

Divergent trophic responses to biogeographic and environmental gradients

Miguel G. Matias^{1,2}, Cátia Lúcio Pereira¹, Pedro Miguel Raposeiro⁴, Vitor Gonçalves⁴, Ana Mafalda Cruz^{4,*}, Ana Cristina Costa⁴ and Miguel Bastos Araújo^{1,3}

¹InBio/CIBIO, Univ. of Évora, Largo dos Colegiais, PT-7000 Évora, Portugal

²Imperial College London, Silwood Park Campus, Buckhurst Road, SL5 7PY Ascot, Berkshire, UK

³Center for Macroecology, Evolution and Climate, Natl Hist. Mus. of Denmark, Univ. of Copenhagen, Copenhagen, Denmark

⁴InBio/CIBIO, Univ. dos Açores, Ponta Delgada, Portugal

*The authors dedicate this article to the memory of Ana Mafalda Cruz, a promising aquatic ecologist, co-author and friend.

Corresponding author: M. G. Matias, InBio/CIBIO, Univ. of Évora, Largo dos Colegiais, PT-7000 Évora, Portugal. E-mail: mail.miguelmatias@gmail.com

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(ABSTRACT)

Following environmental changes, communities disassemble and reassemble in seemingly unpredictable ways. Whether species respond to such changes individually or collectively (e.g. as functional groups) is still unclear. To address this question, we used an extensive new dataset for the lake communities in the Azores' archipelago to test whether: 1) individual species respond concordantly within trophic groups; 2) trophic groups respond concordantly to biogeographic and environmental gradients. Spatial concordance in individual species distributions within trophic groups was always greater than expected by chance. In contrast, trophic groups varied non-concordantly along biogeographic and environmental gradients revealing idiosyncratic responses to them. Whether communities respond individually to environmental gradients thus depends on the functional resolution of the data. Our study challenges the view that modelling environmental change effects on biodiversity always requires an individualist approach. Instead, it finds support for the longstanding idea that communities might be modelled as a cohort if the functional resolution is appropriate.

INTRODUCTION

Understanding how communities change through time and space has long been a central topic in ecology (Gleason 1926, Elton 1949, Andrewartha and Birch 1954, Hutchinson 1959, MacArthur and Wilson 1967). Analyses of historical data-series have revealed that communities disassemble and reassemble in seemingly unpredictable ways following changes in environmental conditions (Graham and Grimm 1990). One of the prevalent ideas is that species respond individually to environmental changes (Whittaker 1956, Davis et al. 1998) with local communities being near-random samples from regional species pools (Ricklefs 2004). An alternative view proposes that individualism is only apparent, with concordant biological responses to environment being detectable at the functional level (e.g., trophic groups; Aebischer et al. 1990, Walther 2010). Studies predicting the consequences of climate change on species distributions often start with the assumption that species respond individually to environmental gradients (Baselga and Araujo 2009). In other words, predictions are typically made after modelling individual responses to environmental gradients without consideration of potential community dynamics or biotic interactions. Such assumption is debatable not least because theoretical (e.g., Travis et al. 2005, Araújo and Rozenfeld 2014) and modelling studies (e.g., Araújo and Luoto 2007, García-Valdés et al. 2015) have shown that biotic interactions can modify individual species responses to environmental change. While there is much debate regarding the scale in which biotic interactions operate (Pearson and Dawson 2003), there is mounting evidence that interactions can constrain distributions of species at broad geographical scales (Gotelli et al. 2010, Araújo and Rozenfeld 2014). Yet, the question of whether species respond to environmental changes individually or whether there is concordance in patterns of change across multiple species distributions at higher levels of organization (e.g., functional groups) is still unresolved.

Following environmental changes, communities are known to go through re-organizations that can have serious consequences for ecosystem structure and functioning (Scheffer and Carpenter 2003). These reorganizations are expected to be of greater magnitude when functional groups, for example trophic groups, are affected differently (Edwards and Richardson 2004). For example, it has been shown that higher trophic groups (e.g., predators) are more sensitive to sudden changes in the environment (Voigt et al. 2003), with potentially destabilizing effects on natural communities under climate change. Investigating such dynamics is complex since, for most natural systems, there are no detailed temporal series. An alternative approach to study such temporal dynamics is to compare contemporary communities along geographical (or environmental) gradients to infer potential responses to them (e.g., thermal gradients nutrient loading, Valiela et al. 1992, thermal gradients, Meerhoff et al. 2007). Such space-for-time approaches can be particularly valuable for investigating compositional changes across space since compositional turnover has been shown to correlate with climate in both space and time (Buckley and Jetz 2008).

In this study, we investigate the spatial concordance within and among trophic groups to gain insight how they might respond to environmental change over time (Araújo and Rahbek 2006, Blois et al. 2013). Spatial concordance (also called congruence) occurs when composition (e.g., richness; Heino 2010) or community structure (e.g., nestedness; Soininen and Kõngäs 2012) of different trophic groups (or taxa) is correlated across space. Despite many examples of highly concordant taxonomical groups (e.g., Paszkowski and Tonn 2000, Bini et al. 2007, Grenouillet et al. 2008), many other studies have reported weak or non-concordant spatial patterns (e.g., Paavola et al. 2003, Declerck et al. 2005, Tolonen et al. 2005, Longmuir et al. 2007). Taken together, these studies raise the question of whether trophic groups mimic dynamics observed at individual species level or, more meaningfully, whether variation of multiple trophic groups affect whole-community dynamics and how they might be predicted forecasts of environmental change effects on biodiversity and ecosystems.

Here, we investigate changes in the composition of aquatic communities along biogeographical and environmental gradients using species occurrences from 19 freshwater lakes across four different islands in the Azorean archipelago. In particular, we examine whether species distributional patterns are spatially concordant 1) within and 2) among trophic groups (see maps in Supplementary material Appendix 1, Fig. A1). Sampling covered the main aquatic trophic groups: producers (benthic diatoms, phytoplankton), micro-consumers (copepods, water fleas) and macro-consumers (insect larvae, crustaceans, molluscs). The data, involving different lakes within islands across archipelagos, provide a unique opportunity to measure the relative contributions of environmental variability (e.g., lake size, productivity) and biogeography (e.g., island-size, distance between islands) on the compositional variation of species across space.

The lack of concordance among trophic groups might affect ecosystem functioning (Burthe et al. 2012), particularly when perturbations alter resource flow to upper trophic groups (Walther 2010). When different trophic groups are spatially concordant, it has been suggested that environment variables might be driving changes among groups in the communities in similar ways (e.g., Paavola et al., 2003); in contrast, when trophic groups are not spatially concordant divergent responses to environmental gradients

are more likely (e.g., Jackson and Harvey 1993, Allen et al. 1999, Korhonen et al. 2011). Our results show that spatial concordance in individual species distributions within trophic groups is greater than expected by chance, while little spatial concordance was found in patterns of change of compositional variation among trophic groups along biogeographic and environmental gradients. Our results invite the interpretation that lack of spatial concordance among trophic groups might lead them to change asynchronously to environmental changes leading to potential cascading effects within communities.

METHODS

Study area. We use data from the Azorean archipelago (Portugal; Northeast Atlantic Ocean; latitude: 36°55 – 39°43 N; longitude: 24°46 – 31°16 W). The archipelago consists of nine islands and several islets (Appendix 1, Fig. A1), and spans across 615 km while being located *ca.* 1300 km west of Portugal and 1900 km east of North America. The Azorean freshwater systems are unique due to the volcanic origin, climate conditions and level of isolation of the islands. Volcanism determines the geological formation and geomorphology of watersheds and strongly influences the hydrological regime of lakes and rivers of the Azores (Cruz et al. 2006). The relative young age of the islands (0.27–8.1 Myr), their isolation from mainland territories, the small size of the islands and the archipelagic dispersion of the islands, create barriers hard to overcome for many aquatic species (Raposeiro et al. 2009). This level of isolation is thought to be responsible for the reduced freshwater species diversity, frequently differentiated: organisms with greater dispersal ability are well represented and are often dominant, contrary to those who are poor dispersers or do not persist for very long periods. Such particular biogeographical context leads to freshwater communities that are different from those in the temperate continental regions of Europe and North America or those in tropical regions (Raposeiro et al. 2009, Raposeiro et al. 2012). The data were compiled from extensive field surveys conducted under the Water Framework Directive (WFD) and aimed at determining the status of water bodies across Europe. The original dataset includes surveys of bodies of water > 0.01 km² between 2003–2012 across four different islands: Corvo, Pico, Flores and São Miguel (Supplementary material Appendix 2, Table A1). Lakes are located between 260–900 m of altitude encompassing a gradient of disturbance ranging from almost pristine to eutrophic or suffering from extreme anthropogenic disturbance (Porteiro 2000, Gonçalves 2008, Pereira et al. 2014; Table B1). We used a subset of the original dataset with data on all three major trophic groups. Our sampling units included data from surveys in 2011 and 2012. The final dataset consisted of 19 lakes across four islands which corresponded to 73% Archipelago's lakes (i.e. >0.01 km²).

Biotic and environmental sampling.

Lakes were surveyed using specific methodologies for each trophic group: (i) producers (i.e., benthic diatoms and phytoplankton); (ii) micro-consumers (e.g., copepods, water fleas) and (iii) macro-consumers (i.e. > 500 µm; insects larvae, crustaceans, molluscs). Producers consisted of two main groups of organisms: benthic diatoms and phytoplankton. Note that we did not include data on submerged macrophytes because there was no comparable dataset with matching temporal and spatial coverage. Benthic diatoms were sampled mostly on lake margins, between 0.3 and 0.5 meters depth. Lake margins sampling sites were selected based on the natural rocky substrates and macrophytes. In each lake, two to four sampling sites were selected, depending on lake size, and taking into account the lake morphology and the structure of the watershed. Both epilithic and epiphytic diatoms were collected by scraping at least 5 cobbles and by washing macrophytes, respectively and immediately preserved in 4% neutralized formalin (Kelly et al. 1998). Slides with diatoms were mounted with Naphrax and diatoms were identified under oil-immersion phase contrast light microscopy (Zeiss Axioimage A1 and Olympus BX50F). Phytoplankton samples were taken using Van Dorn bottle and plankton net of 10 µm mesh size (Beisner et al. 2006) at lake maximum depth point. This procedure was shown to be appropriate due to the high coefficient of circularity, which leads to great environmental homogeneity of the limnetic zone and the horizontal uniformity at both physicochemical and plankton levels (Gonçalves 2008). All samples were preserved with 1 % Lugol solution (v/v) and taxa were identified to the lower taxonomical level possible using light microscopy (Zeiss Axioimage A1 and Olympus BX50F). Consumers were divided in two broad groups (i.e., micro- and macro-consumers) that corresponds a division in terms of body-size, taxonomical groups and functional traits. Micro-consumers consisted mainly of copepods, water fleas, rotifers and were sampled using a Shindler-Patalas 30 L trap with 61 µm mesh size (Bio et al. 2008). Samples were preserved with 10% formalin saturated with sucrose and taxa were identified using a Zeiss Axioimage A1 and Olympus BX50F microscopes. Macro-consumers consisted mainly of macro-invertebrates (i.e. macroscopic organisms larger than 500 µm) and were sampled using a 30 x 30 cm “D-frame net” with a 500 µm mesh size by sweeping across all accessible margins of each lake. This method allows surveying a variety of microhabitats across the lake margins and has been widely used in surveys of macroinvertebrates across European water bodies (e.g., Davies 2001). Samples were rinsed through a

sieve of 500 μm mesh size and preserved in 96 % ethanol (approximately 70 % final concentration). Macro-invertebrates were sorted and identified using Zeiss Stemi 2000-C and Olympus SZX7 magnifiers. Physicochemical profiles (e.g., nutrients, salts) of each lake were determined by collecting water samples using a Van Dorn bottle for posterior laboratory analysis; multi-parametric probes were used to measure *in situ* variables (e.g. pH, conductivity; Appendix 2, Table A1).

Taxonomical resolution

The dataset consisted of 448 taxa: producers (315; mean: 24.2 ± 0.5 SE), micro- (94; mean: 10.6 ± 0.3 SE) and macro-consumers (39; mean = 6.6 ± 0.3 SE). Producers consisted mainly of benthic diatoms, cyanobacteria and green microalgae. From the 173 taxa of benthic diatoms, the most representative families were Naviculaceae (35 taxa), Fragilariaceae (28 taxa) and Bacillariaceae (21 taxa). The most representative groups of phytoplankton were the green algae Conjugatophyceae and Chlorophyceae (45 taxa each) and blue-green algae Cyanophyceae (19 taxa). Micro-consumers consisted mostly of rotifers (59 taxa) and arthropods, particularly “water fleas” (order Cladocera, with 19 taxa) and copepods (16 taxa). Macro-consumers consisted mostly of arthropods (32 taxa), particularly insects (25 taxa) and arachnids (4 taxa). Other phyla contributed to the diversity of macro-consumers, such as annelids (3 taxa), molluscs (2 taxa) and flatworms (Platyhelminthes; 2 taxa). Despite not all taxa being identified to species level, over 98 % of all taxa were identified to family or lower taxonomic levels. Producers consisted mainly of benthic diatoms, cyanobacteria and green microalgae. From the 173 taxa of benthic diatoms, 4.6 % were identified to genus level, 95.4 % to species level. 142 phytoplankton taxa were identified, of which 14.79 % were identified to the genus level and 85.2 % to the species level. The 94 taxa of micro-consumers were identified to family (3.2 %), genus (27.7 %), or species (63.8 %) level. The remaining 5.3 % of total taxa were identified at higher taxonomic levels. A total of 39 taxa of macro-consumers, from which, 33.3 % were identified to family; 30.8 % to genus; and 33.3 % species level. The remaining 2.6 % of total taxa were identified at higher taxonomic levels. Preliminary analyses have shown the level of resolution (up until family) had no bearing on the results being presented in this study. It has been shown that patterns of site-to-site differences in community composition are maintained for genera and families when species data are not available (Terlizii et al. 2009), which suggests that genera or families might be used as effective taxonomic surrogates to detect spatial differences in community dissimilarity.

Measuring spatial concordance within trophic groups. The level of spatial concordance among individual species within a community can be measured by calculating the dispersion (or variance) of the eigenvalues of the correlation matrix (Peres-Neto and Magnan 2004). This measure has been used to estimate correlatedness of different functional traits (e.g., morphological measurements, Peres-Neto and Magnan 2004, Pavlicev et al. 2009). The same principles apply for a correlation matrix calculated from a community matrix with species occurrences across several sites. To account for dependencies on the size of the matrix when eigenvalue variance is compared among matrices, we can define the relative eigenvalue variance by dividing the observed eigenvalue variance by the maximum eigenvalue variance for the particular number of species (or traits) in each trophic group. The maximum expected variance equals the number of species. The relative eigenvalue variance is independent of the number of species and can thus be used to compare spatial correlation across different matrices. This measure ranges from zero to one. If spatial correlatedness is high (i.e., species are concordant), the first few dimensions present large eigenvalues in relation to the latter and the variance of eigenvalues is relatively high. If spatial correlatedness approaches zero, all axes have similar eigenvalues and the variance is low. Eigenvalue variance scales linearly with the square of the mean correlation, while the standard deviation of the eigenvalues scales with the average level of correlation.

We used the measure of spatial correlatedness to test whether individual species' variability from lake-to-lake reflected the overall compositional variability within each trophic group using two approaches. The first approach consisted of testing whether species pairwise correlations (or, more precisely, spatial correlatedness; see details above) from lake-to-lake were different from what would be expected by chance (i.e., whether observed values different from frequency distribution of randomized values). We generated a distribution of expected values of spatial correlatedness to test whether observed values were different from that expected by chance (see *Null models* section for full description). We performed the permutation test in four steps: (1) we generated random assemblages of species; (2) we calculated spatial correlatedness of each species matrix generated in step 1; (3) we performed steps 1 and 2 a 1000 times; and (4) we tested whether the observed value was greater than 95% of the spatial correlatedness values accumulated in step 3 (Peres-Neto and Magnan 2004). This measure is statistically independent of the number of species and can thus be used to compare spatial correlatedness across different groups of species (Peres-Neto and Magnan 2004). The second approach consisted in comparing the distribution of the expected and observed values of spatial correlatedness based on random subsets of species within each trophic group. The test was done in three steps: (1) we generated random assemblages; (2) we calculated spatial correlatedness between subsets of species (i.e., 30) within each trophic group; and (3) we then compared mean spatial correlatedness values using one-way ANOVA with “trophic group” and

“expected vs observed” as main factors ($n=1000$). These two complementary analyses allowed us to test whether spatial correlatedness within each group was different from that expected by chance.

Measuring spatial concordance in community composition. We tested whether trophic groups were spatially concordant among them by correlating their pairwise species compositional dissimilarities. Comparing assemblages of species with differences in numbers of species may overestimate pairwise dissimilarities due to differences in numbers of species between two local communities (e.g., Anderson et al. 2011; Chase et al. 2011). Given that there are substantial differences in the numbers of species (i.e., local and regional scales) among trophic groups, we used multiple approaches to measure spatial variability in community composition to assess whether differences among trophic groups resulted from changes in their underlying spatial variation across the archipelago or, instead, were due to differences numbers of species among them.

We compared the variation in community structure across different trophic groups using three approaches. First, we compared differences in community variability within each trophic group using Jaccard’s pairwise dissimilarities. We tested for differences in mean pairwise dissimilarities using one-way ANOVA’s with “trophic group” as main factor and illustrates the results using the overall summary statistics (box plots). Box plots have been shown to provide an intuitive way to graphically compare average mean pairwise dissimilarities measures using incidence-based metrics (e.g. Myers et al. 2013). Preliminary simulations examining the effect of number of lakes in the calculation of community variability showed differences among trophic groups regardless of the numbers of lakes considered (Appendix 6, Fig. A7).

Second, we tested whether differences in observed pairwise dissimilarities were different from expected based on random expectations (“effect-sizes” *sensu* Myers et al. 2013). This was achieved by comparing observed pairwise dissimilarities with the expected values between communities assembled from random sampling of the regional species pool. This procedure considers the regional species pool as the entire set of species observed within each trophic group whilst maintaining the species frequencies in the observed community matrix by fixing the overall matrix structure of randomly generated communities (see below *Null models* section; Crist et al. 2003; Kraft et al. 2011; Myers et al 2013). We generated null matrices using the “permatfull” function in R package vegan (Oskenen et al. 2013).

Third, we calculated the standardised effect-size of observed pairwise dissimilarities (or b-deviation in Kraft et al. 2011) as the difference between the observed and mean expected dissimilarity (i.e., mean value from 9999 iterations of the null model), divided by the standard deviation of expected values (Myers et al. 2013). Note that we ran preliminary analysis with a range of different null models with different degrees of dispersal limitation which yield qualitatively similar results (see below *Null models* section). The signal of the deviation indicates whether observed communities diverge from what would be expected by random chance: positive deviations indicate higher dissimilarity than expected by chance; deviations approaching zero indicate that observed pairwise dissimilarities are similar to what would be expected from random sampling (and higher b-diversity *sensu* Myers et al. 2013). Finally, we used a complementary approach using the probabilistic Raup-Crick metric that instead of expressing dissimilarity among pairwise communities per se, expresses dissimilarity among two communities as a probability relative a null expectation of what that dissimilarity could be (Chase and Myers 2011, Kraft et al. 2011). This metric minimizes the dependence of classical incidence-based measures on differences in local richness between pairs of communities (Chase et al. 2011).

We examined the effect of sample size (i.e., number of lakes) by running calculating the community variability for random subsets of increasing number of lakes (Appendix 7, Figure A8). These preliminary analysis showed that differences in community variability across different trophic groups arise with just a few lakes and decrease when greater numbers of lakes are included in the analysis, even though the hierarchy of the different trophic groups remains the same.

Null models. We implemented a series of null models (Gotelli and Graves 1996, Gotelli 2000) to assess whether observed patterns of community variability were different than expected by chance. We used three different null models to generate “null communities”: unconstrained (U), geographical (G) and environment-constrained (E). Unconstrained null models generate null communities by taking into account species’ incidence frequency and species richness of each site in the original species distribution matrix (Gotelli et al. 1997, Peres- Neto et al. 2001). The unconstrained models simulate community assembly in which all sites could be successfully colonized by any species under chance alone.

There are two main variants of such unconstrained models: fixed–fixed (FF) and the fixed–equiprobable (FE). FF null models maintain the total number of species at each site (i.e., fixed column totals) and the total number of occurrences of each species (i.e., fixed row totals). FE null models generate communities by assuming that colonization is equiprobable across all sites (i.e., only row totals are fixed; Gotelli 2000).

We implemented both types of unconstrained models and found no qualitative differences (see Appendix 4, Fig. A4). Hereafter we only present results for FF models. Spatially constrained null models are used to

generate null communities that retain the spatial structure between different sites, thus determining the probability of colonization as a function of distance between lakes. We established the constraints based spatial hierarchical cluster analysis to group lakes based on geographical distances (i.e., Euclidean distances calculated using geographical coordinates), reflecting different levels of dispersal limitation. The distance clusters were implemented based on inter-lake distances, which also reflect the isolation of islands since the distance between islands is, in the majority of cases, larger than the distance between lakes within islands. Based on the results of the cluster analysis we ran five different simulations, each with different spatial clustering thresholds: 500, 250, 25 and 5 km between pairs of lakes (see Appendix 4, Fig. A5). The outcome of the cluster analysis was used to restrict randomizations to groups of lakes in each distance class. For example, randomizations using the 5 km threshold simulated communities within 7 clusters of lakes, thus simulating dispersal limited colonization. This procedure was implemented by clusters of lakes (or “strata”) to constraint FF null models in function “permatfull” in R package vegan (Oksanen et al. 2013). Environment (or habitat-) constrained null models were used to generate null communities that retain species associations with a particular environment (or habitats; Peres- Neto et al. 2001, Azeria et al. 2012). We used hierarchical clustering of lakes based on their pairwise environmental distances (see Appendix 4, Fig. A6) to group lakes based on their environmental characteristics. These environmental clusters were incorporated into the null model using four different levels of pairwise dissimilarity (see Appendix 4, Fig. A4). We contrasted all combinations of parameters and found that simulated communities were always significantly more dissimilar than observed values of community dissimilarity, regardless of the choice of the null model. Based on these results, all subsequent analysis were conducted with the most restrictive versions of geographical (<5 km threshold; 7 groups of lakes) and environmental (6 groups of lakes) constrained null models.

Partitioning of compositional variability across biogeographical and environmental gradients. We further investigated compositional variability across biogeographical and environmental gradients by identifying and measuring the contribution of the key variables explaining compositional variability from lake-to-lake. We calculated Pearson product moment correlations between environmental variables to identify and remove variables, which were collinear thus preventing amplification of environmental signal (Pearson $r > 0.80$; Myers et al. 2013); variables that did not meet the criteria were excluded from the analysis. A total of 11 environmental variables were retained and used in analysis (see full set of variables in Appendix 2, Table A1). We also used an alternative approach by calculating the principal components (PCA) on the entire set of variables, and used the orthogonal PCA axes as proxies for the environmental gradients. There was a strong significant correlation between the two sets of variables ($r = 0.75$; $df = 169$; $P < 0.001$). We found no qualitative differences between the environmental variables and PCA axes and for that reason we performed the subsequent analysis using the full set of variables. About 58% of all possible pairwise comparisons included in the analyses were between lakes in different islands, which implies that there could be a correlation between environmental distances and the main biogeographical gradients of the archipelago. Pearson’s correlations revealed no significant correlation between environmental and geographic distances ($F = 0.55$; $P > 0.4$ with 1,169 df.), suggesting that the direction and/or magnitude of environmental and geographical effects were not correlated. We calculated a matrix of Euclidean distances based on the UTM coordinates of each lake and converted them to kilometres. Additionally, we also analysed geographical variables using Principal Components of Neighbour Matrices (PCNM; Dray et al. 2006), which provides greater resolution of small-scale variation in continuum geographic variables in constrained ordinations (Anderson et al. 2011). PCNM analysis yielded six eigenfunctions with positive eigenvalues although we found no major qualitative differences between using raw geographical distances or PCNM eigenfunctions.

We used distance-based redundancy analysis (dbRDA) to partition variation in community structure using either (i) full set of variables (Supplementary material Appendix 2, Table A1) or (ii) subset of variables selected using a forward-model selection procedure (“ordiR2step” in R package vegan; Appendix 5, Table A2). We only performed forward-model selection when full models (i.e., with all explanatory variables) were statistically significant (‘global tests’). We then ran the analysis with selected variables to determine the best model for each trophic group (Appendix 5, Table A3). Finally, we partitioned the variation in community composition matrices of each trophic group with respect to matrices of environmental variables or geographic distances using the function “varpart” in R package vegan (Anderson et al. 2011, Chase et al. 2011). The dbRDA analysis outputs adjusted R-squared values that correspond to unbiased estimates of the proportion of variation explained by each of the four fractions: environment, geography, spatially structured environmental variables and unexplained variance (Oksanen et al. 2013).

RESULTS

Our results revealed that spatial correlatedness of individual species distributions across the Azorean lakes is greater than expected by chance, within trophic groups, but indiscernible among trophic groups. Individual species of macro-consumers showed the greatest within trophic group congruence in all of the three trophic groups. Although not all individual species varied in the same way within trophic groups, as indicated by low overall correlatedness values, they were more concordant across lakes than expected if species would be assigned to each lake randomly (see Null models section details on different types of random communities). Moreover, subsets of species from each of the three trophic groups showed significantly greater spatial concordance than similar subsets from the community as a whole (post-hoc comparisons in Fig. 1).

When we analysed compositional changes across trophic levels we found significant differences among them (ANOVA: $F_{3,662} = 20.37$; $P < 0.001$). While compositional variability of producers across space was distinguishable from the whole-community, micro- and macro-consumers showed significantly different mean pairwise dissimilarity values (Tukey multiple comparisons of means at $P < 0.05$; Fig. 2a). Micro-consumers showed greater compositional variability than producers; in contrast, changes in composition of macro-consumers were the smallest amongst all three trophic levels. Analysis of the effect-sizes of mean pairwise dissimilarities showed significant differences among trophic levels ($F_{3,662} = 206.5$; $P < 0.001$). However, in contrast with the previous analysis, there was a clear discrimination between producers and consumers: micro- and macro-consumers showed significantly greater pairwise dissimilarities than producers and the whole-community (Fig. 2b). Note that the effect-sizes of micro- and macro-consumers approached 0, which indicates that variation in community composition in the whole-community was considerably lower than expected by chance (Fig. 2b). In contrast, producer- and whole-community compositional variation showed changes across space that were substantially different from what would be expected by chance.

In general, adjoining trophic groups showed similar compositional variability from lake-to-lake: producers and micro-consumers showed divergent patterns of distribution ($r=0.03$; $P>0.05$) and the same was true for micro-consumers and macro-consumers ($r=0.05$; $P>0.05$; Fig. 3; Supplementary material Appendix 5, Table A3). Results of the analysis using the Raup-Crick metric were consistent with the previous observation that changes in the distributions of producers vs. micro-consumers, and micro-consumers vs. macro-consumers were not spatially concordant ($r=0.01$, $P>0.05$; and $r=0.12$; $P>0.05$ respectively).

We investigated the driving forces underlying non-concordant changes in trophic composition. When analysed separately, trophic groups varied consistently with geographical distances between lakes, environmental gradients or to both simultaneously. Producers responded strongly to changes in the environment ($r=0.59$; $P<0.001$) but not to geographical distances between lakes ($r=0.01$; $P>0.05$). In contrast, micro-consumers did not appear to be correlated to changes in the environmental variables selected ($r=0.11$; $P>0.05$) but they did covary consistently with pairwise geographical distances between lakes ($r=0.24$; $P<0.001$). Finally, macro-consumers covaried significantly with the environment ($r=0.17$; $P<0.05$) and varied consistently with geographical distances ($r=0.18$; $P<0.01$; Supplementary material Appendix 5, Table A3). These results are consistent with the view that each trophic group is responding to different biogeographical or environmental variables.

To identify which particular variables explain divergent responses in community composition among trophic groups, we used a distance-based Redundancy Analysis (dbRDA; Fig. 4). Compositional variation in producers was largely explained (>60 %; Fig. 4) by the environment, particularly by variables such as water conductivity and phosphorus concentration (Appendix 5, Table A2). Comparatively, environmental and biogeographical gradients explained far smaller amounts of compositional variability of micro-consumers, not exceeding 25%, with increased importance of variables such as pH and NO_2 . Finally, macro-consumers responded to all three sources of variation: environment (7%), geography (16%) and spatially structured environmental variables (13%; Fig. 4). Our analysis clearly demonstrated that trophic groups respond to different environmental gradients and are differently constrained by the geographical distances between lakes.

DISCUSSION

Do individual species within functional groups respond concordantly to spatial variation and environmental pressures? Does functional group composition change concordantly too? Using extensive food webs in aquatic communities across the Azorean archipelago, we show that, within trophic groups, there is greater spatial concordance than expected by chance. Assuming that variation across space is a reasonable substitute for variation across time (Voigt et al. 2003), the observation of spatially concordant variation in species composition across gradients supports the view that communities behave more like a cohort and not individualistically to environmental change. However, when changes in community composition are examined across trophic groups evidence is for non-concordant responses. That is, species of different trophic groups respond in different ways to spatial and environmental variation, thus supporting the assumption of individualism. Our interpretation of these patterns is based on the assumption that compositional turnover through space reflects how trophic groups would vary through time when responding to analogous changes in climatic or environmental gradients. Taking in consideration that mechanisms of community assembly and biotic interactions drive compositional turnover within and across communities, measuring compositional turnover across environmental gradients can be interpreted as a proxy of how communities vary in relation to environmental change. Recent studies using space variation as a proxy for temporal responses have shown that, in the majority of the cases, spatial variation provides a good approximation to temporal variation and thus being a reasonable approach to investigate potential species responses to environmental change (Araújo and Rahbek 2006, Blois et al. 2013). In fact, certain aspects of climate (e.g., temporal variability, covariance among critical variables) are detectable with greater degree of accuracy when measured across space rather than through time (Blois et al. 2013).

Despite this evidence, we acknowledge that the spatial and temporal dimensions of species distribution patterns may not always be fully comparable but seen as an approximation to each other. Further investigation is needed to unravel how these spatial and temporal components contribute to concordant patterns species composition and determine in which cases they may not be comparable.

Whether species respond individualistically or more like a cohort within communities is thus likely to depend on the scale of the observation. The longstanding dichotomy between individualistic versus organismal responses of communities to environmental gradients (Williams and Jackson 2007) is probably a consequence of comparing data with different functional resolutions. As our results show, within functional groups (or guilds), responses are more congruent than among groups. Also, found that spatial concordance within trophic groups is not constant for species of different groups. Greater degree of concordance was recorded for macro-consumers, despite comprising a broad range of species that can exhibit differential responses depending on particular traits (Peres-Neto et al. 2006). Robert H. Whittaker, who pioneered the theory of gradient analysis in ecology (Clements 1916, Gleason 1926), championing the idea of individualism, was working almost exclusively with plants across environmental gradients (Whittaker 1967). Our observations are consistent with his, in the sense that primary producers in the Azorean lake communities (i.e. benthic diatoms and phytoplankton) also displayed relatively weaker concordance with spatial and environmental gradients when compared with other groups. But others studies, analysing macrofossil deposits of vertebrates found that responses of species to past environmental change were individualistic at the taxonomic level alone. When analysis focused on food web structures, changes in composition were synchronous with environmental change (Whittaker 1956). Unravelling the underlying drivers of this divergence in trophic responses is key to understand the dichotomy between individual and organismal responses.

What are the processes that drive species to respond as a group (i.e., as an assemblage of species) or as individuals? One important factor influencing community composition is how species move from one lake to the other. Dispersal mediates how communities are able to adapt to changing environmental conditions (Mendoza and Palmqvist 2008) and is therefore a key driver of species diversity and functioning of local communities (Loreau et al. 2003). Trophic groups that are mainly composed of good dispersers (e.g. microbes and phytoplankton) are expected to respond to environmental gradients (Leibold et al. 2004). Most primary producers in aquatic systems have passive modes of dispersal (e.g., diatoms, phytoplankton) and are more effective in reaching new lakes than organisms with active modes of dispersal (Beisner et al. 2006). We predict that such increased dispersal ability promotes biotic homogenization of lake communities within archipelago as result of their great success in colonizing most lakes. Our prediction is supported by the observation that producers had the lowest lake-to-lake variability in community composition. Note that this assertion is specific to micro-producers (e.g., diatoms, phytoplankton) and might not hold true for macrophytes. Since macrophytes are passive dispersers with propagule sizes (i.e., seed size), comparable to those of large macroinvertebrates (e.g., molluscs), they might have similar spatial patterns to those of trophic groups that are constrained by dispersal (i.e. consumers) and, therefore, are more likely to depend on spatial dynamics such meta-populations (Soininen et al. 2007, Shurin et al. 2009, Bie et al. 2012). Micro-consumers which are

generally considered to have poor dispersal (or meta-communities sensu Leibold et al. 2004, Bie et al. 2012), did not respond to environmental gradients (Shurin et al. 2009). Similarly, macro-consumers – generally considered to have lower dispersal abilities –, showed greater lake-to-lake variability (i.e., spatial turnover) in community composition as a consequence of many species not having been yet able to colonize all islands. Our results showing that higher trophic groups are more likely to have greater spatial turnover than lower trophic groups are in agreement with recent theoretical (Beisner et al. 2006) and empirical studies (Gravel et al. 2011). Observed variation in community composition is likely the result from a series of deterministic (e.g. host-parasite networks; Roslin et al. 2013) as well as stochastic processes (e.g., environmental gradients, life history traits, etc.; Harrison et al. 1992, Veech and Crist 2007). The combined effects of such contrasting processes determines community structure at local scales, as a function of the processes shaping the regional pool of species at regional scales (e.g. dispersal limitation; Hubbell 2001).

Our findings suggest that the relative importance of deterministic (e.g., environmental filtering) and stochastic processes (e.g., dispersal) might vary within the food web as the result of a distribution of traits within each trophic group (see also Leibold et al. 2004, Ricklefs 2004). Unravelling the functional traits and ecological processes that determine whether species respond individualistically or concordantly will be determinant towards making better predictions of dynamics of food webs under changing environments.

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FIGURE LEGENDS

Figure 1 – Spatial concordance within trophic groups in relation to unconstrained (Un), environmental (En) or geographically (Sp) constrained null models. Spatial concordance was measured using a correlation metric based on the variance of eigenvalues of the species correlation matrix within each trophic group. Letters indicate post-hoc Tukey tests comparing means of observed values of spatial inter-correlation. Symbols indicate significance levels of permutation test comparing observed (Ob) with expected values (see Peres- Neto et al. 2001).

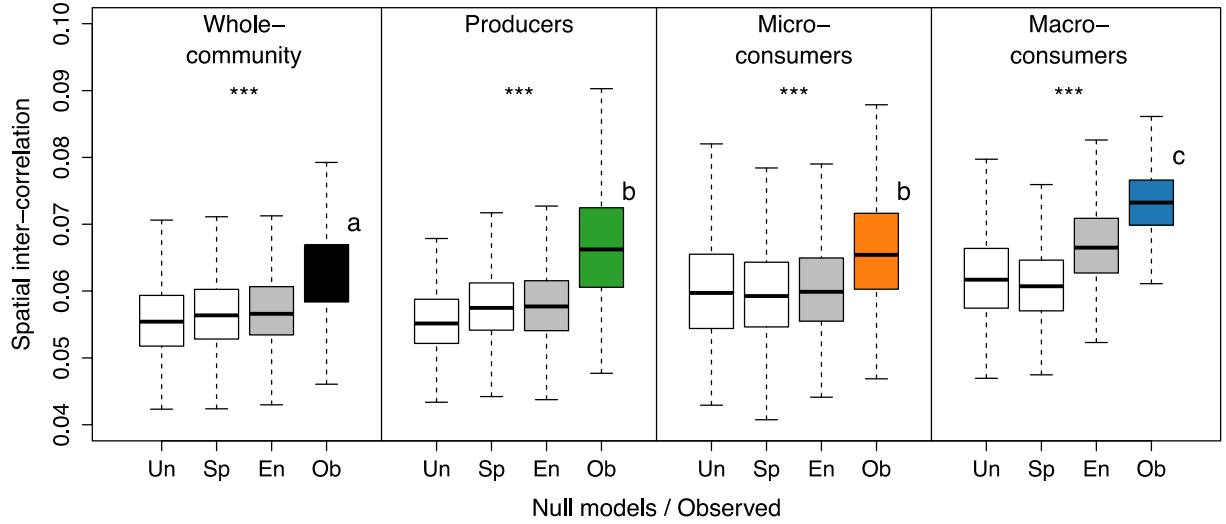


Figure 2 – Variation in community structure across multiple trophic levels: mean pairwise (beta diversity) dissimilarities for each trophic level and effect-sizes (beta deviations) from expected pairwise dissimilarities based on random expectations (Kraft et al. 2011; Myers et al. 2013). Pairwise dissimilarity values closer to zero indicate that distributions are close to what would be expected from random chance; values away from zero indicate environmental filtering determining spatial patterns. Letters indicate post-hoc Tukey tests comparing means of observed values of spatial inter-correlation.

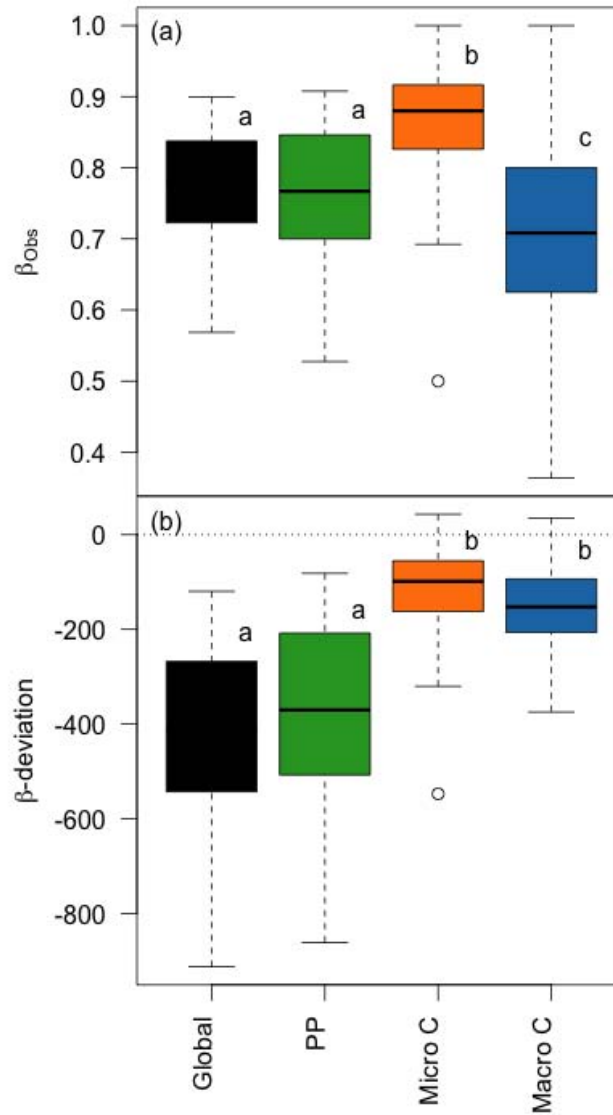


Figure 3 – Relationships among trophic groups and biogeographical (i.e. Euclidean distances calculated using geographical coordinates) or environmental gradients (i.e. Euclidean distances calculated using a matrix of selected environmental variables; see *Methods* section for details). Abbreviations indicate geographical (Geo) and environmental distances (Env). Full lines linking boxes indicate significant correlations (at $P < 0.05$); numbers indicate correlation coefficients (see details in Appendix 5, Table A3).

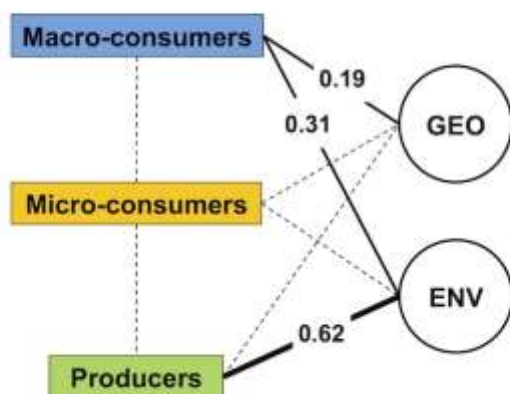


Figure 4 – Partitioning of the variation in community structure in response to biogeographical or environmental gradients across multiple trophic groups. The proportion of variation explained by constrained ordinations (dbRDA) was calculated using the probabilistic Raup-Crick index. Variation is partitioned in four fractions: environment (light grey), geography (black), spatially structured environment (dark grey) and unexplained variance (white). In each case, the proportion of variation explained was calculated with the best subset of variables selected by forward-selection method (Supplementary material Appendix 5, Table A3; see also biplots in Appendix 6, Fig. A7). The full list of variables can be found in Appendix 2 Table A1. Note that there is a clear discrimination between producers and consumers.

