PERMANOVA.
223
224 *3.1. Midshore habitat*
225 Differences between the urban and the extra-urban condition in pseudo-variance
226 components of assemblages were not consistent across sampling times, systems and spatial
227 scales (Fig. 2A and Appendix B). At Time 1, assemblages on the mainland were more
228 heterogeneously distributed in extra-urban compared to urban areas. This pattern at the area
229 scale was reversed in the insular system, where, by contrast, a greater multivariate variance in
230 the extra-urban condition was shown at the two larger scales, i.e. between locations and
231 regions. More heterogeneous assemblages were also found at Time 2 on the mainland at the
232 regional scale, and on the islands at the quadrat scale (Fig. 2A).
233 A significant interaction involving all experimental factors was detected for the variance
234 of articulated calcareous algae, corticated algae, filamentous algae (Appendix C), encrusting

235 algae and gregarious invertebrates (Appendix D). Larger variation in the extra-urban than in
236 the urban condition was shown by: articulated calcareous algae at the regional scale on the
237 mainland and at both the quadrat and the location scale in the insular system, at Time 2 only
238 (Fig. 3A); corticated algae at both the quadrat and the location scale on the mainland and at the
239 location scale on the islands at Time 1, and at all, but the between-areas, scales on the mainland
240 and at the area scale on the islands at Time 2 (Fig. 3C); filamentous algae at the quadrat and the
241 location scale in the insular system at Time 1 (Fig. 3D); encrusting algae at the two smallest
242 scales on the islands at Time 1, and at the quadrat scale on the mainland at Time 2 (Fig. 4A).
243 The opposite pattern in extra-urban *vs.* urban differences was shown by: corticated algae at the
244 area and the regional scale on the islands at Time 1 only (Fig. 3C); filamentous algae at the
245 quadrat scale on the islands at Time 2 (Fig. 3D); encrusting algae at the quadrat scale on the
246 mainland at Time 1 (Fig. 4A); gregarious invertebrates at the location scale on the mainland at
247 Time 2 (Fig. 4C).
248 Irrespectively of the sampling time, differences in the urban *vs.* extra-urban variance of
249 both the foliose (Appendix C) and the canopy-forming algae (Appendix D) depended on the
250 system and scale. However, the detected significant patterns were all in the direction of a
251 relatively larger heterogeneity of these taxa in the extra-urban condition. For foliose algae, this
252 occurred at the location scale in both the mainland and the insular system, and at the scales of
253 areas and regions on the mainland and of quadrats on the islands (Fig. 3B). Such more
254 heterogeneous distribution in the extra-urban condition characterized canopy-forming algae
255 only at the smallest spatial scale in the insular system (Fig. 4D).
256 In all combinations of factors displaying significant differences, grazers were more
257 heterogeneously distributed in the urban condition (Fig. 4B and Appendix D). Such a situation
258 was shown, in particular, on the mainland at both sampling times, irrespectively of the spatial
259 scale, and at both the quadrat and the location scale, consistently across times and systems.

Predatory, detritus-feeding and solitary sessile animals and invasive algae were not formally tested as consistently too low abundant (Appendix G, panels G, H, I and K, respectively).

Besides the above illustrated patterns, it was also evident that the main contribution to the spatial variability of midshore assemblages was provided by the 'extreme' scales (among-quadrats and between-regions: Fig. 2A). Several single groups of organisms also showed the largest proportion of variance at the smallest scale (Fig. 3 and Fig. 4). However, very small to null variances, leading to obvious significant or non-significant patterns, were generally associated to very small to null mean abundance values (Appendix G).

3.2. Lowshore habitat

Urban *vs.* extra-urban differences in the variance of lowshore assemblages also varied with sampling times, systems and scales (Fig. 2B and Appendix B). More heterogeneous assemblages in the urban than in the extra-urban condition were found, at Time 1, at the location scale on the mainland. At Time 2, the same urbanization-related pattern was shown at both the area and the location scale on the mainland and at the regional scale on the islands. Conversely, a relatively larger heterogeneity of extra-urban assemblages was found, only at Time 2, at the largest and smallest scales in the mainland and in the insular system, respectively (Fig. 2B).

Significant urbanization-related differences depending on combinations of all other factors were shown by grazers, gregarious sessile animals and invasive algae (Appendix F). At Time 1, grazers on the mainland were more heterogeneously distributed in the urban condition at all scales excepted the between-areas one; such a pattern at the location scale was maintained at Time 2, when, instead, the variability of this group at the regional scale switched to a relatively larger value in the extra-urban condition (Fig. 6B). Noticeably, however, grazers were virtually absent in the lowshore habitat in the islands, which was associated to minimal or

null variances and the consequent lack of any significant difference within this system (Fig. 6B and Appendix H, panel F). Gregarious animals were also virtually absent in the insular system at this shore level (Appendix H, panel J), hence significant differences between conditions were limited to the mainland. These consisted in a larger variance in the urban condition at the regional scale at Time 1 and at the area scale at Time 2, while the opposite pattern occurred at the quadrat scale at Time 2 (Fig. 6C and Appendix F). Conversely, relatively large and frequent cover values of invasive algae were found only at Time 1 in the extra-urban condition of the islands (Appendix H, panel K), resulting in larger variance at both the quadrat and the area scale, compared to the urban condition (Fig. 7A and Appendix F).

Urban *vs.* extra-urban differences varying with the sampling time and spatial scales, but consistent across the two systems, were shown by articulated calcareous, corticated, filamentous and encrusting algae (Appendix E). Relatively larger variance in the urban condition characterized articulated calcareous algae at the regional scale at both sampling times and at the location scale at Time 2 (Fig. 5A), and corticated algae at the location scale at both sampling times (Fig. 5C). Larger variance in the extra-urban condition was shown by: articulated calcareous algae at the smallest scale at Time 2 (Fig. 5A); corticated algae at the area and the regional scale at Time 1 (Fig. 5C); filamentous algae at the quadrat scale at both sampling times, at the area scale at Time 1 and at the regional scale at Time 2 (Fig. 5D); encrusting algae at the area and the regional scale at Time 1 and Time 2, respectively (Fig. 6A).

Irrespectively of the spatial scale, urbanization-related patterns of variance of articulated calcareous, foliose and encrusting algae varied between sampling times and systems (Appendix E). Only at Time 2, the first group was more heterogeneously distributed in the urban condition in both systems, although the difference was more pronounced in the mainland (Fig. 5A). In the islands, urbanization was associated to a larger variance of foliose algae at both times, while the opposite occurred in the mainland, but only at Time 2 (Fig. 5B). Encrusting algae in

311 the islands were relatively more heterogeneous in the extra-urban condition at Time 1 (Fig.
312 6A).
313 The variance of foliose algae in the urban *vs.* the extra-urban condition also varied
314 between systems and among scales, independently of the sampling times (Appendix E). In the
315 mainland, this variable was relatively larger in the extra-urban condition at both the quadrat
316 and the location scale, while the opposite occurred in the islands at the quadrat scale (Fig. 5B).
317 The 'Sy x Co x Sc' interaction was significant also for canopy-forming algae (Appendix F).
318 The variance of this group at the quadrat and the regional scale was larger in the urban
319 condition, but only in the insular system (Fig. 7B). Although algal canopies were absent at
320 most locations in both systems, this pattern matched their much smaller and close to zero mean
321 cover values on the mainland compared to the islands (Appendix H, panel L).
322 Analogously to the midshore habitat, the distribution of most single groups of lowshore
323 organisms was characterized by the largest variability at small (among-quadrats) scale (Fig. 6
324 and Fig. 7).
325 Other groups were not tested as consistently too low abundant (Appendix H, panels G, H
326 and I).
327
328 **4. Discussion**
329 This study compared patterns of variation of whole intertidal assemblages and individual
330 groups of organisms at a range of scales between the urban and the extra-urban condition,
331 testing whether urbanization-related differences in homogeneity/heterogeneity were consistent
332 between mainland and insular systems. This hypothesis was not supported by present findings,
333 as a multiplicity of different, in several cases contrasting, responses was found both between
334 and within systems and depending on the sampling time and scale. Under these circumstances,
335 it is difficult to draw conclusions on patterns of variability of rocky intertidal organisms that
336 would generally discriminate the urban and the extra-urban condition over and above the

337 variability of different systems due to the effects of other drivers acting there. Nevertheless, the
338 large context-dependency of more or less heterogeneous distributions of populations and
339 assemblages could be considered itself as a common characteristic of urbanization-affected
340 environments. In fact, while increased variability among samples has been hypothesized to be a
341 main and general trait of stressed environments (Warwick and Clarke, 1993), it was
342 empirically demonstrated only in some cases (e.g. Oliveira et al., 2014a). Other studies
343 reported that the degree of variability of assemblages within control (undisturbed) and
344 disturbed conditions were comparable (Chapman et al., 1995), or dependent on the examined
345 spatial scale more than on the disturbance gradient itself (Bishop et al., 2002).
346 A likely critical point is that coastal urbanization is a general concept comprising a wide
347 range of types and intensities of sources of disturbance, including, *inter alia*, water quality and
348 action (Balata et al., 2008), chemical pollution (Koop and Hutchins, 1996) and nutrient input
349 (Carpenter et al., 1998). For example, storm disturbance, even when possibly occurring in
350 comparable ways in urban and extra-urban environments, may exert drastically different effects
351 when associated with varying levels of other local anthropogenic stress (Oliveira et al., 2014b).
352 Separately examined, the ecological effects of some of these stressors in terms of increased or
353 decreased homogenization of biodiversity may be rather predictable. Conversely, when they
354 are combined with each other and superimposed on fluctuations of environmental conditions
355 and to the influence of other factors not directly related to urbanization varying at a range of
356 spatial and temporal scales, generalizations become much more difficult, if not impossible
357 (Fraterrigo and Rusak, 2008). This might be well the case of the present systems, which,
358 analogously to almost any other worldwide, are likely exposed to multiple and concomitant
359 stressors acting from local to global scales and true pristine conditions, if actually existing, are
360 increasingly difficult to find (Airoldi and Beck, 2007; McKinney, 2008). On the other hand,
361 both the identification of current impacts and the possible implementation of future
362 management and mitigation strategies can not be effectively achieved if the scales and the

363 context-dependency of such variability are not explicitly taken into account in sampling
364 designs aimed at assessing impacts (Underwood, 1993; Bishop et al., 2002). In this context, the
365 importance attributed to variability *per se* as an indicator measure of the actual effect of natural
366 or anthropogenic disturbance has raised in the last decades, in association with increasing
367 concern by ecologists about the need for examining it even independently of changes in the
368 mean (Benedetti-Cecchi, 2003). As a result, the present variable findings should not be
369 interpreted as the failure of this study to identify general patterns related to urbanization, but as
370 an accurate representation of a key characteristic of systems exposed to urbanization. Such a
371 characteristic could not be described and appreciated through a sampling design including, for
372 instance, a single system examined at a single time at a single or smaller number of spatial
373 scales. This option would potentially lead to extrapolate to general context patterns that were
374 applicable to that specific situation only. In both studied systems, urbanization, in particular,
375 seemed unable to exert a strong enough influence to overwhelm other natural or anthropogenic
376 drivers of variability of most examined response variables, as their significant variation at a
377 range of scales was observed in both the urban and the extra-urban condition. In the future,
378 specifically designed studies should focus on particular combinations of system, habitat, scale
379 and time here identified as being associated to significant urban *vs.* extra-urban differences,
380 and quantify the relative contribution of possible weak effects of particular urbanization-related
381 disturbance and of strong effects of other concomitant factors to such differences.

382 In spite of the inconsistency of present findings, some other general considerations can be
383 done based on the most consistent results of this study.

384 First, when significant differences were found, urbanization tended to be associated to a
385 more homogeneous distribution of most algal groups and to an increased spatial variance of
386 most invertebrates. Identifying and testing the actual mechanisms of such responses was
387 beyond the present goals, but it could be suggested that the net influence of urbanization-
388 related pressures affected negatively several algal groups, which were relatively more abundant

389 (but not as dominant as to generally monopolize space with, consequently, a very
390 homogeneous distribution) in the extra-urban condition. Such overall reduced abundances may
391 have directly reduced their variability between different patches of the substratum. This was
392 evident, for instance, for corticated and foliose algae from the midshore habitat, which were, in
393 general, relatively less abundant and more homogeneously distributed in the urban than in the
394 extra-urban condition in both systems. Although not consistent through time, a smaller
395 variability, particularly at small scale, of algae (*Enteromorpha* spp.) was also documented by
396 Bishop et al. (2002) in close proximity, compared to larger distance, to a shoreline sewage
397 outfall. Such a response, however, was likely driven by the increased abundance of such algae
398 close to that particular source of disturbance, leading to their dominance of space and
399 consequent more homogeneous distribution there. By contrast, sessile invertebrates, such as the
400 gregarious group here examined, for which the available space is a critical resource, are likely
401 to respond negatively to larger covers of algae. This would explain their generally lower
402 abundance in the urban condition. Moreover, they could have occurred only within small
403 portions of the substratum left available by dominant algal competitors, resulting in a more
404 heterogeneous distribution compared to the extra-urban condition. Concomitantly, the overall
405 trend of the difference between the urban and the extra-urban condition in the abundance of
406 grazers was in the opposite direction of that of dominant algal group. Although grazers might
407 directly and positively respond to fluctuations in the abundance of their food resources, their
408 activities can also be jeopardized in patches monopolized by sessile organisms, including algae
409 (Underwood and Jernakoff, 1981). Accordingly, it is not surprising that their overall abundance
410 was relatively larger in the urban condition where potential algal food items were also more
411 abundant, but their trend in spatial variability reversed that of algae.
412 Second, but strictly related to the previous point, smaller and larger variances of most
413 groups of organisms were found where these were, respectively, less or more abundant.
414 Analogous evidence was obtained by previous studies examining patterns of abundance and

distribution of rocky shore organisms in response to urbanization in general (Oliveira et al., 2014a) and to particular human-related disturbances (Benedetti-Cecchi et al., 2006). Independently of the driving factors and underlying mechanisms of changes in abundances, this circumstance can be interpreted as a direct consequence of the scaling relationship between the mean and the variance, according to which very low mean values of a variable would intrinsically hinder large fluctuations around them (Taylor, 1961).

Third, irrespectively of any other examined factor, most variability of the majority of examined response variables was found at the smallest (among-quadrats) scale. This seems to be an ubiquitous feature of benthic assemblages in coastal habitats (Fraschetti *et al.*,, 2005) in response to local physical and biological processes which are common in marine systems (e.g. Coleman et al., 2002; Terlizzi et al., 2007). In this context, provided that changes in small-scale variability have been suggested as indicative of impacted assemblages (Warwick and Clarke, 1993), examining in detail, such as in the present study, the direction of such changes in a range of systems and habitats is essential to separate the variability due to the examined disturbance from the large variability characterizing assemblages even in non-impacted conditions.

Fourth, contrarily to the reported positive relationship between urban-related influences and the number and/or spread of biological invasions (Bulleri and Airoldi, 2005; Tyrrell and Byers, 2007), urbanization in our study systems did not appear to facilitate invasive species. Almost all locations where these species were present and/or relatively abundant belonged, instead, to the extra-urban condition. Once again, the specific drivers of this pattern could not be elucidated by the present study, but it is worth noting that several previous studies reporting a facilitation of invasions in marine systems focused on the role of artificial structures within urban environments (Bulleri and Airoldi, 2005; Glasby et al., 2007; Tyrrell and Byers, 2007). The same circumstances did not apply here as present comparisons were all done on natural rocky substratum. There is evidence, however, that gradients of urbanization *per se* may be

441 poor predictors of patterns of distribution and abundance of invasive macroalgae. These
442 might, instead, respond more directly to the relative availability of favourable and
443 unfavourable habitats, a variable that is not necessarily related to urbanization and to its
444 associated overall degradation of environmental conditions in a consistent way (Bulleri et al.,
445 2011).
446 Finally, especially in the midshore habitat, canopy-forming algae in the islands were
447 generally more abundant in the extra-urban condition, while on the mainland they tended to
448 be less abundant or completely absent everywhere. This finding agrees in part with previous
449 evidence of the loss of canopy-forming algae along gradients of urbanization (Benedetti-
450 Cecchi et al., 2001; Connell et al., 2008; Mangialajo et al., 2008) and of their larger
451 abundance in insular compared to mainland systems (Benedetti-Cecchi et al., 2003).
452 Moreover, there is the general perception that algal canopies, such as kelp beds, that used to
453 be common along the Portuguese continental coast have now dramatically declined (Assis et
454 al., 2009). Hence, it can be suggested that rocky shores far from urban areas in the islands are
455 relatively more pristine compared to those sampled on the mainland. As such, they would
456 represent a spatial refuge for structurally complex species, which may undergo local
457 extinction on the mainland due to past and current excessive disturbance even relatively far
458 from coastal cities (e.g. Benedetti-Cecchi et al., 2003).
459 In conclusion, although the particular mechanisms underlying the complex set of
460 urbanization-related responses still need to be elucidated, the present study provides the first
461 example where the influence of urbanization on patterns of distribution of whole assemblages
462 and individual taxa were tested across mainland and insular systems. This is crucially
463 important as mainland and insular environments may differ in their isolation and size and/or
464 in local relevant processes, with consequent different patterns of distribution and abundance
465 of populations and assemblages in response to anthropogenic pressures in urban areas.
466 Addressing such issues is important to assess whether islands provide unique environments

relatively ‘safe’ from pervasive urbanization-related influences, or such influences are as strong and pervasive as to determine patterns of biodiversity comparable to those on the mainland. Present findings suggest that effects of urbanization in the studied systems might not be strong enough to overwhelm those of other processes making the islands and the mainland system intrinsically different, but also that specific patterns of distribution and abundance of rocky shore organisms in response to urbanization are evident in islands too. In a broader perspective, these results strengthen the notion, supported by previous evidence from intertidal (e.g. Bishop et al., 2002; Benedetti-Cecchi et al., 2003), subtidal (e.g. Chapman et al., 1995; Balestri et al., 2004; Terlizzi et al., 2007) and terrestrial (e.g. Pryke and Samways, 2015) systems, that multiple spatial scales should be simultaneously examined, by means of proper sampling designs, in assessments of responses of coastal assemblages to human disturbance. As a direct consequence, any effective management and conservation strategy would require to include (for instance, within implemented protected areas) representative assemblages and their relevant scales of variation associated to gradients of urbanization, both on the mainland and the islands.

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694

FIGURE CAPTIONS

Figure 1. Map of the study locations (nTGC indicates the rocky shore adjacent to the Terminal of General Cargo breakwater in the Sines city area).

Figure 2. Multivariate square root-transformed variance (mean + SE, n = 3) of the structure of midshore (A) and lowshore (B) assemblages from the urban and the extra-urban condition at four spatial scales (Qua = quadrat, Are = area, Loc = location, Reg = region) and two times of sampling at the mainland and the island system. Stars above bars indicate significantly different (* = $p < 0.05$, ** = $p < 0.01$) means (SNK tests; only comparisons within each scale are appropriate).

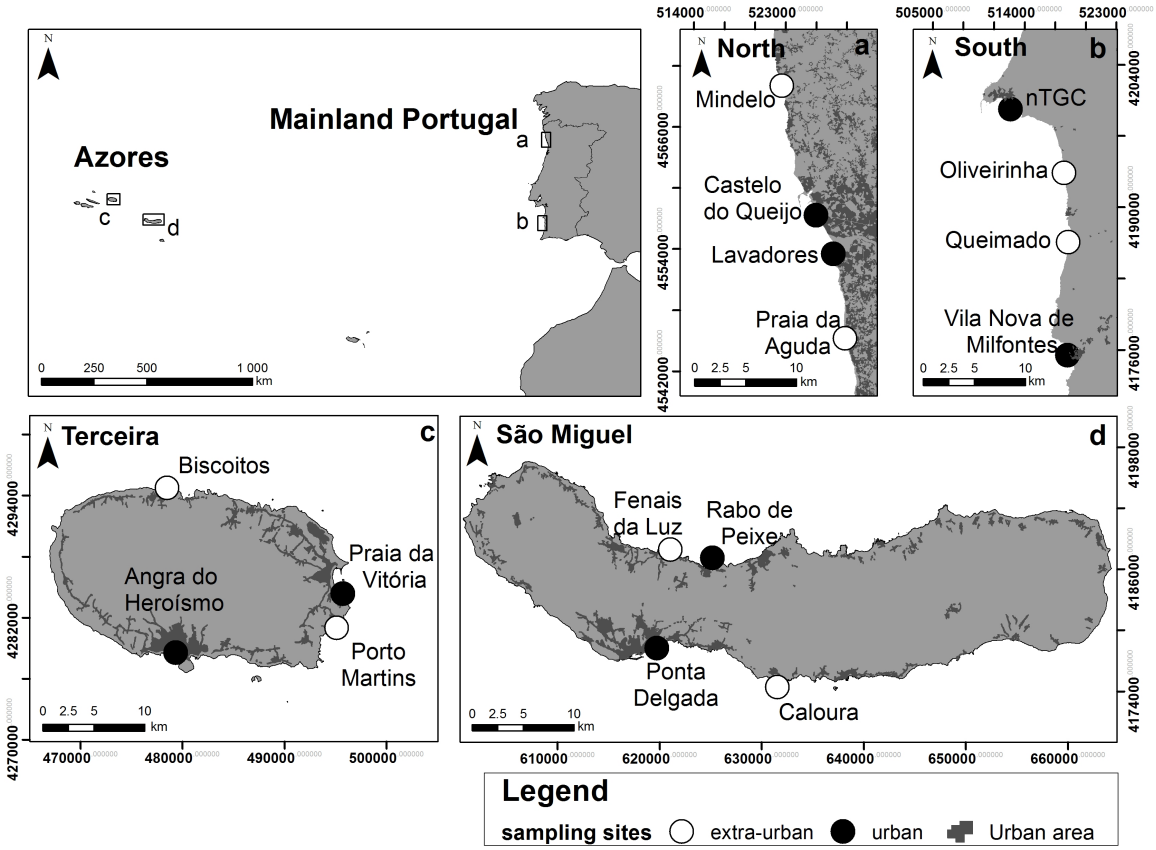
Figure 3. Univariate measures of variance (mean + SE, n = 3 in both panels A, C and D, n = 6 in panel B) of the abundance of morpho-functional groups of algae at midshore height. Symbols and abbreviations as in Figure 2. Panels A, B and C are on logarithmic scale, panels D are on untransformed scale.

Figure 4. Univariate measures of variance (mean + SE, n = 3 in both panels A and C, n = 12 in all panels B, n = 6 in panel D) of the abundance of morpho-functional groups of algae or invertebrates at midshore height. Symbols and abbreviations as in Figure 2. Panels A, C and D are on untransformed scale, panels B are on square root-transformed scale.

Figure 5. Univariate measures of variance (mean + SE, n = 12 in both the first and the third panel A and B, n = 6 in all other panels) of the abundance of morpho-functional groups of algae at lowshore height. Symbols and abbreviations as in Figure 2. All panels A are on square root-transformed scale, panels B and C are on logarithmic scale, panels D are on untransformed scale.

Figure 6. Univariate measures of variance (mean + SE, n = 12 in all panels A, n = 3 in panels B and C) of the abundance of encrusting algae and grazers and gregarious sessile animals at lowshore height. Symbols and abbreviations as in Figure 2. Panels A are on square root-transformed scale, panels B and C are on untransformed scale.

Figure 7. Univariate untransformed measures of variance (mean + SE, n = 3 in both panels A, n = 6 in panel B) of the abundance of invasive and canopy-forming algae at lowshore height. Symbols and abbreviations as in Figure 2.



725 Fig. 1 Bertocci et al.

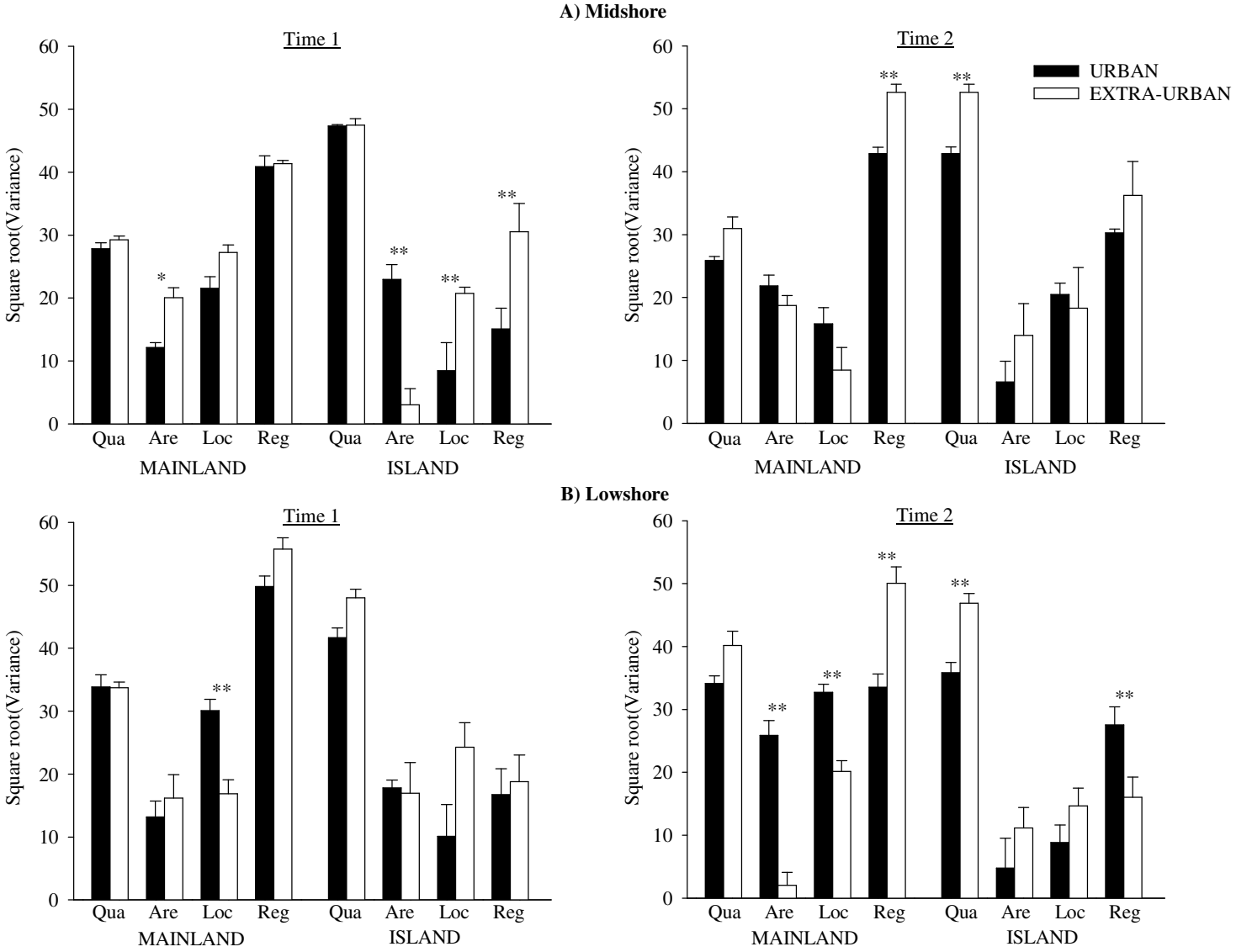


Fig. 2 Bertocci et al.

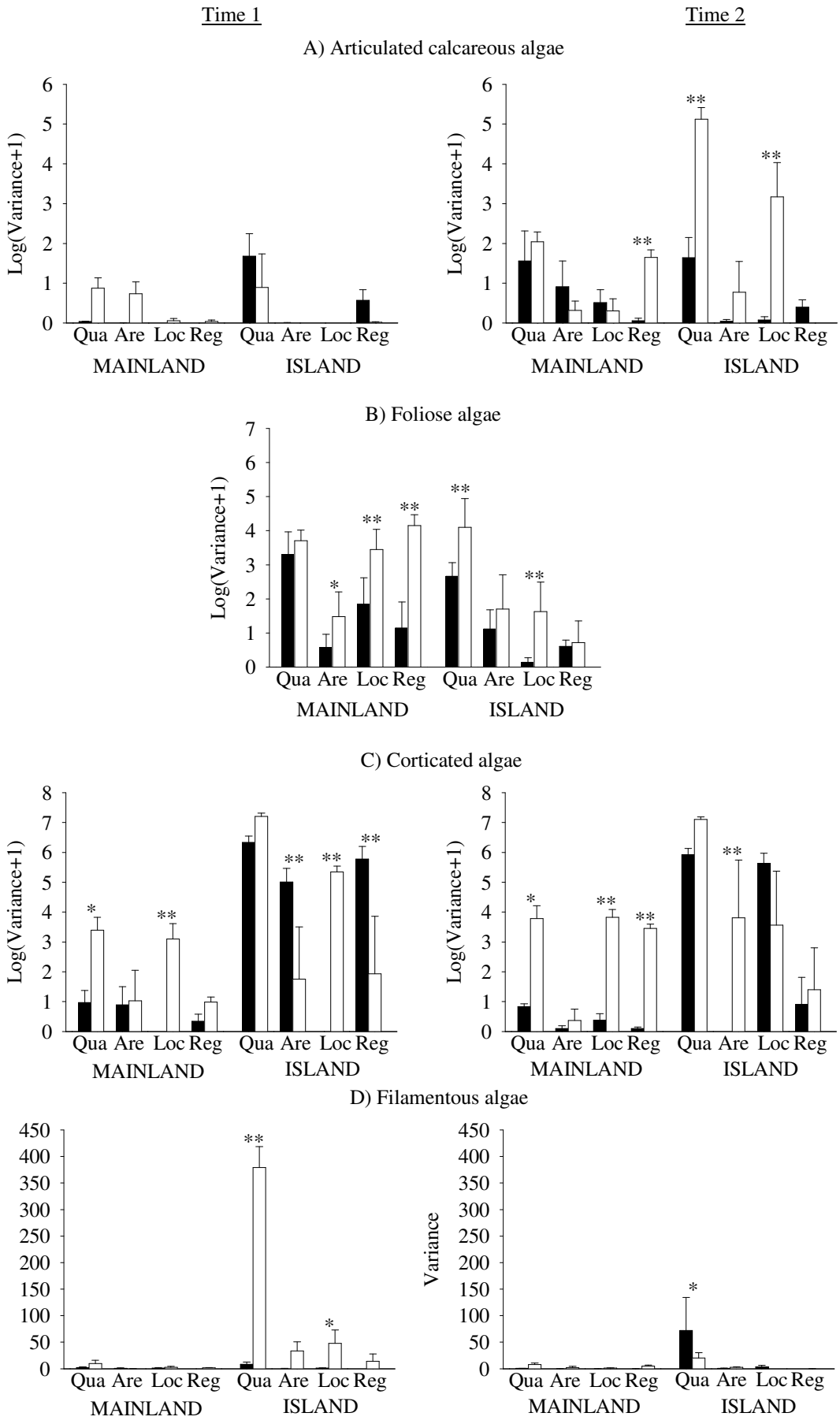


Fig. 3 Bertocci et al.

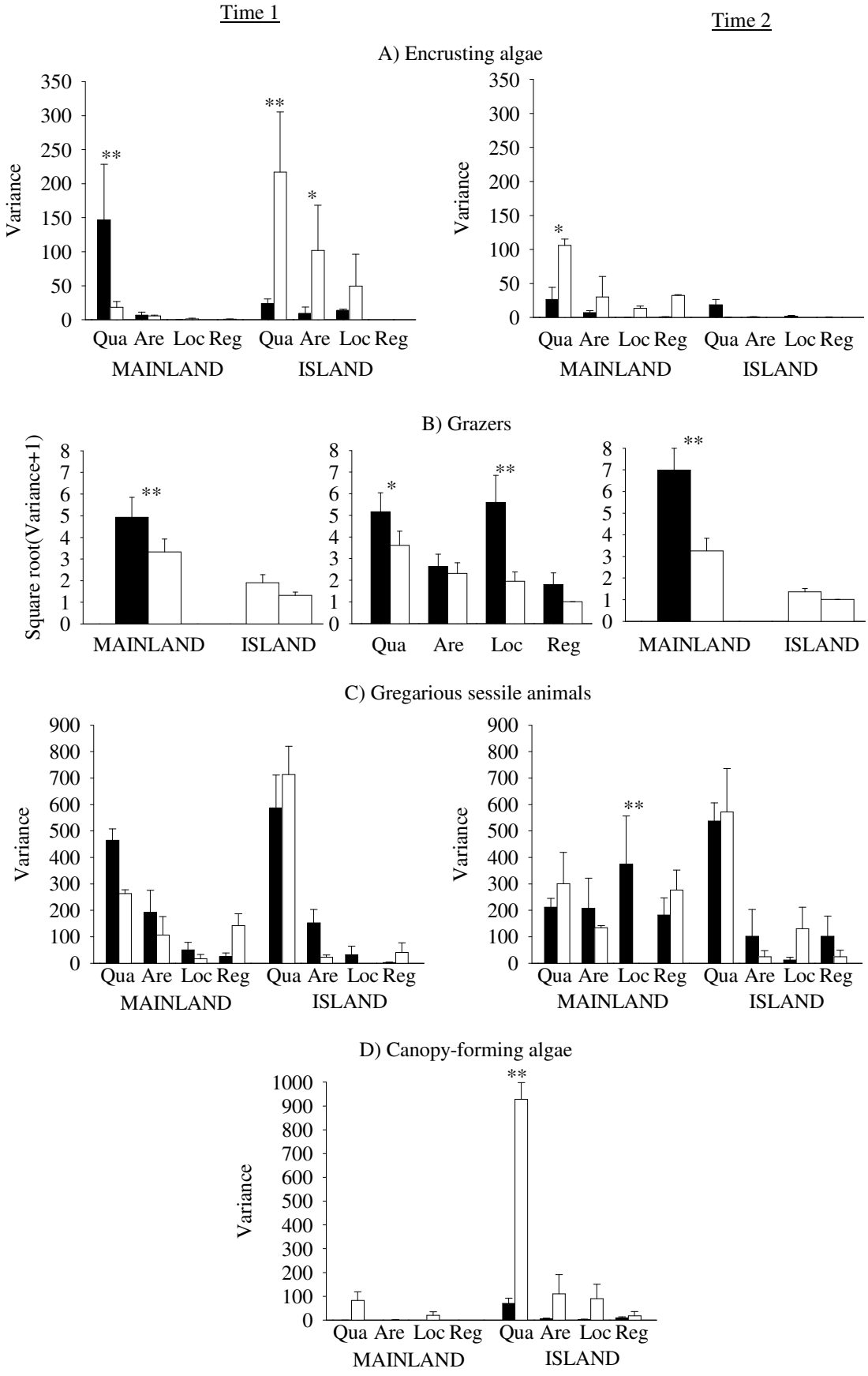


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Fig. 4 Bertocci et al.

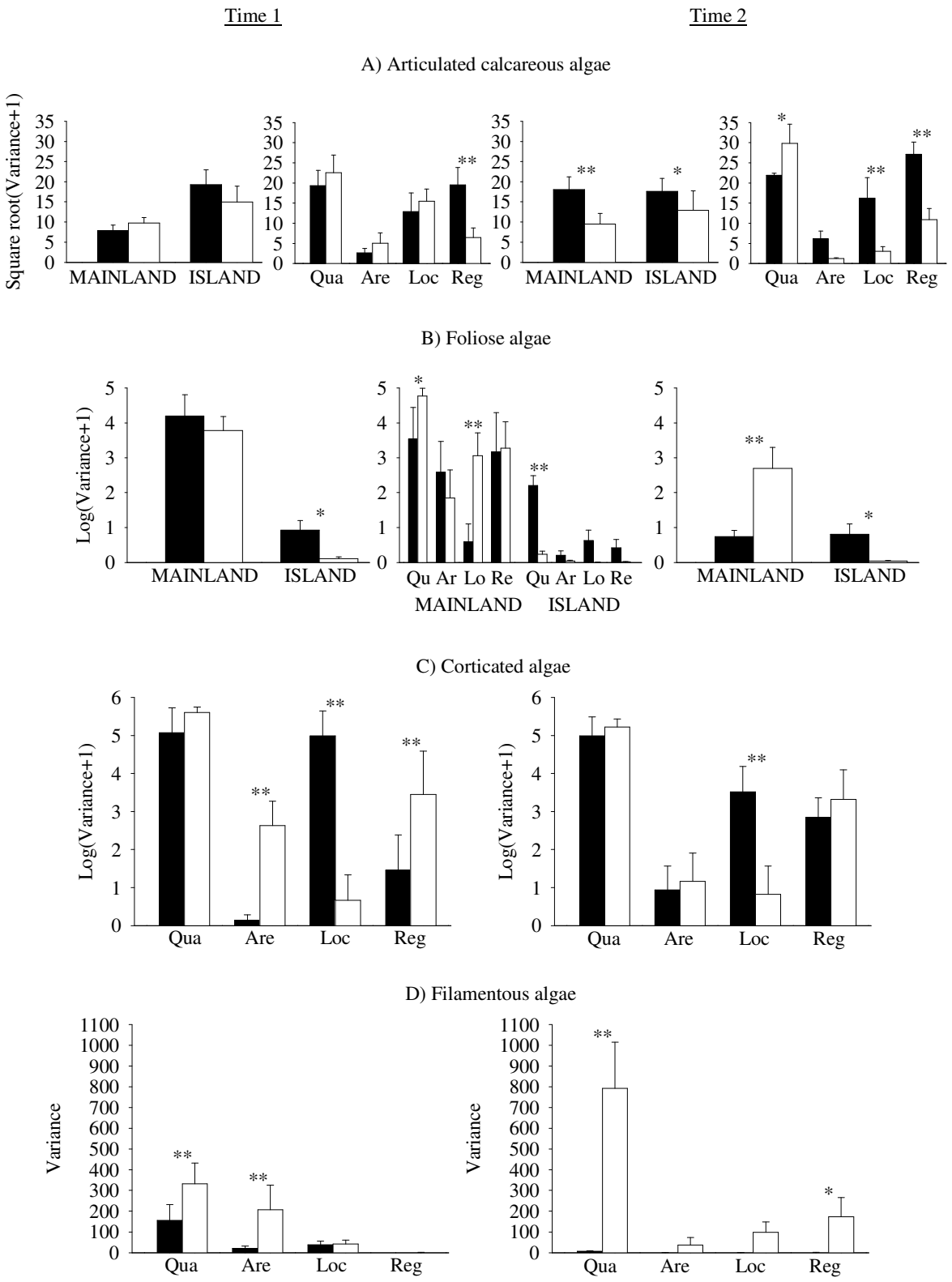
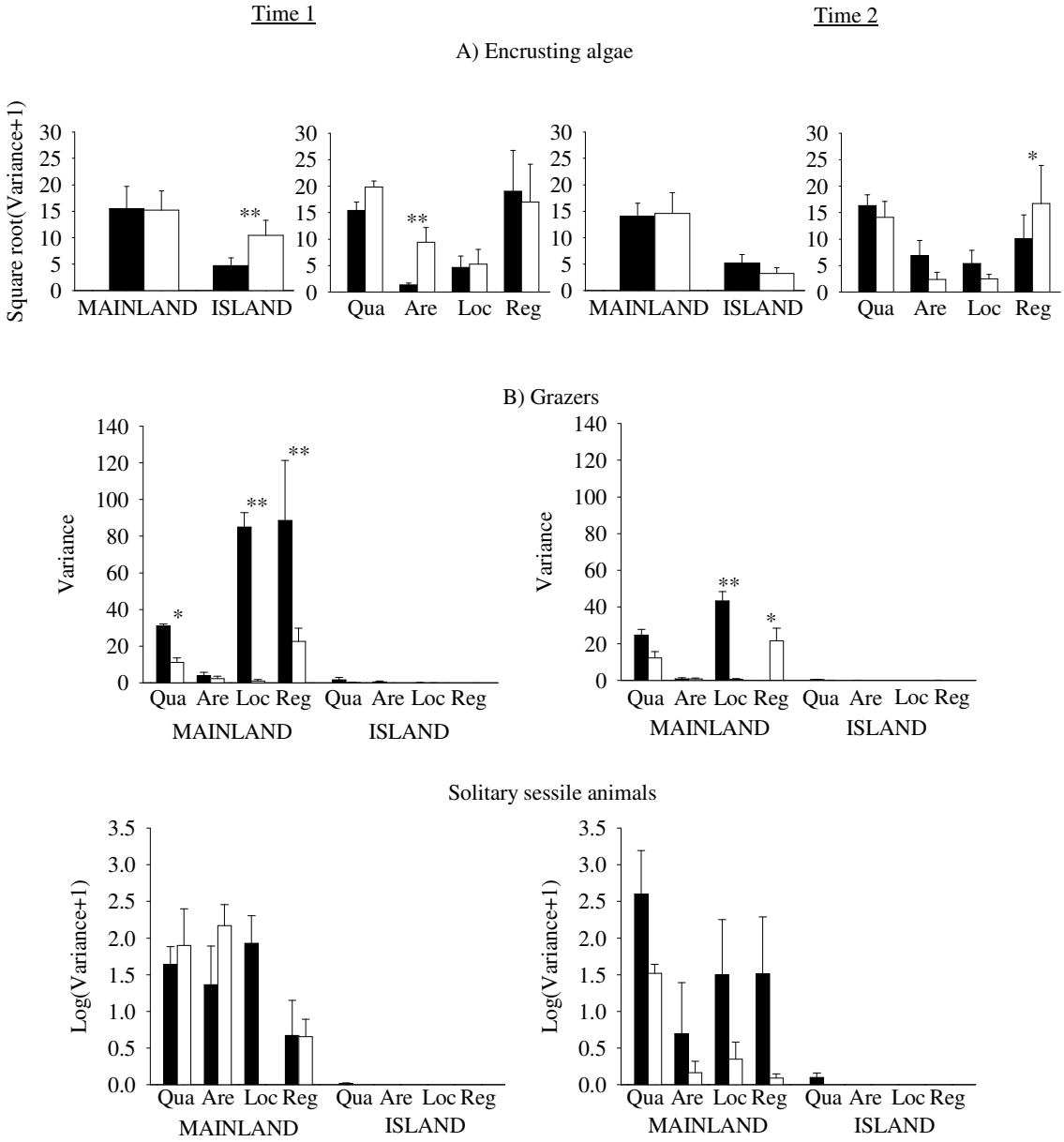


Fig. 5 Bertocci et al.



735 Fig. 6 Bertocci et al.

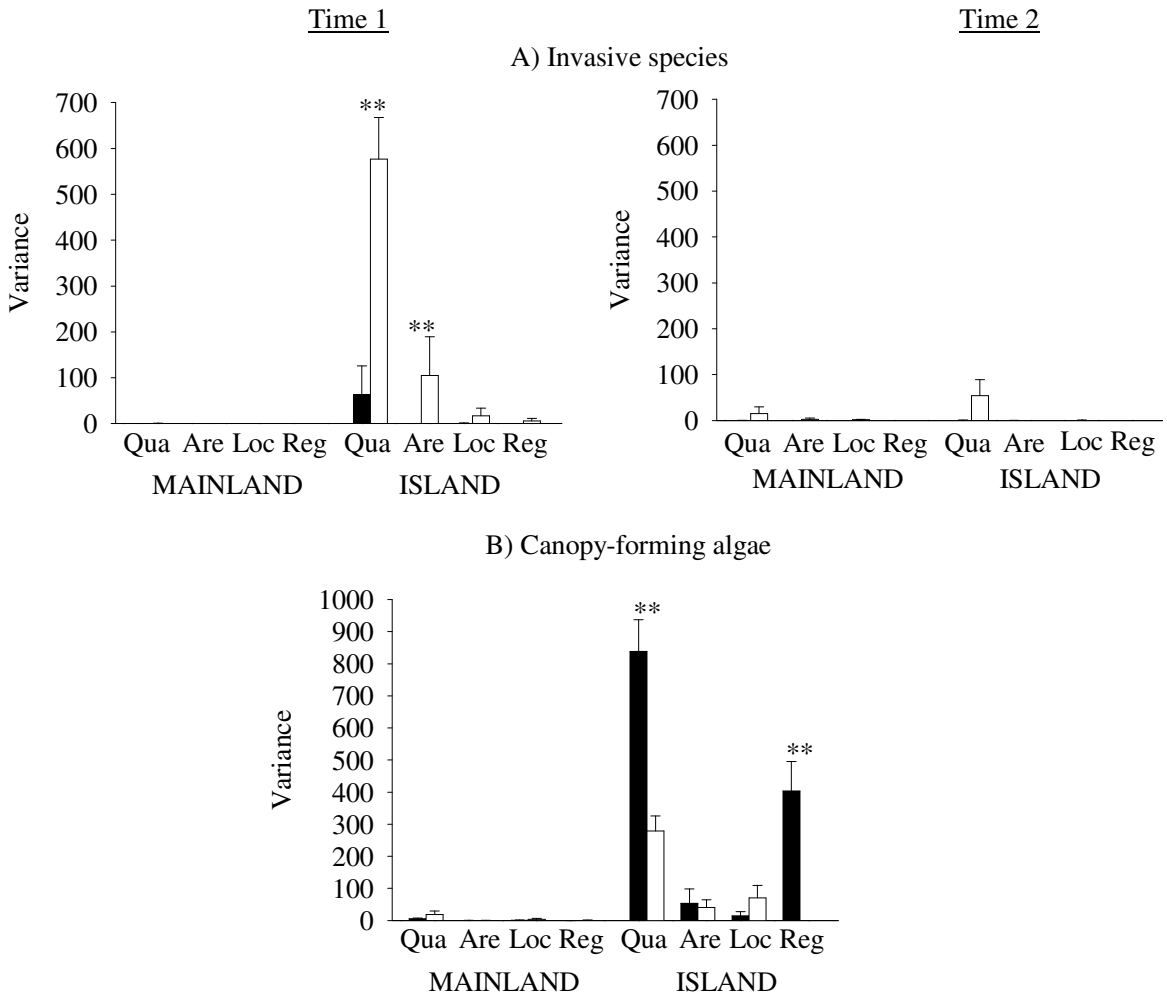


Fig. 7 Bertocci et al.