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Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: a multiscaled approach

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Running Head: Organization of shallow water algae

ABSTRACT: We conducted a mensurative survey to investigate spatial variability and the effect of wave exposure at a range of spatial scales including islands (100s of kilometres apart), locations within islands (10s of kilometres apart), and sites within locations (100s of meters apart), on the composition, abundance and distribution of shallow water algal assemblages across subtidal hard bottoms of the Canarian Archipelago (eastern Atlantic). A multi-scaled hierarchical sampling design provided the framework for quantifying the variation among samples due to each spatial scale and level of wave exposure. Haphazardly placed 50 x 50 cm quadrats were deployed in shallow rocky-reefs to assess community structure and dominance. Non-parametric multivariate techniques, as well as univariate tests, provided evidence to collectively suggest that shallow water algal assemblages differed between protected (leeward) and exposed (windward) shores, with a consistency of its effects across islands, while different spatial scales were also involved in the variability and patchiness of these assemblages. In this sense, differences were clearly taxon and/or group-

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specific. In general, the presence and abundance of frondose fucoid species was greater at exposed shores compared to protected shores, whereas turf-algae dominated protected shores at each island. Dissimilarities between islands for the overall algal assemblage generally increased with the distance between islands. In particular, the presence and abundance of fucoid species was larger in the eastern islands, while in contrast turf and bush-like algae increased in the western islands. The large-scale gradient of the oceanographic conditions in an east-to-west direction across the Canarian Archipelago provided a parsimonious explanation for this observation, yet some inconsistencies were observed in the overall regional pattern.

KEY WORDS: Algae • Phytobenthic assemblages • Hierarchical design • Spatial variability • Wave exposure • PERMANOVA • Canary Islands

INTRODUCTION

Differences in environmental conditions play an important role in landscape heterogeneity at different scales, from local patchiness to variation along biogeographic gradients (Levin 1992, Tilman & Kareiva 1997, Fraschetti et al. 2001, Garrabou et al. 2002, Fraschetti et al. 2005). Consequently, linkages across multiple scales are increasingly being considered by ecologists (Brown 1995, Fraschetti et al. 2005). The use of macroecology to reconcile biogeography and ecology has focused mainly on terrestrial systems (Boero 1999), with scarce application of these concepts to marine habitats (Fraschetti et al. 2001); most studies have focused on a narrow range of spatial scales in a limited number of habitats (Fraschetti et al. 2005). In this sense, linkages between local geography and ecological features have seldom been considered for the composition, distribution and structure of subtidal assemblages on rocky reefs.

The main biological engineers of temperate rocky-reefs are macroalgae (Steneck et al. 2002, Graham 2004). The existence of algae is influenced by pre-recruitment processes (Hoffmann & Ugarte 1985, Andrew & Veijo 1998, Coleman 2003), environmental conditions (e.g. wave exposure) (Santelices 1990, Coleman 2003, Taylor & Schiel 2003), post-recruitment biotic processes (Underwood & Jernakoff 1981, Jernakoff 1983, Benedetti-Cecchi & Cinelli 1994), and physical stress and disturbance (Kennelly 1987, Kendrick 1991). The role played by different processes operating at different scales in the composition, distribution and structure of algal assemblages is a growing field of interest, and remains largely untested in the majority of coastal areas (Fraschetti et al. 2005). In this context, hierarchical spatially structured sampling programs provide a means of partitioning and quantifying the magnitude of variation at different spatial scales (Underwood & Chapman 1996, Underwood 1997, Menconi et al. 1999, Benedetti-Cecchi 2001, Benedetti-Cecchi et al. 2003, Anderson & Millar 2004, Dethier & Schoch 2005, Fraschetti et al. 2005).

The Canary Islands lie between 100 and 600 km offshore from the north-west coast of Africa (~28ºN) and comprise seven major islands, as well as a group of small islets (Chinijo Archipelago) (Fig. 1). Nearshore waters of north-western Africa are characterized by almost year-round wind-driven upwelling that brings cold, nutrient-rich sub-surface waters to the surface, extending as a 50–70 km band along shore (Davenport et al. 2002). Consequently, the Canarian Archipelago lies in the transition between the oligotrophic open ocean and the northwest African upwelling (so-called Northwest African Coastal Transition Zone [NACTZ]). Large spatial variation in sea surface temperature (SST) occurs across an east–west gradient perpendicular to the African coast (Davenport et al. 2002), with an average difference of 2ºC between the eastern and western islands (Barton et al. 1998, Davenport et al. 2002). As a result, marine assemblages at widely separated islands (100s of km) are subjected to different oceanographic conditions and regimes of 'bottom-up' effects (*sensu* Menge 2000), that produce qualitative and quantitative differences between the eastern and western islands, as has been observed for demersal fish (Tuya et al. 2004a). At the same time, persistent trade winds induce strong turbulence (swell and wind) at exposed north and northeast facing shores, while south and southwest facing shores are more sheltered.

Islands have provided valuable systems to test hypotheses about the effect of environmental heterogeneity on the spatial patterns of natural subtidal assemblages (Benedetti-Cecchi et al. 2003, Lindegarth & Gamfeldt 2005, Micheli et al. 2005). We took advantage of the natural conditions across the Canarian Archipelago to assess the role played by environmental factors in determining the composition, structure and organization of shallow water algal assemblages on rocky reefs. In this sense, we conducted a mensurative, multi-scaled, observational experiment (*sensu* Underwood 1997, Anderson & Millar 2004, Fraschetti et al. 2005) to study the effects of: (i) the degree of wave exposure and spatial variability associated with a hierarchy of spatial scales ranging from (ii) islands (100s of kilometres apart), to (iii) locations within islands (10s of kilometres apart), and (iv) sites within locations (100s of meters apart) on the composition, abundance and distribution of shallow water algal assemblages at a regional context (< 1000 km). More specifically, we tested the hypothesis that the role of wave exposure is significant in determining the structure and organization of shallow water algal assemblages, and assessed the consistency of this pattern across the islands constituting the Canarian Archipelago. Since frondose fucoid algae may be considered as temperate-water elements of the shallow subtidal zone (Lüning 1990, Steneck et al. 2002), whereas turf and bush-like algae are more common in tropical waters (Lüning 1990), we additionally hypothesized that the presence and abundance of fucoid algae should be larger in the eastern islands, while in contrast turf and bush-like algae should increase in the western islands. Algae can be expected to be more susceptible to disturbance by wave action and/or have lower capabilities to recover after disturbance when other factors make the environment stressful. As a result, we predicted that the effects of wave exposure would interact with variability among islands, and that the different algal taxa and/or algal groups would show different patterns in this regard.

MATERIALS AND METHODS

Area of study and sampling design. The study was carried out on basaltic rocky bottoms between 2 to 8 m of depth at the Canarian Archipelago (28º N, eastern Atlantic Ocean), during March 2005. In this region, the long-spined black sea urchin, *Diadema antillarum* (Philippi), plays a key role on the structure of subtidal rocky reefs (Tuya et al., 2004a), transforming areas previously covered by erect algae to unvegetated substrates. In general, water turbulence inhibits considerably the presence of *D. antillarum* within the first meters of the subtidal across the eastern Atlantic (Alves et al. 2001). As a result, the distribution of benthic communities along the bathymetric axis shows usually a clear vertical zonation pattern. Within the shallowest zone, extensive stands of algal assemblages dominate the community with a scarce presence of *D. antillarum* (densities typically range between 0 to 1 ind m^{-2}). Intensive grazing by *D. antillarum* produces clear interfaces between these shallow water algal stands and deeper areas devoid of vegetation (densities usually range between 2 to 12 ind m^{-2}, Tuya et al. 2004a). The contribution of other herbivorous fauna to the organization of subtidal reefs is negligible compared to *D. antillarum* (Tuya et al. 2004b). For example, echinoid species such as *Paracentrotus lividus* or *Arbacia lixula* are found at low densities across all the Canary Islands, in contrast to the nearby Mediterranean Sea.

Responses of algae to environmental variability are best tested with a functional group approach instead of using specific species (Steneck & Dethier 1994). Fleshy, canopy-forming, algae were categorized into three morphological groups, by taking into account the algal form groups reported in the literature (Steneck & Dethier 1994, Garrabou et al. 2002, Fowler-

Walker & Connell 2002, McClanahan et al. 2003), especially those from the nearby Mediterranean (Ruitton et al. 2000), as well as our own experience. Turf algae (hereafter TA) consist of small cushion-shaped and filamentous species, usually < 5 cm in height, such as *Codium* spp., *Colpomenia sinuosa*, *Dasycladus vermicularis* and, principally, *Lobophora variegata*. Bush-like algae (hereafter BA) are sheet-shaped, jointed non-crustose calcareous and thick leathery-shaped species (e.g. *Asparagopsis* spp., *Corallina elongata*, *Dyctiota* spp., *Padina pavonica*, *Stypocaulon scoparium*, *Stypopodium zonale*, *Taonia atomaria*, *Zonaria tournefortii,* etc.), from 1 to 15 cm in height, which constitute either large algal cushions or thin sheets with mixtures of algal species. Corticated, large, canopy-forming brown macrophytes (hereafter BM) are erect, frondose, coarsely-branched fucoid species (the genera *Cystoseira* and *Sargassum*), usually > 15 cm in height, and in general forming low diversity algal stands. Understory algae were excluded from the surveys as their coverage is hard to determinate, and a meticulous investigation of the whole substratum is too time-consuming. However, crustose coralline algae (e.g. the genera *Lithothamnion, Lithophyllum*, *Neogoniolithon*, *Titanoderma*, etc) were counted when not overgrown by other algae.

Our sampling design tested the effect of the degree of wave exposure to the dominant, trade wind-induced NE-swells (categorized as high *versus* low exposure = exposed or windward *versus* protected or leeward shores, see Lindegarth & Gamfeldt 2005 for a discussion on this topic) at each of the seven islands constituting the Canary Islands, as well as a group of small islets, the "Chinijo Archipelago", to the north of Lanzarote Island (Fig. 1). We selected a total of 32 locations across the Canarian Archipelago as spatial replicates of the 16 defined treatments (2 levels of degree of wave exposure x 8 islands), with 2 locations separated by 10s of kilometres per treatment (Fig. 1). Exposed locations directly received the prevailing swells and winds from the northeast, whereas protected locations lay to the south on the opposite side of each island (Fig. 1). Swells from the south are significantly rarer (Martín Ruiz 2001).

Additionally, we surveyed two randomly-selected sites separated by 10s of meters within each location. As a result, a hierarchical, structured, sampling design (*sensu* Underwood 1997, Fraschetti et al. 2005) provided the framework for quantifying the variation among samples due to each spatial scale and both levels of wave exposure at a regional scale (< 1000 km).

Sampling and data analysis. At each site, a SCUBA-diver quantified *in situ* the percent cover of algae in four 50 x 50 cm quadrats (0.25 m^2), following point-quadrat procedures with a grid of 121 points per quadrat. Quadrats, several meters apart, were haphazardly laid out. This is a rapid, non-destructive, technique to assess community structure and dominance of sessile biota (Fowler-Walker & Connell 2002, McClanahan et al. 2003). Final values for each taxon were expressed as percentages. Taxa presented in less than a 4% cover were omitted. Unidentified filamentous turf consisted principally of red algae belonging to the families Ceramiaceae and Rhodomelaceae.

Hypotheses were tested using multivariate and univariate procedures. To test for differences in the algal community caused by the two levels of wave exposure across the hierarchy of spatial scales, we selected non-parametric approaches (Anderson 2001, Anderson & Millar 2004) and applied a mixed analysis technique by combining the semi-parametric, distance based, Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2004), and non-metric multidimensional scaling (MDS) ordination (PRIMER software; Clarke & Warwick 1994). In both cases, data were transformed to square root and analyses were based on Bray-Curtis dissimilarities. The PERMANOVA incorporated the following factors: (1) 'Wave Exposure' (fixed factor with two levels: protected *versus* exposed) (2) 'Island' (fixed factor with eight levels corresponding to the seven islands plus Chinijo Archipelago, and orthogonal to the previous factor), (3) 'Locations' (random factor with two levels, nested within the interaction term between 'Islands' and 'Wave exposure') and (4) 'Sites' (random factor with two levels, nested within the interaction term between 'Locations', 'Islands' and

'Wave exposure'). PERMANOVA was used to partition variability and provide measures of multivariate variability at different scales in the structured design in a manner analogous to univariate partitioning using ANOVA (Anderson & Millar 2004, Fraschetti et al. 2005). We applied this technique to the overall community dataset, as well as to each of the three defined morphological groups of algae. When appropriate, pairwise *a posteriori* comparisons were executed using permutations (Anderson 2004).

To visualize multivariate patterns, non-metric multidimensional scaling (MDS) ordinations were carried out. The MDS was applied for three different scenarios, gradually increasing the complexity of the analysis. Firstly, we analyzed the algal community structure by considering only the 16 established treatments (8 islands x 2 levels of wave exposure) by pooling the overall data within each treatment. In the second step, we included replicated locations within each treatment; and in the third step, we included replicated sites within locations for each treatment. Stress values are a measure of goodness of fit of data points in the MDS, and stress equals zero when data are perfectly represented (Clarke & Warwick 1994). If the stress levels are greater that 0.2, plots are considered difficult to interpret. Since an acceptable stress value (< 0.14) was only obtained for the first scenario, we used only this analysis.

The SIMPER procedure (Clarke & Warwick 1994) was carried out to assess average similarities and dissimilarities within and between treatments, respectively; as well as to identify the contribution of each algal taxon to the differences within and between levels of wave exposure and islands. As a result, prominent taxa contributing to differences among treatments were identified and used in subsequent univariate analyses.

A mixed four-factor ANOVA univariate model (Underwood 1997) was applied to each of the three groups of algae, as well as to the prominent taxa detected by the SIMPER protocol, to test for significant differences attributable to the above-considered factors. Hence, ANOVAs tested the same hypotheses described above for multivariate data, but in a univariate context.

When the factor 'Islands' was significant for some of the ANOVAs, pairwise *a posteriori* SNK tests were used. Before analysis, the Cochran's test was used to check for homogeneity of variances. Although no transformation rendered homogeneous variances in the majority of cases (Cochran's test, $p < 0.01$), the ANOVA was carried out as it is robust to heterogeneity of variances, particularly for large balanced experiments (Underwood 1997). The significance level was thus set at the 0.01 level instead of 0.05 (Underwood 1997).

Finally, we assessed the geographical affinities in the composition and structure of algal assemblages across the Canarian Archipelago by means of a correlation analysis between the average pairwise dissimilarities matrix among islands for the entire dataset and a pairwise matrix containing the minimum lineal distances (in km) between each pair of islands. We used the pairwise average dissimilarities matrix output from both the SIMPER procedure and the PERMANOVA.

RESULTS

A total of 39 algal taxa were observed in the 256 quadrats conducted at the 32 study locations (Appendix 1). The prominent taxa within the TA were, in decreasing order, *Lobophora variegata* (40.6% frequency of occurrence in the 256 quadrats), unidentified filamentous turf (38.6%) and *Jania* spp. (32.4%). The BA group was mainly dominated by *Dyctiota dichotoma* (68.7%), *Padina pavonica* (31.6%) and *Asparagopsis* spp. (21.9%). Finally, the BM group was represented by *Cystoseira* spp. (21.9%) and *Sargassum* spp. (11.3%).

Multivariate analysis

Multivariate techniques revealed large and significant differences in the composition and structure of the algal community for the different factors. Firstly, the multivariate ANOVA performed on the entire algal dataset (Table 1) detected significant variability at the three spatial scales considered by our study: differences among islands, differences between locations within each island and level of wave exposure, and differences between sites within locations within each island and level of wave exposure ($p < 0.001$, Table 1). Significant variability attributable to differences in the degree of wave exposure was found ($p = 0.01$, Table 1); its effect was otherwise consistent across the islands (Table 1, 'I x WE', $p > 0.05$). Secondly, the two-dimensional MDS (Fig. 2, stress value = 0.09) revealed a separation of the treatments along the ordination diagram, with the eastern islands (Chinijo, Lanzarote, Fuerteventura and Gran Canaria) falling in the left side of the plot with the exception of exposed locations in Lanzarote (LZ-E in Fig. 2); whereas the western islands (Tenerife, Gomera, La Palma and El Hierro) were positioned in the right side of the plot. Several islands (Fuerteventura, Gran Canaria, Tenerife and Gomera) had similar assemblages in both protected and exposed locations, while the rest of the islands showed a clearer separation between protected and exposed locations in the ordination space (Fig. 2). *A posteriori* permutational tests among islands revealed a total of 10 significant differences of the overall 28 possible comparisons (p-Monte Carlo < 0.01) with 8 significant differences including El Hierro or La Palma islands. This result was indicative of the different composition, abundance and structure of the algal assemblages of these two islands compared to the rest of the islands. Moreover, the MDS plot also revealed this difference (Fig. 2), with the majority of locations within El Hierro and La Palma positioned at the top of the plot.

Alternatively, we found group-specific results when we analyzed the output of the PERMANOVA for each algal group (Table 1). Coverage of the BM group was significantly greater at exposed shores compared to protected shores ($p < 0.01$, Table 1) across islands (Table 2, 'I x WE', $p > 0.05$); while TA cover differed among islands ($p < 0.01$, Table 1), which was corroborated by some significant pairwise comparisons (Table 1). In all cases, we detected substantial variability at the medium (differences between locations) and small (differences between sites) spatial scales ($p < 0.01$, Table 1).

SIMPER analysis indicated that the average similarity among protected locations (38.46%) was greater that the average similarity among exposed locations (28.80%), suggesting a greater heterogeneity of exposed algal assemblages. Eight taxa contributed extensively to the differences between both levels of wave exposure accounting for the 57.97% of the overall dissimilarity (Appendix 2). In general, these taxa, as well as the fucoids *Cystoseira mauritanica* and *Sargassum* spp., accounted for dissimilarities among islands, although the relative importance of each taxon varied for each pair of comparisons (Appendix 2).
Average dissimilarities between pairs of islands were significantly correlated with lineal distances in km between them ($r_s = 0.49$, $0.001 < p < 0.01$ using the output from the SIMPER procedure; $r_s = 0.36$, $0.01 < p < 0.05$ using the output from the PERMANOVA).

Univariate analyses

Mean percentage covers across the study area (islands, locations within islands, and sites within locations) for three defined algal groups: TA, BA and BM are shown in Figures 3, 4 and 5, respectively. Results from the ANOVAs performed on the three groups are presented in Table 2. Although the ANOVAs indicated a significant effect of the variability between sites separated by 10s of m within locations only for the BM, we detected substantial spatial heterogeneity at the medium spatial scale (differences between locations separated by 10s of km within each island and level of wave exposure) for the three morphological groups ($p < 0.01$, Table 2). This large variability prevented the detection of significant differences caused by some of the two main effects in the three ANOVAs. However, the power of the ANOVAs was sufficient to reject some null hypotheses. In this sense, the BM group was significantly more abundant on exposed shores ($p < 0.01$, Table 2; Fig. 5), whereas the TA group was more abundant on protected shores ($p < 0.01$, Table 2; Fig. 3). In both cases, the effect of the 'wave exposure' was consistent across the islands (Table 2, 'I x WE', $p > 0.05$). Significant differences caused by the different islands were not detected for BM ($p > 0.01$, Table 2), although visual inspection of the results (Fig. 5) suggests the existence of differences. In contrast, significant differences caused by 'Islands' were detected for TA ($p < 0.01$, Table 2) and BA ($p = 0.01$, Table 2), and can be seen in Figs 3 & 4. *A posteriori* SNK tests (Table 2) indicated the TA group dominated the western islands, whereas BA dominated the central and eastern islands with the exception of Chinijo Archipelago.

Results from the ANOVAs performed on the prominent algal taxa are presented in Table 3. Again, the analyses indicated substantial variability at the medium and low spatial scales (differences between locations 10s of kilometres apart within each island and level of wave exposure, and between sites 10s of meters apart within locations, respectively). Due to the variability between locations within each treatment, detection of significant differences among islands and between levels of wave exposure was only found for *Lobophora variegata*, *Jania* spp., and the unidentified filamentous turf (Figs 6, 7 & 8, respectively). *Lobophora variegata* (Fig. 6) monopolized the rocky bottoms of both El Hierro and La Palma with mean percent coverages up to 90% per location, and it was significantly more abundant in these islands than all other islands ($p < 0.01$, SNK tests, Table 3). *Jania* spp. (Fig. 7) appeared to be more abundant in the eastern islands ($p < 0.01$, SNK tests, Table 3). Finally, the unidentified filamentous turf (Fig. 8) was significantly more abundant in Gomera and Tenerife than the rest of the islands ($p < 0.01$, SNK tests, Table 3).

DISCUSSION

The presence of multiple islands along an oceanographic gradient with shores exposed to different hydrographic conditions provided an ideal opportunity to test hypotheses about the separate and combined effects of geographical and physical processes on the whole subtidal shallow water algal assemblages. Collectively, the findings of this study showed that subtidal algal assemblages differ consistently between protected and exposed shores across surveyed islands. Additionally, clear differences between islands situated at the opposite sides of the Canarian Archipelago were observed.

The analysis of pattern in distribution and abundance of marine organisms has direct relevance to the identification of underlying causal processes (Benedetti-Cecchi et al. 2003 and references therein, Fraschetti et al. 2005). Biotic processes and behaviour are usually implicated in the maintenance of small-to-medium scale spatial patchiness (e.g. differences between sites and locations separated by 100s of meters to 10s km), whereas oceanographic conditions and climate largely dictate regional, large-scale patterns operating at 100s of km (Underwood & Chapman 1996, Menconi et al. 1999). Our results support, in part, these conclusions. In particular, certain important group-specific differences within islands can be attributable to differences in levels of wave exposure, while significant differences at a regional scale (differences among islands 100s of kilometres apart) were found for some groups and taxa.

Variability associated with differences in the level of wave exposure

The combined indirect and direct hydrodynamic effects of wave action on nearshore biota are often grouped under the term 'wave exposure' (Taylor & Schiel 2003). Distinct patterns arose when the results of our study on the effect of 'wave exposure' were interpreted at a morphological group level. In general, the presence and abundance of species within the BM group (frondose fucoid species) was clearly greater at exposed locations (mean coverage for all exposed locations = 22.00 ± 5.61, mean ± SE) compared to protected locations (mean coverage for all protected locations = 1.56 ± 1.07, mean ± SE). Subtidal fucoid plants tend to be better adapted to exposed or semi-exposed conditions compared with other algal species in the Canary Islands (Medina & Haroun 1993, Haroun et al. 2003).

However, the ecological mechanisms underlying this difference are unknown. Variation in hydrographic conditions at the scales considered by our sampling design probably influence algal assemblages through the temporal variability and intensity of swells and storms, and the release of propagules from the water column (Micheli et al. 2005). Usually, water motion (i) enhances nutrient uptake by reducing or breaking the boundary layer, (ii) removes epiphytes and waste products, and (iii) allow algal stands to use light more efficiently by stirring their fronds, ensuring that no frond is either always shaded or always in the sun (Diez et al. 2003 and references therein). These mechanical advantages are accompanied by a continued mechanical stress that only morphologically adapted species can resist. Algae in these disturbed environments are characterized by a flexible thallus and an efficient attachment mechanism, such as the basal disc of certain species belonging to the genera *Cystoseira* and *Sargassum*.

Alternatively, this pattern could be related to anthropogenic perturbations. There is an increasing trend for long-term, and perhaps permanent, loss of canopy-forming algae to occur along human-impacted coasts (Russell & Connell 2005 and references therein). The loss of canopy-forming algae typically results in the immediate colonisation and spatial dominance of turf algae (Russell & Connell 2005). In this context, Benedetti-Cecchi et al. (2001) found that frondose, coarsely-branched algae were virtually absent from urban areas in the Mediterranean, with replacement by turf-forming algae. These authors argued that this group of fucoid algae (e.g. the genus *Cystoseira*) is highly sensitive to human disturbances. In the Canarian Archipelago, the most important urban areas associated with the tourist industry are located in the protected southern shores of each island (Martin-Ruiz 2001). As a result, the large number of sewage discharges, and subsequently the nutrient enrichment, along these human-perturbed areas could be involved in the lack of BM in the protected locations of our study. It is possible that a combination of wave action and anthropogenic disturbance is important in this variability within each island. However, lack of historical data on these assemblages and of direct quantification of the intensity and distribution of disturbances on the islands make it impossible to conclusively link these observed patterns to human impacts. The pattern detected for the BM group clearly contrast with that observed for TA, and in particular, for the patterns observed for the unidentified filamentous turf group. As a general pattern, TA dominated protected locations within each island with the exception of La Palma. For example, the unidentified filamentous turf group was twice as abundant in protected locations (coverage for all protected locations = 20.84 ± 5.70, mean ± SE) than exposed locations (coverage for all exposed locations = 10.37 ± 4.03, mean ± SE) for the overall study. Consequently, our observations reinforce the findings of other investigations that have highlighted the important role that wave exposure plays in shaping shallow marine benthic communities in temperate waters (Blanchette et al. 1999, Benedetti-Cecchi et al. 2003, Taylor & Schiel 2003, Lindegarth & Gamfeldt 2005, Micheli et al. 2005).

Variability at the medium and small spatial scale: differences within islands

In all cases analyzed by means of the multivariate ANOVAs, sampled locations within each island and level of wave exposure, as well as sites within locations, were quantitatively different. Considerable heterogeneity at these spatial scales highlights the complex nature of these assemblages; small-scale variability is a general property of benthic assemblages in marine coastal habitats (Underwood & Chapman 1996, Menconi et al. 1999, Benedetti-Cecchi 2001, Fowler-Walker & Connell 2002, Benedetti-Cecchi et al. 2003, Coleman 2003, Fraschetti et al. 2005). Differences among locations within each island and level of wave exposure were often as large as differences among islands or level of wave exposure. Variability at the location level probably obscured differences in cover between levels of wave exposure and islands for some algal groups and taxa. We can only speculate on the underlying causes of this variation, which are likely to involve complex interactions among several physical (e.g. availability of resources, habitat attributes) and biological processes (e.g. competition, predation). Clearly, different explanations can be proposed for different taxa according to their life-history strategies and biology.

Variability at the large spatial scale: differences among islands

Dissimilarities between islands for the overall subtidal algal community generally increased with the distance between islands. For example, El Hierro and La Palma, the westernmost islands, constituted a different assemblage 'block' compared to the rest of the islands. However, significant differences among islands were group, or more specifically, taxon-specific.

What are the underlying mechanisms that could account for differences among islands? Generally, differences in patterns of water circulation, availability of resources and type of substratum affecting recruitment, growth and mortality of algae have been proposed as explanations of variability at large spatial scales (from 10s to 100s of kilometres) (Santelices 1990, Menconi et al. 1999). The large-scale gradient in oceanographic conditions, such as SST and nutrients, in an east-to-west direction across the Canarian Archipelago (Barton et al. 1998, Bode et al. 2001, Davenport et al. 2002) provides a parsimonious explanation for this observation. Variation in oceanographic conditions usually results in differences in local productivity potential, which, in turn, can result in a visible and predictable change in the algal community (Steneck & Dethier 1994). In this context, our results agree with those of Schils and Coppejans (2003), who attributed differences in the composition, abundance and structure of subtidal algal communities in the Socotra Archipelago, Indian Ocean, to differences in SSTs and bottom-up resources caused by upwelling. The drawback of this approach is that islands may differ in other respects than differences in bottom-up availability of resources. Hence, caution is necessary in ascribing differences in the observed algal assemblages; causality can only be determined through experimental manipulation (Dulvy et al. 2004).

We hypothesized that the presence and abundance of fucoid species should be larger in the eastern islands, where SSTs are about 2ºC lower than the western islands, while in contrast the TA and BA groups should increase in the western islands. Our results generally support this pattern. For example, the fucoid alga *Cystoseira mauritanica* was only recorded at Chinijo Archipelago; whereas turf algae, and specially *Lobophora variegata*, were most abundant in the westernmost islands (El Hierro and La Palma). This result is consistent with the composition and structure of populations of the genus *Cystoseira* across subtidal and intertidal habitats of the Canarian Archipelago (Medina et al. 1995, Haroun 1997). Nevertheless, we found some inconsistencies in this general pattern. For example, no fucoid species (BM) were observed in Fuerteventura Island, while this algal group was relatively abundant in the westernmost island (El Hierro). The origin of the potential mechanisms explaining the 'temperate vs. tropical' differences in the algal assemblages are unknown, though differences in the availability of 'bottom-up' resources apparently play an important role explaining such differences. More work is desirable to empirically assess the reasons of this pattern.

Consequently, generalization of patterns and the establishment of a regional framework for the composition, abundance and distribution of shallow water algal assemblages along the overall Canarian Archipelago is complicated. Many environmental factors covary across large spatial gradients (Harley et al. 2003); making temperate rocky reef assemblages highly variable and dynamic at a regional scale (Micheli 2005). Within-island variability also obscures the hypothesized regional pattern. As a result, increasing the spatial replication at the smallest spatial scales (replicated quadrats within sites, and sites within locations) would probably help to decrease the 'noise' associated with other sources of environmental variability. To understand the generality of patterns in algal assemblages is difficult using a hierarchy of spatial scales covering < 1000 km (Fowler-Walker & Connell 2002). We therefore suggest increasing the spatial scale of observation (> 1000 km) to encompass a wider area of study along the warm-temperate waters of eastern Atlantic in the northern hemisphere. Probably, this approach could provide evidence of the existence of simple underlying rules (*sensu* Fowler-Walker & Connell 2002, Fraschetti et al. 2005) in the organization of shallow water algal assemblages.

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LITERATURE CITED

Alves FMA, Chicharo LM, Serrao E, Abreu AD (2001) Algal cover and sea urchin spatial distribution at Madeira Island (NE Atlantic). Sci Mar 65:383-392

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance in ecology. Aust Ecol 26: 32-46

Anderson MJ (2004) PERMANOVA_2factor: a FORTRAN computer program for permutational multivariate analysis of variance (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, New Zealand

Anderson MJ, Millar RB (2004) Spatial variation and effects of habitat on temperate reef assemblages in north eastern New Zealand. J Exp Mar Biol Ecol 305: 191-221

Andrew NL, Veijo RM (1998) Ecological limits to invasion of *Sargassum muticum* in northern Spain. Aquat Bot 60: 251-263

Barton ED, Arístegui J, Tett P, Cantón M, García-Braun J, Hernández-León S, Nykjaer J, Almedia C, Almunia J, Ballesteros S, Basterretxea G, Escánez J, García-Weill L, Hernández-Guerra A, López-Laatzen F, Molina R, Montero MF, Navarro-Perez E, Rodriguez JM, van Lening K, Velez H, Wild K (1998) The transition zone of the Canary Current upwelling region. Prog Oceanog 41: 455-504

Benedetti–Cecchi L, Cinelli F (1994) Recovery of patches in an assemblage of geniculate coralline algae: variability at different succesional stages. Mar Ecol Prog Ser 110: 9-18

Benedetti–Cecchi L. (2001) Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Mar Ecol Prog Ser 215: 79-92

Benedetti–Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbances: large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser 214: 137-150

Benedetti–Cecchi L, Maggi E, Bertocci I, Vaselli S, Micheli F, Osio GC, Cinelli F (2003) Variation in rocky shore assemblages in the northwestern Mediterranean: contrasts between islands and the mainland. J Exp Mar Biol Ecol 293: 193-215

Blanchette CA, Thornber C, Gaines S (1999) Effects of wave exposure on intertidal fucoid algae. Proceedings of the California Islands Symposium 5: 347-355

Bode A, Barquero S, Varela M, Braun JG, De Armas D (2001) Pelagic bacteria and phytoplankton in oceanic waters near the Canary Islands in summer. Mar Ecol Prog Ser 209: 1-17

Boero F (1999) Macroecology returns. J Evol Biol 12: 999-1001

Brown JH (1995) Macroecology. University of Chicago Press, Chicago, USA

Clarke KR, Warwick RM (1994) Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environment Research Council, United Kingdom

Coleman MA (2003) The role of recruitment in structuring patterns of small-scale spatial variability in intertidal and subtidal algal turfs. J Exp Mar Biol Ecol: 131-145

Davenport R, Never S, Helmke P, Perez-Moreno J, Llinás O (2002) Primary productivity in the northern Canary Islands region as inferred from Seawifs imagery. Deep Sea Research II 49: 3481-3496

Dethier MN, Grahan ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover estimations: "objective" is not always better. Mar Ecol Prog Ser 96: 93-100

Dethier MN, Schoch GC (2005). The consequences of scale: assessing the distribution of benthic populations in a complex estuarine fjord. Estuar Coast Shelf Sci 62: 253- 270

Diez I, Santolaria A, Gorostiaga JM (2003) The relationship of environmental factors to the structure and distribution of subtidal seaweed vegetation of the western Basque coast (N Spain). Estuar Coast Shelf Sci 56: 1041-1054

Dulvy NK, Freckleton RP, Polunin NVC (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. Ecology Letters 7: 410-416

Fowler-Walker MJ, Connell SD (2002) Opposing states of subtidal habitat across temperate Australia: consistency and predictability in kelp canopy-benthic associations. Mar Ecol Prog Ser 240: 49-56

Fraschetti S, Bianchi CN, Terlizzi A, Fanelli G, Morri C, Boero F (2001) Spatial variability and human disturbances in shallow subtidal hard substrate assemblages: a regional approach. Mar Ecol Prog Ser 212: 1-12

Fraschetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. Mar Ecol Prog Ser 296: 13-29

Garrabou J, Ballesteros E, Zabala M (2002) Structure and dynamics of North-western Mediterranean rocky benthic communities along a depth gradient. Estuar Coast Shelf Sci 55: 493-508

Graham MH (2004) Effects of local deforestation of the diversity and structure of southern California giant kelp forest food webs. Ecosystems 7: 341-357

Harley CDG, Smith KF, Moore VL (2003) Environmental variability and biogeography: the relationship between bathymetric distribution and geographical range size in marine algae and gastropods. Global Ecology and Biogeography 12: 499-506

Haroun RJ, Afonso-Carrillo A (1997) Flora marina de Canarias y su biodiversidad In: Pérez de Paz P (ed) Ecosistemas Insulares Canarios. Usos y aprovechamientos en el territorio. Consejería de Política Territorial, Gobierno de Canarias, p 163-168

Haroun R, Gil-Rodríguez MC, Wildpret de la Torre W (2003) Plantas marinas de Canarias. Canseco Press, Talavera, Spain

Hoffman AJ, Ugarte R (1985) The arrival of propagules of marine macroalgae in the intertidal zone. J Exp Mar Biol Ecol 92: 83-95

Jernakoff P (1983) Factors affecting the recruitment of algae in a midshore region dominated by barnacles. J Exp Mar Biol Ecol 67: 17-32

Kendrick GA (1991) Recruitment of coralline crusts and filamentous turf algae in the Galapagos Archipelago: effect of simulated scour, erosion and accretion. J Exp Mar Biol Ecol 147: 47-63

Kennelly SJ (1987) Physical disturbance in an Australian kelp community: 1. Temporal effects. Mar Ecol Prog Ser 40: 145-153

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943-1967

Lindegarth M, Gamfeldt L (2005) Comparing categorical and continuous ecological analyses: effects of "wave exposure" on rocky shores. Ecology 86: 1346-1357

Lüning K (1990) Seaweeds: their environment, biogeography, and ecophysiology. Wiley, New York

Martín Ruiz JF (2001) Geografía de Canarias. Sociedad y medio natural. Ediciones del Cabildo de Gran Canaria

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones IV SH (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Mar Ecol Prog Ser 261: 135-147

Medina M, Haroun RJ (1993) Preliminary study on the dynamics of *Cystoseira abies-marina* populations on Tenerife (Canary Islands). Courier Forsch: 109-112

Medina M, Haroun RJ, Wildpret W (1995) Phytosociological study of the *Cystoseira abies-marina* community in the Canarian Archipelago. Bull Museu Mun Funchal 4: 433-439

Menconi M, Benedetti–Cecchi L, Cinelli F (1999) Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the northwest Mediterranean. J Exp Mar Biol Ecol 233: 1-23

Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. J Exp Mar Biol Ecol 250: 257-289

Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Chato Osio G, Romano F (2005) Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. Ecological Monographs 75: 81-102

Ruitton S, Francour P, Boudouresque CF (2000) Relationships between algae, benthic herbivorous invertebrates and fishes in rocky sublittoral communities of a temperate sea (Mediterranean). Estuar Coast Shelf Sci 50: 217-230

Russell BD, Connell SD (2005) A novel interaction between nutrients and grazers alters relative dominance of marine habitats. Mar Ecol Prog Ser 289: 5-11

Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanogr Mar Biol Annu Rev 28: 177-276

Schils T, Coppejans E (2003) Spatial variation in subtidal plant communities around the Socorra Archipelago and their biogeographic affinities within the Indian Ocean. Mar Ecol Prog Ser 251: 103-114

Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. Oikos 69: 476-498

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MT (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental Conservation 29: 436-459

Taylor DI, Schiel DR (2003) Wave-related mortality in zygotes of habitat-forming algae from different exposures in southern New Zealand: the importance of "stickability". J Exp Mar Biol Ecol 290: 229-245

Tilman D, Kareiva P (1997) Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, NJ

Tuya F, Boyra A, Sánchez-Jerez P, Haroun RJ, Barberá C (2004a) Relationships between rocky-reef fish assemblages, the sea urchin *Diadema antillarum* and macroalgae throughout the Canarian Archipelago. Mar Ecol Prog Ser 278: 157-169

Tuya F, Boyra A, Sánchez-Jerez P, Haroun RJ, Barberá C (2004b) Can alone one single species determine the structure of a rocky benthic community: the case of the black long-spined sea urchin *Diadema antillarum* in the eastern Atlantic. Hydrobiologia 519:211-21

Underwood AJ (1997) Experiments in Ecology: their logical design and interpretation using Analysis of Variance. Cambridge University Press, Cambridge

Underwood AJ, Jernakoff P (1981) Interactions between algae and grazing gastropods in the structure of a low shore algal community. Oecologia 48: 221-254

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution on intertidal invertebrates. Oecologia 107: 212-224

Table 1: Analysis of the effects of Islands (fixed), Wave exposure (fixed and orthogonal), Locations (random and nested within islands and both levels of wave exposure), and Sites (random and nested within locations, islands and levels of wave exposure) on the multivariate algal assemblages by PERMANOVA. p-values were obtained using 4999 random permutations. CH: Chinijo, LZ: Lanzarote, FV: Fuerteventura, GC: Gran Canaria, TF: Tenerife, GO: Gomera, LP: La Palma, EH: El Hierro

		Overall algal dataset			Brown Macrophytes			Turf Algae			Bush-like Algae		
Source of variation	df	MS	F	p(perm)	MS	F	p(perm)	MS	F	p(perm)	MS	F	p(perm)
Islands = I	7	33008.85	3.9300	0.0002	8821.11	1.4240	0.1900	29818.99	3.3717	0.0010	17632.73	1.5323	0.0230
Wave exposure = WE	1	25228.32	3.0061	0.0124	48821.18	7.8814	0.0010	20309.00	2.2964	0.0480	16408.93	1.4260	0.1810
Locations (I x WE)	16	8392.32	6.5029	0.0002	6194.44	2.8576	0.0010	8843.78	2.6911	0.0010	11507.23	3.1114	0.0010
Sites (Lo (I x WE))	32	1290.55	2.6304	0.0002	2167.68	2.5944	0.0010	3286.32	1.2498	0.0190	3698.43	1.3257	0.0010
I x WE	7	8119.42	0.9675	0.5264	6473.99	1.0451	0.4220	9805.97	1.1088	0.3290	13786.41	1.9181	0.2020
Residual	192	490.6209			835.52			2629.50			2789.77		
Pairwise *a posterirori* comparisons								EH > GO; EH > TF; EH >GC; EH > CH LP > GO; LP > TF; LP > CH GC > GO; FV > GO; FV > TF					

Table 2: Analysis of the effects of Islands (fixed), Wave exposure (fixed and orthogonal), Locations (random and nested within islands and both levels of wave exposure), and Sites (random and nested within locations, islands and levels of wave exposure) on the mean percent coverage of the three algal morphological groups. Acronyms for islands as in Table 1. *: $p < 0.01$

		Brown Macrophytes		Turf Algae		Bush-like Algae	
Source of variation	DF	MS	F	MS	F	MS	F
Islands = I	7	0.0777	1.58	0.2448	5.48*	0.3256	4.02 (p = 0.01)
Wave Exposure = WE	1	0.5036	10.22*	0.4399	9.85*	0.0002	0.00
Locations (I x WE)	16	0.0493	8.15*	0.0447	5.38*	0.0811	18.36*
Sites (Locations (I x WE))	32	0.0060	1.79*	0.0083	1.51	0.0044	1.02
I x WE	7	0.0490	0.99	0.0620	1.39	0.0750	0.92
Residual	192	0.0034		0.0055		0.0043	
SNK tests				LP EH GC > CH > FV GO TF LZ		LZ FV GC TF > GO CH LP EH	

Table 3: Analysis of the effects of Islands (fixed), Wave exposure (fixed and orthogonal), Locations (random and nested within islands and both levels of wave exposure), and Sites (random and nested within locations, islands and levels of wave exposure) on the mean percent of coverage of selected algal species. Acronyms for islands as in Table 1. *: $p < 0.01$

		Lobophora variegata		Unidentified filamentous turf		*Dyctiota dichotoma*		*Stypocaulon scoparium*		*Asparagopsis* spp.		*Jania* spp.	
Source of variation	DF	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Islands = I	7	40.1578	23.88*	16.8451	4.80*	13.1876	3.63	0.0385	1.29	4.2593	3.42	4.9245	6.02*
Wave Exposure = WE	1	3.1696	1.88	51.8169	14.77*	0.7873	0.22	0.0078	0.26	0.1253	0.10	1.6889	2.06
Locations (I x WE)	16	1.6819	5.30*	3.5074	4.52*	3.6322	15.84*	0.0298	22.05*	1.2458	1.27	0.8180	3.77*
Sites (Locations (I x WE))	32	0.3174	1.25	0.7758	2.26*	0.2293	0.86	0.0014	1.16	0.9833	4.51*	0.2167	1.29
I x WE	7	3.0250	1.80	1.5045	0.43	1.6675	0.46	0.0240	0.81	3.1134	2.50	0.9106	1.11
Residual	192	0.2546		0.3435		0.2680		0.0012		0.2178		0.1679	
SNK tests		EH LP > GC > CH FV LZ TF GO		GO TF > FV > GC LP CH LZ EH								FV GC > CH LZ > LP TF EH GO	

Table 3 (continued): Analysis of the effects of Islands (fixed), Wave exposure (fixed and orthogonal), Locations (random and nested within islands and both levels of wave exposure), and Sites (random and nested within locations, islands and levels of wave exposure) on the mean percent of coverage of selected algal species. *: $p < 0.01$

		Padina pavonica		*Cystoseira abies-marina*		*Cystoseira mauritanica*		*Sargassum* spp.	
Source of variation	DF	MS	F	MS	F	MS	F	MS	F
Islands = I	7	3.3948	1.27	0.1150	0.95	0.0164	1.62	0.0325	2.11
Wave Exposure = WE	1	2.6661	1.00	0.3494	2.90	0.0038	0.38	0.0627	4.07
Locations (I x WE)	16	2.6696	28.64*	0.1206	31.14*	0.0101	7.95*	0.0154	4.91*
Sites (Locations (I x WE))	32	0.0932	1.11	0.0039	2.03*	0.0013	0.98	0.0031	2.27*
I x WE	7	1.1227	0.42	0.1150	0.95	0.0038	0.38	0.0243	1.58
Residual	192	0.0839		0.0019		0.0013		0.0014	

Legends

Figure 1: Map of study locations within islands. Black circles: locations protected from the NE-swell. Grey squares: locations exposed to the NE-swell

Figure 2: MDS plot comparing the composition and structure of shallow water algal assemblages for each island and level of wave exposure (P: protected, E: Exposed). CH: Chinijo, LZ: Lanzarote, FV: Fuerteventura, GC: Gran Canaria, TF: Tenerife, GO: Gomera, LP: La Palma, EH: El Hierro. Black circles are locations within the western islands; grey circles are locations within the eastern islands

Figure 3: Turf-algae. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

Figure 4: Bush-like algae. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

Figure 5: Brown macrophytes. Mean percentage cover across the study area. Black bars are sites within protected locations (e.g. S1L1 denotes site 1 within location 1) and white bars are sites within exposed locations. Error bars represent SE of means

Figure 6: *Lobophora variegata*. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

Figure 7: *Jania* spp. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

Figure 8: Unidentified filamentous turf (red algae belonging to the families Ceramiaceae and Rhodomelaceae). Mean percentage cover across the study area. Black bars are sites within protected locations (e.g. S1L1 denotes site 1 within location 1) and white bars are sites within exposed locations. Error bars represent SE of means

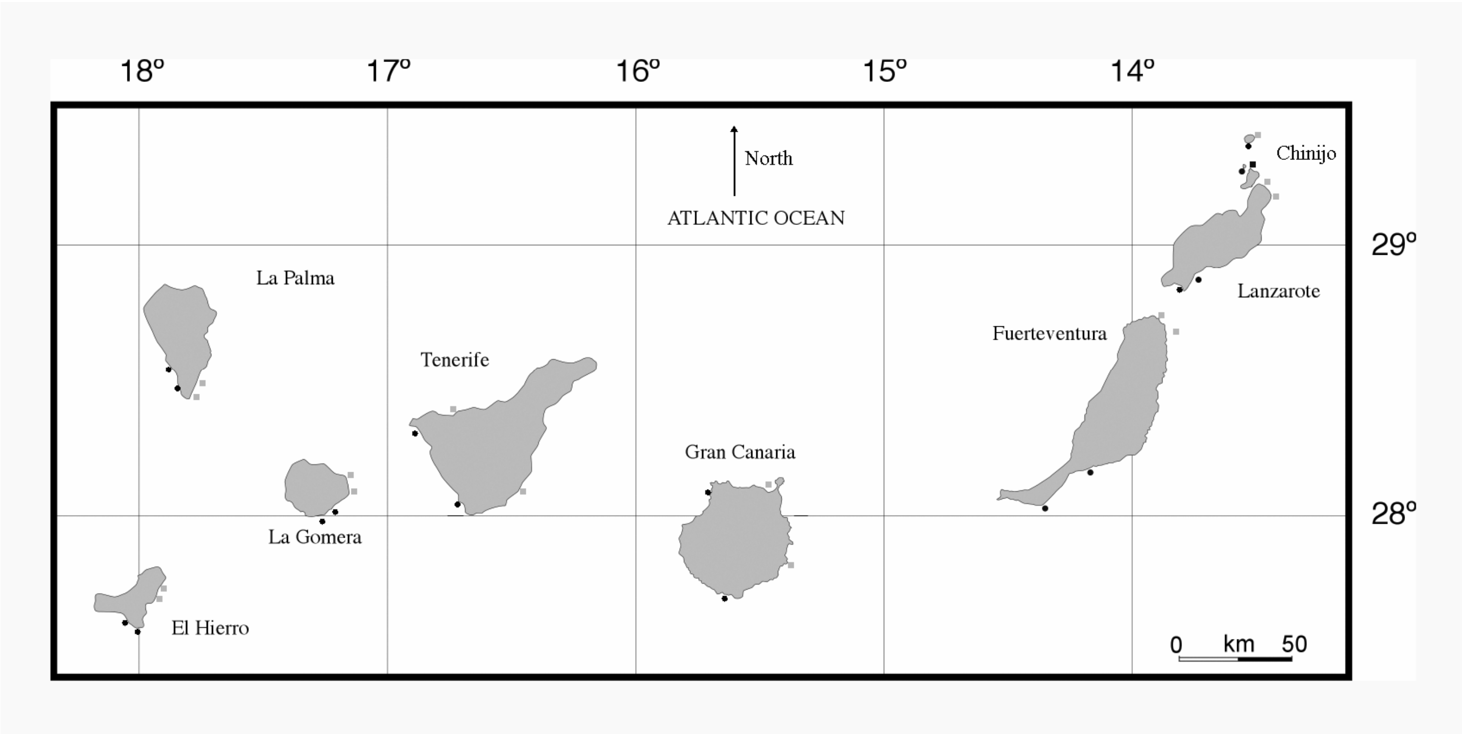
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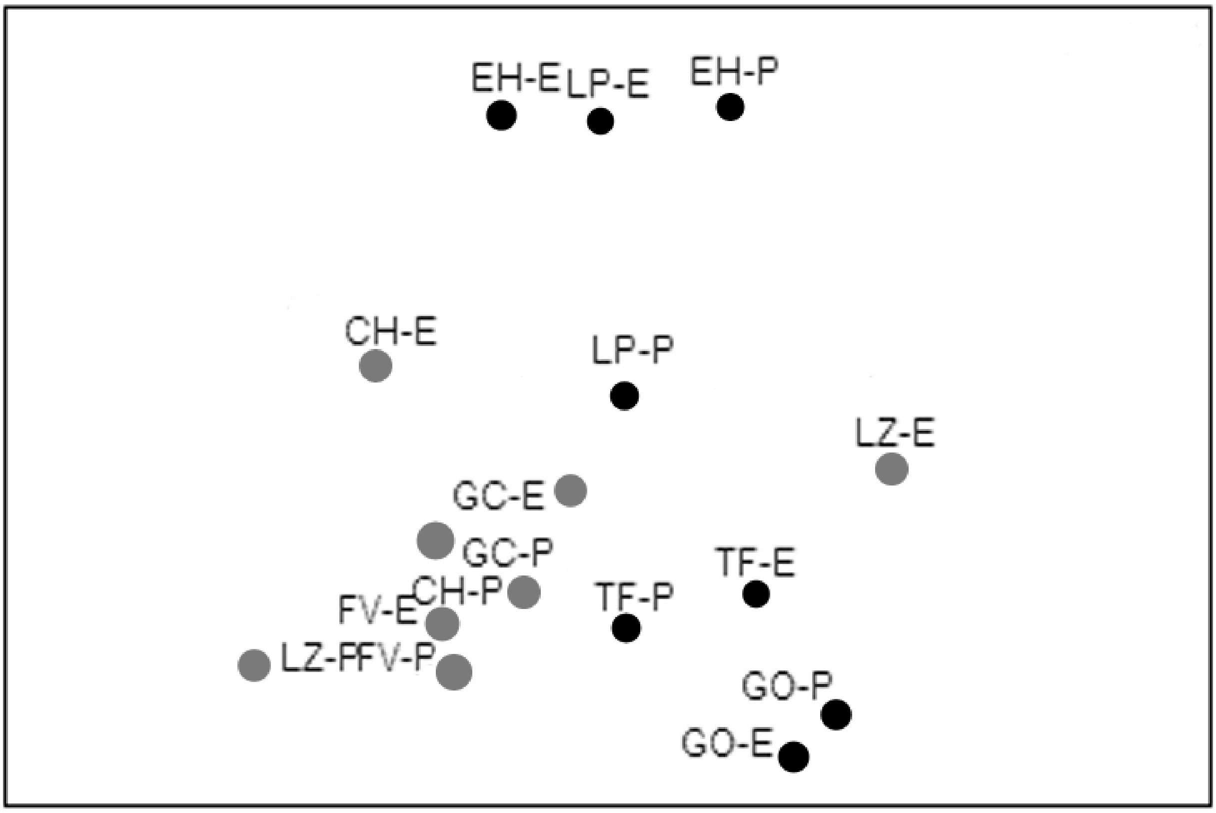
Fig.1



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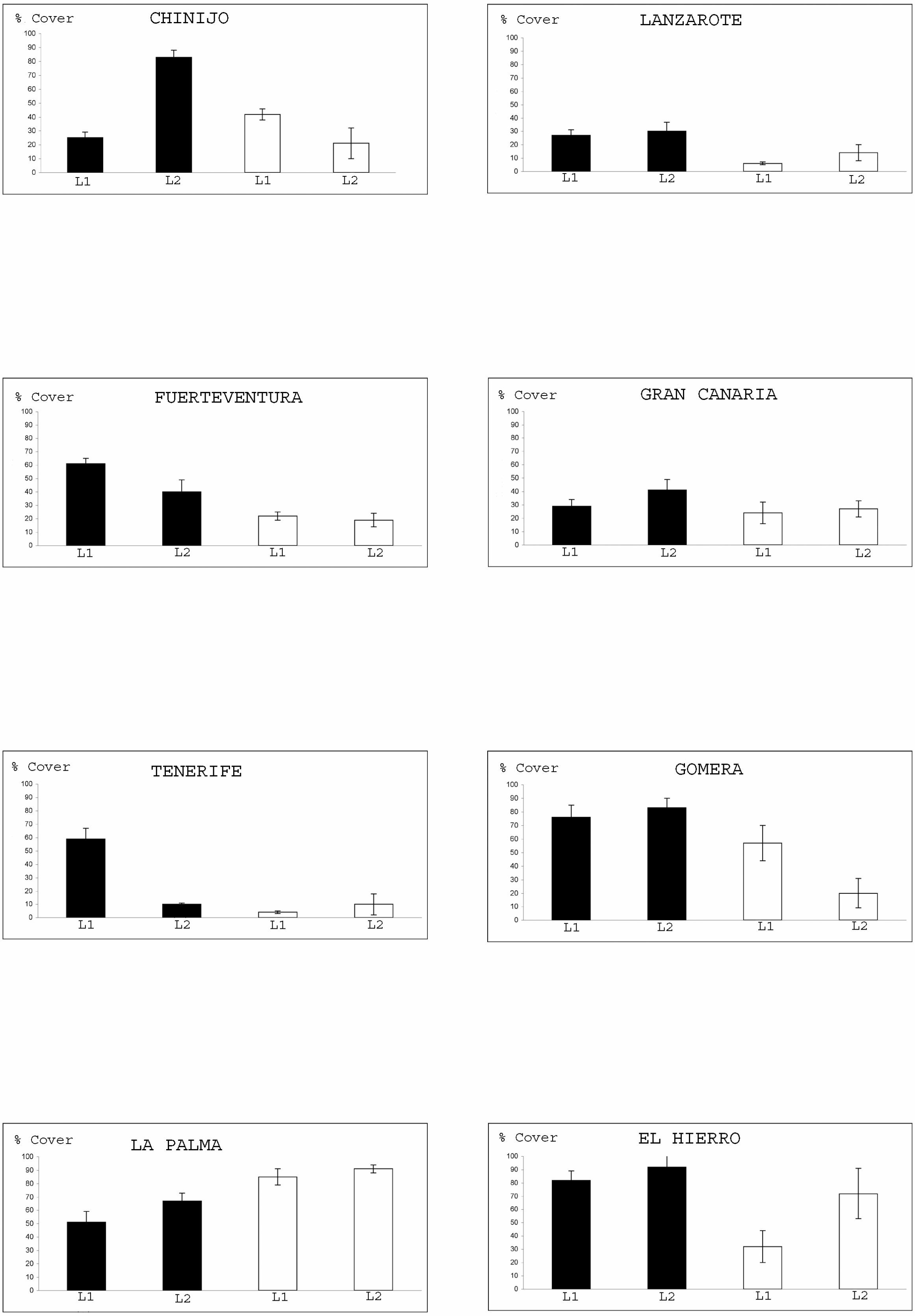
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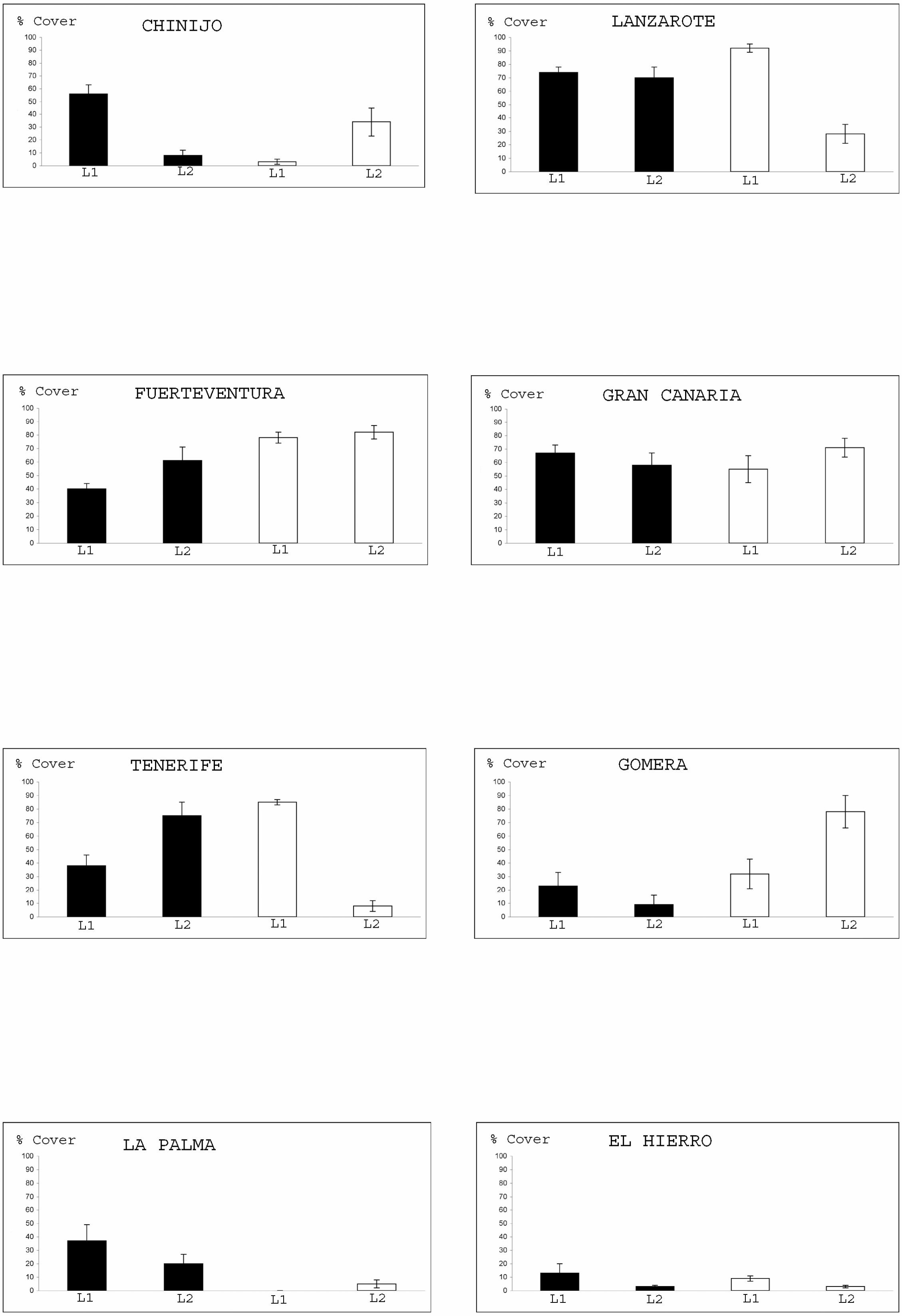
Figure 3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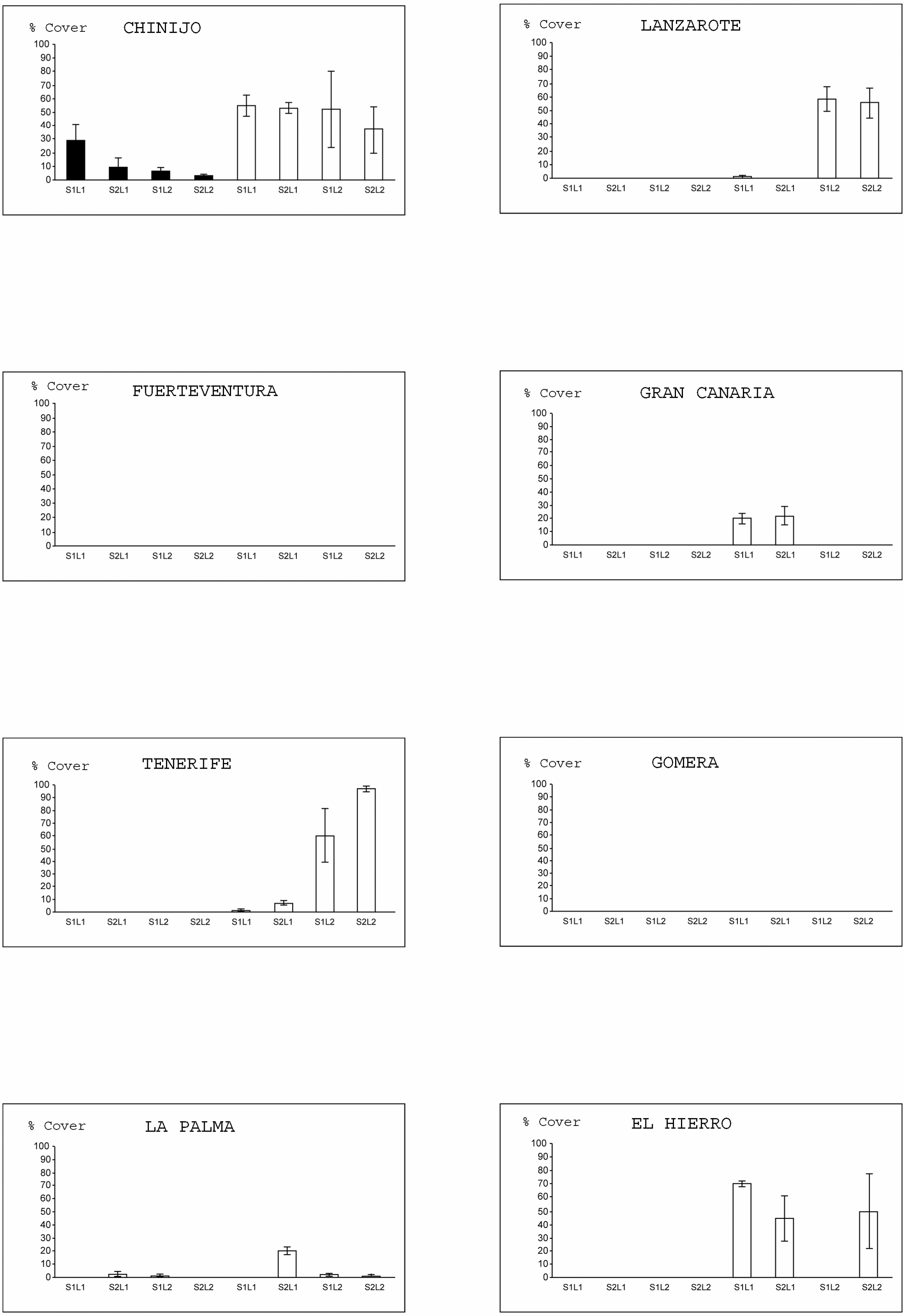
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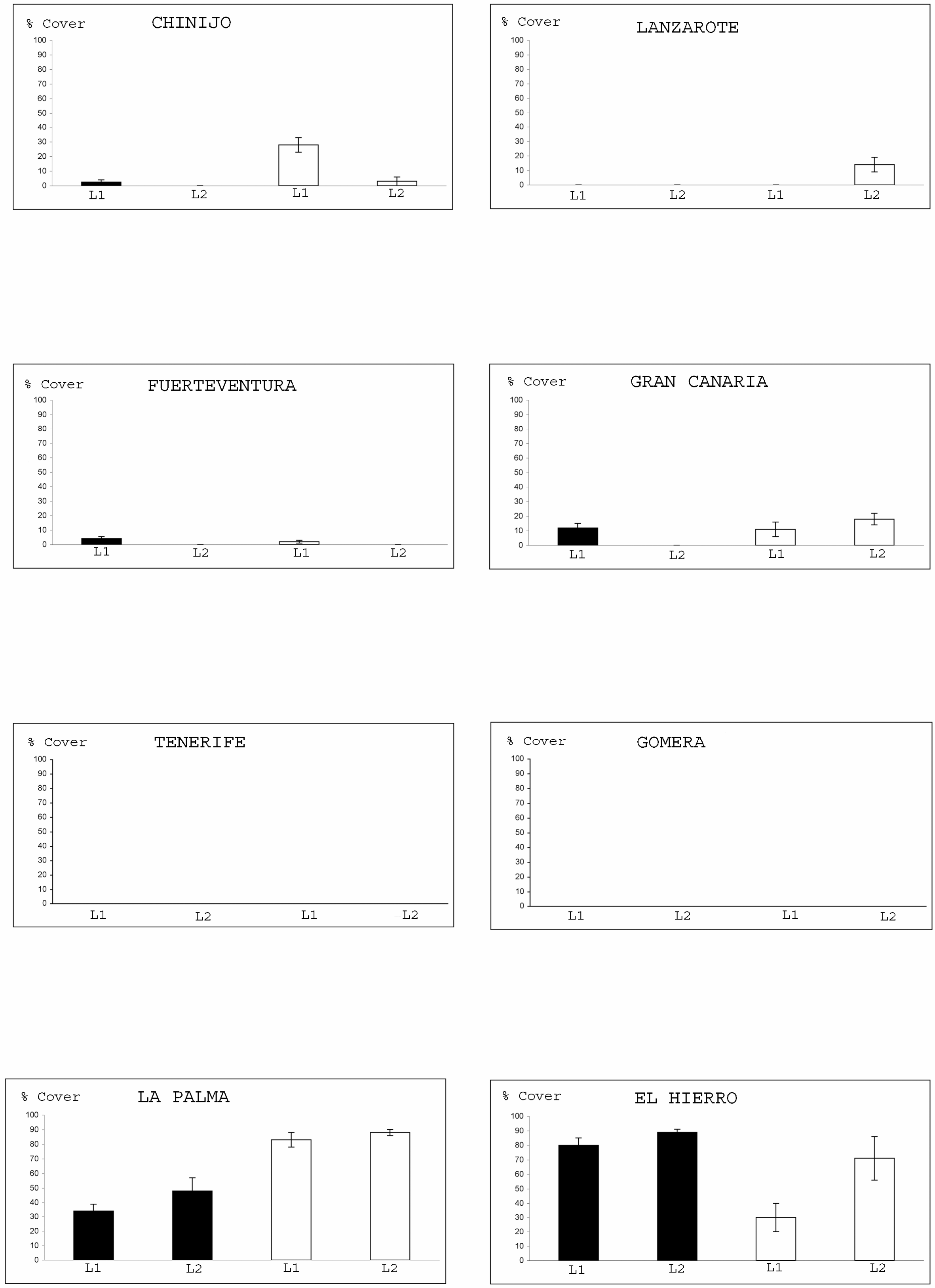
Figure 5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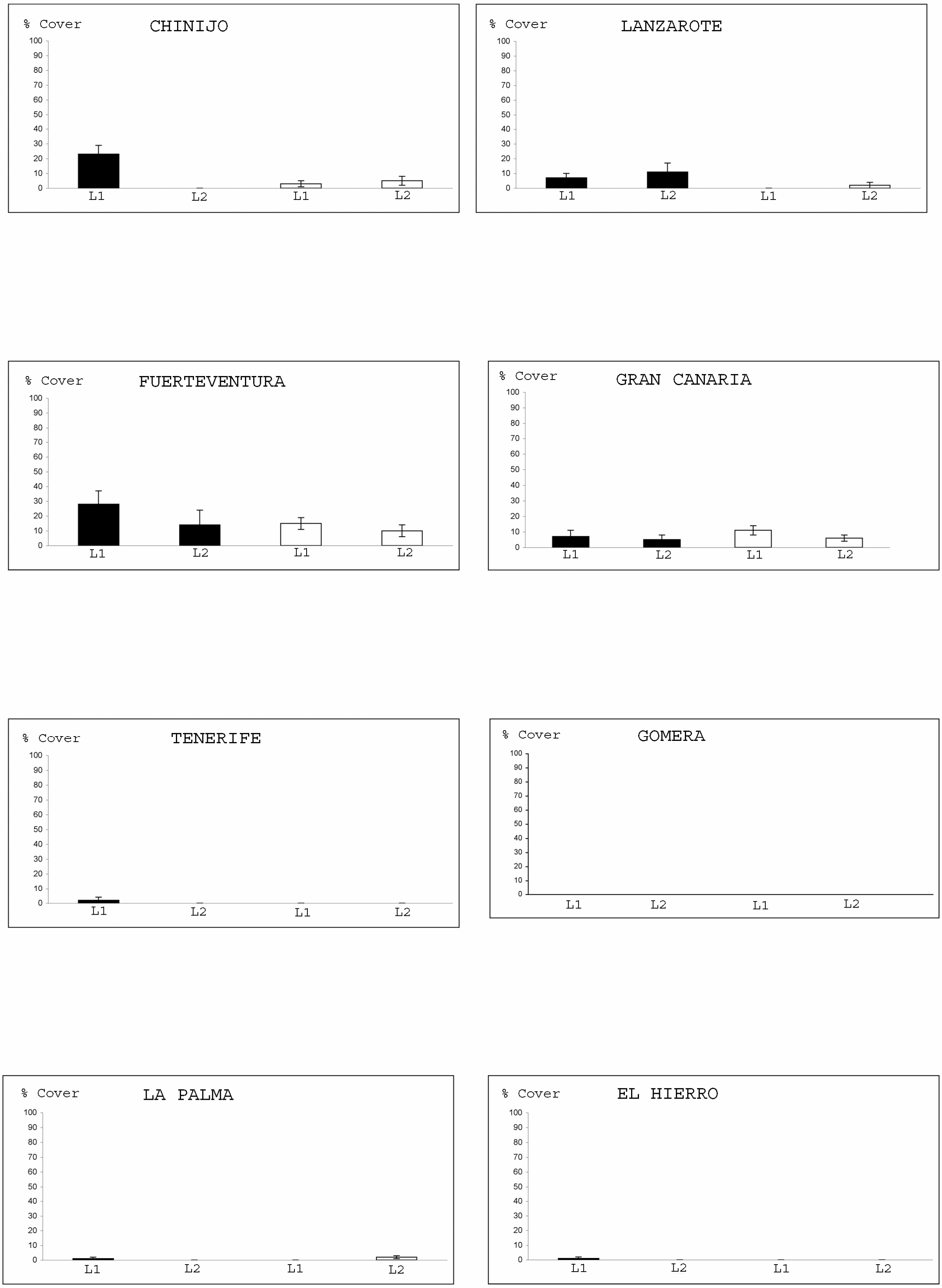

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Figure 7

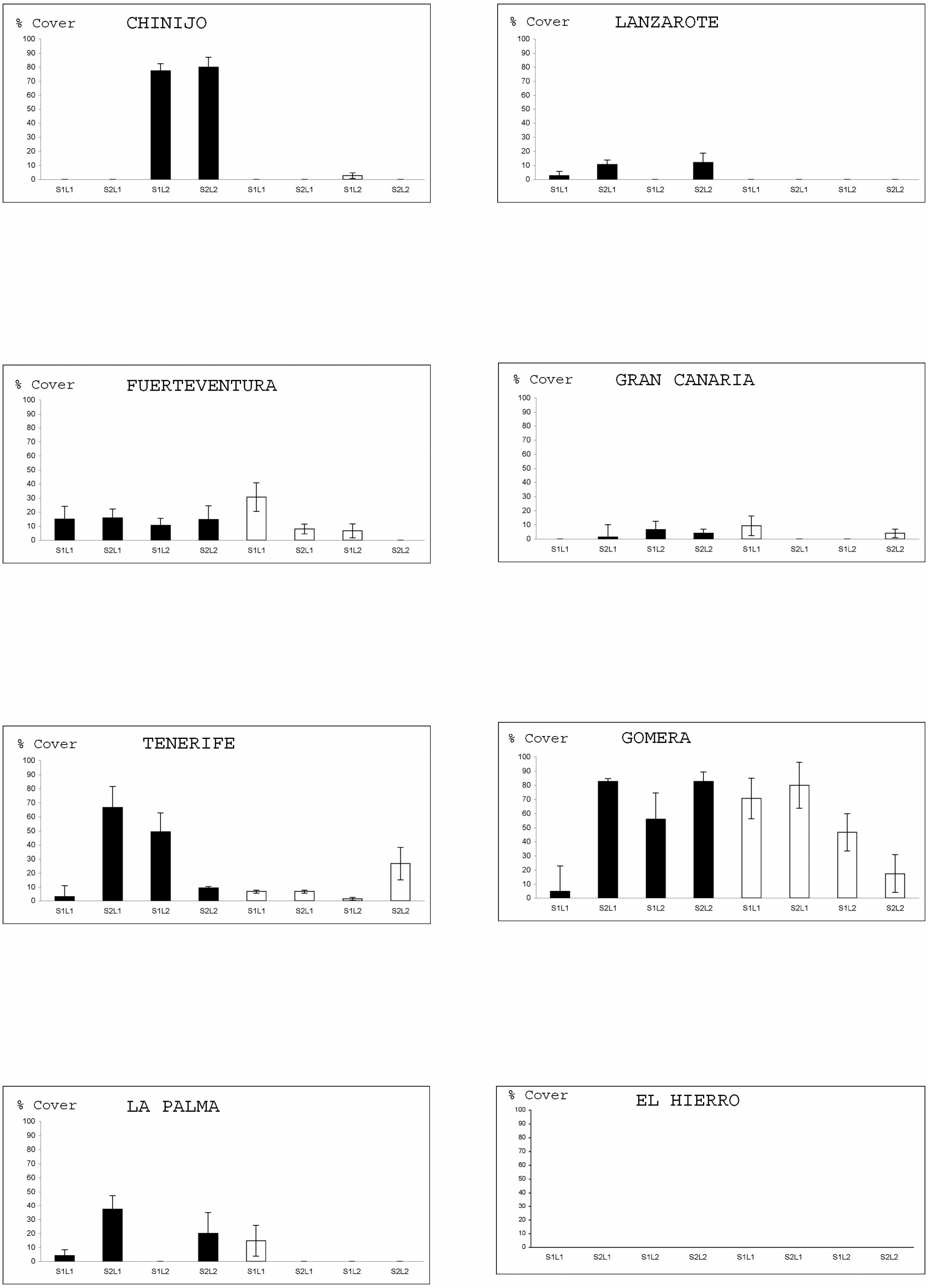
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Figure 8

Supplementary material (Appendices 1 & 2)

Appendix 1. Mean percent cover (%) of each algal taxon in each surveyed locations within each island and level of wave exposure

	Chinijo				Lanzarote				Fuerteventura				Gran Canaria				Tenerife				Gomera				La Palma				El Hierro			
	Protected		Exposed		Protected		Exposed		Protected		Exposed		Protected		Exposed		Protected		Exposed		Protected		Exposed		Protected		Exposed		Protected		Exposed	
	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2	L1	L2
Amphiroa spp.	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anadyomene stellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Asparagopsis spp.	4.5	0	2	23.5	0	0	0	0	1.5	0	7	0	17	0	3.2	6	14	24	0	0	11.5	9.8	18	19.5	2	0	0	0	0	0	0	0.5
Bryopsis spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5	0	0	2.5	2.5	0	0	0	0	0	0	0.5	2.5	0	0
Caulerpa mexicana	0	0	0	0	0	0	11.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caulerpa racemosa (peltata)	0	0	0	0	0	0	0.6	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caulerpa webbiana	0	0	0	0	0	0	4.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
Cladophora spp.	0.5	0	0	0	0	0	0	0	1.5	0	3	2.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Codium spp.	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colpomenia sinuosa	0	9	9.5	11	12.5	8.5	0	0	11	1.5	0.5	5.5	1.5	30	7.6	0	5	0	0	0	0	0	0	0	0	0	0.5	1.5	0	0	0	0
Corallina elongata	0	0	0	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	0	1.5	0.3	0	49.5	14.5	0	0	0	0	0	0	0
Cotoniella filamentosa	0	0	0	0	0	0	0	7	0	0	2	0	0	0	1.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
Cymopolia barbata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cutleria multifida	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cystoseira abies-marina	0	0	0	0	0	0	0.6	56.5	0	0	0	0	0	0	10.5	0	0	0	4	78.5	0	23.6	0	0	0	0	0	0	0	0	0	0
Cystoseira compressa	0	0	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.5	10	1.5	0	0	17	0
Cystoseira mauritanica	14.5	0	0	44.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dasya spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Dasycladus vermicularis	0	0	0	0	0	0	6.8	0	0	0	0	0	0	0	0	1	1.5	0	0	0	2	0.4	0	5	0	0	0	0	0	0	0	0
Dyctiopteris spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0
Dyctiota dichotoma	25	5	1	8.5	10	18.5	3.4	17.5	15.5	6	45	3.5	47.5	24.5	36.2	29.5	17	24.5	52.5	6.5	3	3.1	0	7	11	10.5	0	1.5	1.5	1	2	1.5
Dyctiota bartayresiana	0	3	0	0.5	0	0	1.2	0.5	0	0	5	0	1	0	4.8	1	0	6	5	0	5	1	14	1.5	3.5	3.5	0	0.5	0	0	0	0
Halimeda discoidea	0	0	0	0	0	0	2.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haliptilon virgatum	0	0	0	0	0	0	0	0	0	0	0	0	0	13.5	3.4	0	0	0	0	0	1.5	0.3	0	0	0	0	0	0	0	0	0	0
Hydroclathrus clathratus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1.5	0
Jania spp.	22.5	0	1.5	5.5	7.5	11	0	0	28	15.5	11.5	13	7	2	8.3	6	3	0	0	0	0	0	0	0	0	0.5	0	1.5	1	0	0	0
Laurencia spp.	1.5	0	0	0	0	0	0	0	0	0	13.5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobophora variegata	2.5	0	31	3	0	0	0	14	4	0	2	0	12	0	12.2	18.5	0	0	0	0	0	0	0	0	34.5	48.5	83.5	88	88.5	89.5	30.5	71.5
Lophocladia trichoclados	0	0	0	0	0	0	61.4	0	0	0	0	0	0	0	0	0	0	19	18.5	1.5	0	0.5	0	0	0	0	0	0	0	1	2	0
Nemastoma canariensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0
Padina pavonica	9	0	0	0.5	0.5	37.5	1.4	2.5	11	6.5	0	33	1	14	3.7	3.5	6.5	9.5	8.5	0	0	0	0	0	0	0	0	0	0	0	1.5	0
Microdyction boergesenii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0.5
Sargassum spp.	4.5	4.5	52.5	0	0	0	0	0	0	0	0	0	0	0	1.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	24.5
Scinaia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0
Stypocaulon scoparium	15.5	0	0	0	55	0	4.4	0	10	20	2.5	40.5	0	5.5	2.5	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stypopodium zonale	0	0	0	1	0	14	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2.5	0	1.5	0	0	0.5	0
Zonaria tournefortii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0.5	3.5	0	0	0	0	0	0
Unidentified Filamentous Turf	0	74	0	1	6.5	10.5	0	0	17.5	22.5	8	0	7.5	8.5	3.9	1.5	49	8	4	10	71	54.7	57	14.5	16.5	18	0	0	0	0	0	0
Coralline crustose algae	0	4.5	1	1	0	0	1.8	1.5	0	0	0	0	5	2	1.4	2	4	7.5	7.5	3.5	2	4	11	2.5	11.5	12.5	5	3	5.5	5.5	2	1.5

Appendix 2: Summary of the results from the SIMPER procedure

	Taxon	Contribution to dissimilarity (%)
1. Protected *versus* Exposed locations		
Average dissimilarity = 67.49		
	Lobophora variegata	12.03
	Unidentified Filamentous Turf	10.76
	Dyctiota dichotoma	7.29
	Stypocaulon scoparium	5.87
	Asparagopsis spp.	5.79
	Padina pavonica	5.61
	Jania spp.	5.49
	Cystoseira abies-marina	5.13
2. Dissimilarities among islands		
2.1 Chinijo *versus* Lanzarote		
Average dissimilarity = 70.99		
	Unidentified Filamentous Turf	9.01
	Sargassum spp.	8.84
	Stypocaulon scoparium	8.35
	Cystoseira mauritanica	7.34
	Lobophora variegata	6.85
	Padina pavonica	6.48
	Cystoseira abies-marina	6.28
	Asparagopsis spp.	6.00
2.2 Chinijo *versus* Fuerteventura		
Average dissimilarity = 62.97		
	Unidentified Filamentous Turf	11.42
	Stypocaulon scoparium	10.98
	Sargassum spp.	9.50
	Padina pavonica	8.31
	Cystoseira mauritanica	7.92
	Jania spp.	7.92
	Dyctiota dichotoma	6.42
	Lobophora variegata	6.21
2.3 Chinijo *versus* Gran Canaria		
Average dissimilarity = 56.92		
	Unidentified Filamentous Turf	10.50
	Dyctiota dichotoma	10.49
	Sargassum spp.	9.50
	Cystoseira mauritanica	8.32
	Lobophora variegata	8.11
	Stypocaulon scoparium	7.33
2.4 Lanzarote *versus* Gran Canaria		
Average dissimilarity = 58.14		
	Stypocaulon scoparium	9.79
	Dyctiota dichotoma	8.06
	Lobophora variegata	7.93
	Cystoseira abies-marina	7.92
	Colpomenia sinuosa	7.33

	Asparagopsis spp.	6.97
2.5 Fuerteventura *versus* Gran Canaria Average dissimilarity = 50.20		
	Dyctiota dichotoma	9.54
	Stypocaulon scoparium	9.24
	Lobophora variegata	8.75
	Padina pavonica	7.59
	Colpomenia sinuosa	7.02
	Unidentified Filamentous Turf	6.82
	Asparagopsis spp.	6.50
2.6 Chinijo *versus* Tenerife Average dissimilarity = 68.91		
	Unidentified Filamentous Turf	11.85
	Cystoseira abies-marina	9.30
	Sargassum spp.	9.21
	Cystoseira mauritanica	7.64
	Dyctiota dichotoma	7.52
	Asparagopsis spp.	7.47
2.7 Lanzarote *versus* Tenerife Average dissimilarity = 64.10		
	Cystoseira abies-marina	12.05
	Stypocaulon scoparium	10.50
	Unidentified Filamentous Turf	8.77
	Padina pavonica	8.53
	Asparagopsis spp.	7.34
	Dyctiota dichotoma	6.88
2.8 Fuerteventura *versus* Tenerife Average dissimilarity = 66.15		
	Stypocaulon scoparium	12.35
	Jania spp.	11.28
	Cystoseira abies-marina	9.24
	Lophocladia trichoclados	7.51
2.9 Gran Canaria *versus* Tenerife Average dissimilarity = 53.45		
	Cystoseira abies-marina	11.21
	Lobophora variegata	10.12
	Lophocladia trichoclados	8.85
	Colpomenia sinuosa	8.20
	Asparagopsis spp.	8.05
	Stypocaulon scoparium	7.93
2.10 Chinijo *versus* Gomera Average dissimilarity = 70.98		
	Unidentified Filamentous Turf	15.95
	Sargassum spp.	9.06
	Cystoseira mauritanica	7.51
	Colpomenia sinuosa	7.39
	Asparagopsis spp.	7.04
	Lobophora variegata	6.82
2.11 Lanzarote *versus* Gomera Average dissimilarity = 79.81		
	Unidentified Filamentous Turf	14.70
	Asparagopsis spp.	10.48

	Stypocaulon scoparium	7.13
	Cystoseira abies-marina	7.11
	Padina pavonica	6.56
	Dyctiota dichotoma	5.89
2.12 Fuerteventura *versus* Gomera		
Average dissimilarity = 74.98		
	Unidentified Filamentous Turf	11.36
	Jania spp.	11.24
	Stypocaulon scoparium	11.04
	Padina pavonica	8.27
	Asparagopsis spp.	8.01
	Corallina elongata	7.27
	Dyctiota dichotoma	6.38
2.13 Gran Canaria *versus* Gomera		
Average dissimilarity = 65.89		
	Unidentified Filamentous Turf	13.76
	Dyctiota dichotoma	12.99
	Lobophora variegata	8.31
	Colpomenia sinuosa	7.17
	Jania spp.	6.99
	Stypocaulon scoparium	6.51
2.14 Tenerife *versus* Gomera		
Average dissimilarity = 54.35		
	Unidentified Filamentous Turf	14.20
	Cystoseira abies-marina	13.36
	Dyctiota dichotoma	12.93
	Asparagopsis spp.	9.78
	Lophocladia trichoclados	9.52
	Corallina elongata	8.74
2.15 Chinijo *versus* La Palma		
Average dissimilarity = 68.91		
	Lobophora variegata	18.41
	Unidentified Filamentous Turf	10.33
	Sargassum spp.	9.45
	Cystoseira mauritanica	7.81
	Colpomenia sinuosa	6.79
	Asparagopsis spp.	5.94
2.16 Lanzarote *versus* La Palma		
Average dissimilarity = 77.32		
	Lobophora variegata	20.23
	Stypocaulon scoparium	7.46
	Padina pavonica	6.86
	Cystoseira abies-marina	6.04
	Unidentified Filamentous Turf	5.85
	Dyctiota dichotoma	5.81
2.17 Fuerteventura *versus* La Palma		
Average dissimilarity = 78.21		
	Lobophora variegata	19.30
	Stypocaulon scoparium	10.70
	Jania spp.	9.57
	Padina pavonica	8.02
	Dyctiota dichotoma	7.16
	Unidentified Filamentous Turf	6.42

2.18 Gran Canaria *versus* La Palma		
Average dissimilarity = 64.76		
	Lobophora variegata	16.08
	Dyctiota dichotoma	12.37
	Stypocaulon scoparium	6.69
	Padina pavonica	6.62
	Colpomenia sinuosa	6.55
	Unidentified Filamentous Turf	6.46
2.19 Tenerife *versus* La Palma		
Average dissimilarity = 72.82		
	Lobophora variegata	24.69
	Dyctiota dichotoma	9.34
	Cystoseira abies-marina	9.27
	Unidentified Filamentous Turf	8.83
	Lophocladia trichoclados	7.45
	Asparagopsis spp.	6.31
2.20 Gomera *versus* La Palma		
Average dissimilarity = 71.91		
	Lobophora variegata	25.35
	Unidentified Filamentous Turf	15.97
	Asparagopsis spp.	11.11
	Corallina elongata	7.51
	Cystoseira compresa	5.10
	Dyctiota dichotoma	4.66
2.21 Chinijo *versus* El Hierro		
Average dissimilarity = 71.85		
	Lobophora variegata	19.40
	Sargassum spp.	10.38
	Unidentified Filamentous Turf	8.41
	Cystoseira mauritanica	7.87
	Colpomenia sinuosa	7.80
	Asparagopsis spp.	6.17
2.22 Lanzarote *versus* El Hierro		
Average dissimilarity = 83.98		
	Lobophora variegata	20.30
	Sargassum spp.	7.39
	Stypocaulon scoparium	7.25
	Dyctiota dichotoma	6.14
	Padina pavonica	6.10
	Lophocladia trichoclados	5.87
2.23 Fuerteventura *versus* El Hierro		
Average dissimilarity = 88.50		
	Lobophora variegata	18.54
	Stypocaulon scoparium	9.95
	Jania spp.	9.48
	Unidentified Filamentous Turf	7.23
	Padina pavonica	7.12
	Sargassum spp.	6.65
2.24 Gran Canaria *versus* El Hierro		
Average dissimilarity = 74.00		
	Lobophora variegata	15.45
	Dyctiota dichotoma	13.07

	Sargassum spp.	7.57
	Colpomenia sinuosa	6.77
	Unidentified Filamentous Turf	6.34
	Stypocaulon scoparium	6.13

2.25 Tenerife *versus* El Hierro Average dissimilarity = 81.89		
	Lobophora variegata	23.87
	Unidentified Filamentous Turf	10.78
	Dyctiota dichotoma	9.94
	Cystoseira abies-marina	8.74
	Sargassum spp.	7.67
	Lophocladia trichoclados	6.18

2.26 Gomera *versus* El Hierro Average dissimilarity = 85.44		
	Lobophora variegata	23.20
	Unidentified Filamentous Turf	19.22
	Asparagopsis spp.	10.20
	Sargassum spp.	7.45
	Corallina elongata	6.01
	Dyctiota dichotoma	5.93

2.27 La Palma *versus* El Hierro Average dissimilarity = 48.34		
	Sargassum spp.	13..3
	Unidentified Filamentous Turf	9.33
	Cystoseira compresa	9.14
	Lobophora variegata	8.02
	Dyctiota dichotoma	6.54
	Stypopodium zonale	5.32