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Metacommunities from bacteria to birds: stronger environmental effects in Mediterranean than in tropical ponds.

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Abstract

The metacommunity concept provides a theoretical framework that aims at explaining organism distributions by a combination of environmental filtering, dispersal and drift. With the development of statistical tools to quantify and partially isolate the role of each of these processes, empirical metacommunity studies have multiplied worldwide. However, few works attempt a multi-taxon approach and even fewer compare two distant biogeographical regions using the same methodology. Under this framework, we tested the expectation that temperate (Mediterranean) pond metacommunities would be more influenced by environmental and spatial processes than tropical ones, because of stronger environmental gradients and higher isolation of waterbodies.

We surveyed 30 tropical and 32 Mediterranean temporary ponds and obtained data on 49 environmental variables (including limnological, hydrogeomorphological, biotic, climatic, and landscape variables). We characterized the biological communities of Bacteria and Archaea (from the water column and the sediment), phytoplankton, zooplankton, benthic invertebrates, amphibians and birds, and estimated the relative role of space and environment on metacommunity organization for each group and region, by means of variation partitioning using Generalized Additive Models (GAMs).

The residual (unexplained) variation was larger in tropical pond metacommunities, suggesting a higher role for stochastic processes and/or effects of unmeasured processes such as biotic interactions in the tropics. Environmental filtering was important in both tropical and Mediterranean ponds, but markedly stronger in the latter, probably related to higher environmental heterogeneity. The variability between taxonomic groups in spatial and environmental contributions was very wide, and only some similarities between geographic settings were observed for the environmental effects of passively dispersing organisms, with

rotifers and diatoms being among the most and least affected by the abiotic environment, respectively, in both areas. Overall, these results provide support, in a wide variety of aquatic organisms, for the classical view of stronger abiotic niche constraints in temperate areas compared to the tropics.

Key words— multi-taxon analysis, dispersal limitation, species sorting, tropical and temperate ecology, freshwater metacommunity.

"Tropical species often exhibit patchy geographic distributions that respond to no obvious relations with climate or habitat"

MacArthur 1972

Introduction

Communities are not isolated systems, as they had been classically considered, but are instead conforming networks connected by dispersal, known as metacommunities (Hanski and Gilpin 1991; Wilson 1992). Our understanding of metacommunity organization relies on the role of selection, dispersal, and stochastic processes (Vellend 2010; Leibold and Chase 2018) and the conceptual view of four archetypes, representing extreme scenarios of these processes: species sorting, patch dynamics, mass effects and neutral models (Leibold et al. 2004). Previous studies observed that the relative relevance of these processes largely depends on landscape settings (e.g., connectivity, environmental heterogeneity; Grönroos et al. 2013; Erös et al. 2017; Castillo-Escrivà et al. 2017a) and on the traits of the organisms being investigated (e.g., body size, dispersal mode, trophic level; De Bie et al. 2012; Astorga et al. 2012; Vanschoenwinkel et al. 2010). However, few works have jointly studied a wide variety of organisms in the same type of ecosystems, sampled at the same time and using the same methodology, across biogeographical regions but with similar spatial extents. All these factors may be affecting the outcome of metacommunity analyses and it is therefore important to keep some control on all of them.

When metacommunities are surveyed in different landscapes, they show a general pattern associated with the spatial scale of observation (e.g., stream, basin and ecoregion; Heino et al. 2015; Leibold and Chase 2018). Small spatial scales, with dispersal surplus and/or homogeneous environmental conditions, favour stochastic metacommunity variation, whereas at broad spatial scales, dispersal rates decrease, creating spatial variation associated with

dispersal limitation. Both small and large scales reduce environmental filtering strength, which is relevant at intermediate scales with a heterogeneous environment, allowing moderate dispersal rates to track all the suitable localities. Therefore, keeping spatial extent under control is essential for the comparison of diverse metacommunities. However, few studies explore metacommunity organization comparing distinct biogeographical regions (with large differences in their abiotic setting and biota) but controlling for spatial scale (Myers et al 2013; Heino et al. 2017). Uniform temperature conditions during the whole year in tropical regions should reduce species sorting compared to the heterogeneous and restrictive climatic conditions in temperate areas due to an expected higher environmental heterogeneity in the latter (Leibold and Chase 2018). In this sense, some studies found that temperate communities were more environmentally controlled than tropical ones, which were more spatially structured (Myers et al. 2013; Souffreau et al. 2015). In addition, massive floods during the rainy season increase the aquatic connectivity in the tropical regions (Junk et al. 1989; Bunn et al. 2006; Larsen et al. 2019), reducing dispersal limitation and homogenizing local communities (Thomaz et al. 2007; Brasil et al. 2020), and contrasting with the more intense isolation of the Mediterranean region.

Focusing on distinct organisms at the same locations, other metacommunity studies reveal substantial differences between groups in the underlying processes' relevance (Beisner et al. 2006; Padial et al. 2014; Gálvez et al. 2020). Dispersal mode and body size have been considered important features associated with each organism's potential dispersal rates and, consequently, with the strength of environmental filtering and dispersal limitation (De Bie et al. 2012). For active dispersers, dispersal ability increases with body size, being easier for large organisms to spread among suitable sites (favouring species sorting), thus avoiding dispersal limitation (Grönroos et al. 2013; Csercsa et al. 2019). Contrarily, passive transport of organisms with large sizes may be more limited than in small organisms (which also produce more propagules; Finlay 2002), these being expected to be more structured by environmental filtering

(Van der Gucht et al. 2007). However, some other studies do not support these patterns (Heino et al. 2012; Schulz et al. 2012), or they could differ between biogeographic regions, due to particular environmental processes in each region (e.g. flood pulse in the tropics).

Here, we compared the relative importance of environmental and spatial factors on temporary pond metacommunities in a wide range of taxonomic groups (from bacteria to vertebrates) and between two biogeographic regions (Neotropical and Mediterranean) at the same time, with the same methodology and spatial extent. In both study regions, Costa Rica and Spain, precipitations are distributed seasonally, with a marked dry season that promotes the presence of temporary ponds. Temporary ponds are ideal ecosystems for metacommunity studies due to their well-delimited spatial and temporal boundaries, their isolation in a terrestrial matrix (Leibold and Chase 2018), and the natural alternation of liquid water availability (through freezing or drying; Williams 1983; Williams 2006). In this framework, we hypothesize that i) both environmental and spatial effects must have a lower influence on the tropical pond metacommunity assembly than on the Mediterranean one; ii) we expect different responses among organisms according to their dispersal ability in both regions, showing higher environmental effects in passive dispersers and large-bodied active dispersers than in small ones; and iii) a common pattern in the responses of the different taxa comparing between the two regions.

Methods

Study area

We selected 32 Mediterranean and 30 tropical (seasonal or semipermanent) temporary ponds in a study area of 13,000 km^2 in Eastern Spain and 10,000 km^2 in Northern Costa Rica (Figure 1). We sampled the ponds at the beginning of the hydroperiod (two weeks after infilling), in May 2017 for tropical ponds and January 2018 for Mediterranean ponds. The maximum distances between ponds were 209 and 252 km in Spain and Costa Rica, respectively. When

selecting the ponds, we tried to incorporate each region's heterogeneity, including well preserved temporary freshwater bodies from sea level up to 1,500 m a.s.l. The studied ponds encompass different typologies including coastal wetlands, inland shallow lakes, interdunal ponds and small naturalized farmland ponds. All these water bodies show a shallow depth (< 2 meters), fresh to oligohaline waters (< 7000 µS/cm) and different hydroperiod lengths, varying from six months to a few years. The Mediterranean ponds are distributed in a region with warm mean annual temperature (12.9ºC, SD 3.0ºC) and reduced mean precipitation (537 mm, SD 68.3 mm). The tropical ponds experience almost constant hot temperatures during the whole year (24.9ºC, SD 1.3ºC) and high but variable precipitation (2486 mm, SD 934.7 mm) (Fick and Hijmans 2017).

Environmental characterisation

We measured limnological variables *in situ*, including water transparency with a Snell tube (Van de Meutter *et al.* 2006), water temperature, pH, electrical conductivity, and dissolved oxygen concentration, using a WTW® Multi 3430 Multiparameter Meter (with WTW® SenTix 940 for pH, TetraCon 925 for conductivity and FDO 925 for oxygen concentration). Unfiltered water samples were taken for volumetric analyses of chloride and alkalinity, and filtered water for photometric determination of ammonium, nitrite, nitrate and phosphate (SpectroquantMerk® and AquaMerk® test kits and T90+UV/VIS Spectrophotometer) in the lab. The water used for nutrient content analyses was filtered through Whatmann® Gain Flattening Filters (GFF). We extracted chlorophyll-*a* from these GFF filters with acetone 90% and analysed the extract by spectrophotometry (Jeffrey & Humphrey 1975). Hydrogeomorphological variables included maximum and average depth, measured with a graduated stick. In addition, using Google Earth Pro 7.3.2.5776 (Google Inc.) we determined, for each pond, its maximum and minimum diameter, surface area, and shoreline development, as $DL=L/(2\sqrt{\pi A})$, where L=perimeter and A=area (Aronow 1984). We took six random samples

of sediment, from different depths, to analyse its granulometry (following De Vaasma 2010), and organic and carbonate content (according to Heiri et al. 2001). We estimated the proportion of dry weight represented by different grain sizes (>2mm, 2-1 mm, 1-0.5 mm, 0.5-0.25mm, 0.25-0.063mm, 0.063-0.036mm, <0.036mm), and by organic matter and mineral carbonates. We furthermore estimated hydroregime (seasonal or semipermanent) and the origin of the water (rain, streams or phreatic inputs) from local informants, direct observation and maps. Regarding biotic variables (besides chlorophyll-*a*), we visually determined the percentage of surface area of the pond covered by submerged, floating and emergent vegetation, the presence of fish and the presence of livestock. For the optical study of dissolved organic matter (DOM), GFF filtered water samples were kept refrigerated until analysis in the laboratory. DOM fluorescence parameters were acquired by means of excitation–emission matrices (EEMs) with an F-7000 Hitachi fluorescence spectrophotometer following Stedmon and Markager (2005). To measure landscape variables we also used Google Earth, including elevation above sea level and the percentage of different types of land cover in a circular area of 100 m of diameter around the sampling point, occupied by either agricultural fields, low grass, high grass, scrub, forest or buildings. Landscape heterogeneity was estimated with the Shannon index of the different land cover types. Finally, climatic variables were extracted from WorldClim (Fick and Hijmans 2017) to obtain mean annual, maximum and minimum temperatures, temperature range, mean annual precipitation, and seasonality of each location's precipitation, using the software ArcGIS 10.3 (ESRI 2014). Overall, we obtained two main sets of environmental variables: local (limnological, hydrogeomorphological and biotic variables) and regional (landscape and climate variables).

Biological communities

We surveyed prokaryotes, phytoplankton, zooplankton, benthic invertebrates, amphibians and birds in each studied pond. For prokaryotic organisms, two samples were obtained: a 1-L sterilized bottle with pond water and a microtube with 1 mL of wet pond sediment. Afterwards, we filtered the water through 3 µm pore polycarbonate filters (Nucleopore, Whatman) to remove larger particles in the laboratory. The remaining water was filtered again through 0.2 µm pore polycarbonate filters (Nucleopore, Whatman) to obtain DNA samples for subsequent analysis. Filters and sediment samples were cold-stored in microtubes filled with RNAlater™ reagent, until further processing. DNA extractions, PCR and taxonomic assignment were done following Picazo et al. (2019).

Phytoplankton samples were obtained directly from the water column at the center of the pond (100 mL stored in amber coloured glass bottles) and fixed with 3 mL of Lugol's solution. Phytoplankton taxa were identified to species level whenever possible using mainly Huber-Pestalozzi (1976-1982) and Wolowski and Hindák (2005). Zooplankton samples were taken dragging a hand net (63 µm mesh-size) trough 10-20 m of water column, whenever possible, integrating all different microhabitats and depths. Samples were fixed with formaldehyde 4% and identified to species level (when possible) following Koste (1978) and Segers (1995) for rotifers, Alonso (1996), Elías Gutiérrez et al. (2008), and references therein for branchiopods, Dussart (1967; 1969) and Elías Gutiérrez et al. (2008) for copepods and Bledzki and Rybak (2016) for both branchiopods and copepods.

Benthic invertebrate communities were sampled using a hand net (20 x 20 cm, 250 µm mesh-size). About 10 m (when possible) were sampled, integrating all microhabitats. Samples were fixed with ethanol 96% and invertebrates identified to the lowest taxonomic rank possible following mostly Tachet et al. (2010), Thorp and Covich (2010) and Springer et al. (2010), and references therein, for macroinvertebrates, and Meisch (2000), Karanovic (2012) and references therein for Ostracoda.

The occurrences of amphibian species in the ponds were noted *in situ* using eggs, tadpoles, adults, and calls. Due to the low species richness and the easy detectability of species in Mediterranean ponds, we surveyed each pond with a hand net (800 cm^2, 2 mm mesh pore) with a constant effort of ten minutes, and we examined the surroundings of the pond for ten more minutes. When *in situ* identification of larvae was not possible, we identified them in the laboratory by their oral disk. In tropical ponds, with higher species richness and lower detectability, we performed night surveys looking for individuals in the pond's surroundingswith an effective effort of up to 2 hours per pond, avoiding full moon nights. Bird surveys were performed by 15-minute point-counts per pond. We recorded the presence of species identified visually or by their calls.

Statistical analysis

We quantified the role of environmental filtering, ecological drift and dispersal limitation through the partitioning of the metacommunity variation between environmental variables and spatial functions (Peres-Neto *et al.* 2006), for each organism group and region. The groups considered were: archaea from the sediment, archaea from the water, bacteria from the sediment, bacteria from the water, phytoplankton, rotifers, microcrustaceans, macroinvertebrates, amphibians and birds. We also analysed subgroups of these organisms due to major taxonomic and trophic differences among them. Phytoplankton was separated in Cyanobacteria, Chlorophyceae, diatoms and mixotrophic phytoplankton (including Chrysophyceae, Cryptophyceae, Euglenophyta and Dinoflagellata). Microcrustaceans were split in branchiopods, copepods and ostracods, and macroinvertebrates in molluscs and insects. Moreover, insects were divided in Paleoptera (including Odonata and Ephemeroptera), Heteroptera, Coleoptera and Diptera (considering also chironomids separately as another subgroup). All the groups and subgroups accounted for 23 species matrices based on presence-absence data.

For each group and region, we performed variation partitioning with two methods: Redundancy Analyses (RDA), commonly used for metacommunity analysis (Cottenie 2005; Legendre & Legendre 2012) and Generalised Additive Models (GAMs) (Wood 2011), more recently implemented to explore metacommunity variation (Viana et al. 2021). In RDA, a linear model is computed for each species with a predictor matrix (e.g., environmental variables or spatial functions), and estimating the total variation explained for all the species in the group by means of a weighted mean of the adjusted R^2 of each species. But the performance of this method was recently questioned because it is based on linear regression (which is not suitable for non-linear niches, such as Gaussian responses). Therefore, other flexible models have been proposed to replace linear models in the same context. Here, we used GAMs as non-linear but gradual modelling for environmental and spatial variables, allowing them to fit the data better.

For RDAs, we transformed species presence/absence matrices with the Hellinger method. For GAMs, we used as response matrices the predicted values of Generalized Linear Latent Variable Models (GLLVM, with binomial distribution) with the lowest AIC (Niku *et al.* 2017), due to the high number of zeros in the data (which could be troublesome when performing GAMs). Prior to these analyses, environmental variables were inspected and transformed either logarithmically, with the arcsine of the square root, or squared, depending on the distribution of the raw data, in order to reduce skewness and leverage of extreme values. Due to the large number of CDOM and granulometry variables, rather than using the two whole sets of variables, they were reduced with Principal Component Analysis (PCA) and we used the first three components (which explained more than 95% of the variance). When applying GAMs, due to the small sampling size (30 tropical and 32 Mediterranean ponds), we were limited to a maximum number of three variables, to allow GAMs to generate nine splines per variable (3 variables x 9 splines = 27), maximising the response of the selected variables. As a consequence, before executing GAMs (with quasibinomial distribution), we reduced the

number of environmental predictors by using the first three principal components (PCs) in a PCA of all variables. As spatial predictors in RDAs, we used positively correlated spatial variables derived from Moran's Eigenvector Maps (MEM) analysis (Dray *et al.* 2006). In GAMs, we used spatial functions (the default splines in the mgcv R package) calculated for longitude and latitude coordinates, respectively.

We reduced the number of environmental and spatial predictors introduced in RDAs by means of forward selection, with a double stopping criterion (Blanchet et al. 2008). In GAMs, among the five available variables (three environmental PCs and spatial coordinates), we selected those three variables which contributed more to the explained variation. As a result, RDAs and GAMs provide information on the proportion of metacommunity variation explained by environmental and spatial factors together and separately, determining the pure environmental fraction (E|S; associated with environmental filtering), the pure spatial fraction (S|E; mainly associated with dispersal processes) and the overlap of environment and space (E∩S; which is often assigned to a spatialized environment). The unexplained proportion, or residuals, can be associated with ecological drift, and unmeasured environmental variables, either abiotic or biotic, or other processes such as historical contingency. In both methods (RDA and GAMs), in order to reduce spurious correlations between species distributions and spatialized environment, we used the method based on Moran Spectral Randomization (MSR; Clappe et al. 2018).

Additionally, we carried out a test of homogeneity of multivariate dispersion (betadisper; Anderson 2006) to check the environmental heterogeneity of both regions. Non-parametric comparisons of the proportions of explained variation between regions and between groups of organisms with differing dispersal abilities were carried out with Wilcoxon signed-rank test (Wilcoxon 1945), if paired samples, or with Kruskal-Wallis test if not (Hollander and Wolfe 1973). All analyses were performed with R (v4.0.2; R Core Team 2021) and R packages

vegan (Oksanen *et al.* 2019), *ade4* (Bougeard & Dray 2018), *adespatial* (Dray *et al.* 2019), *gllvm* (Niku *et al.* 2020) and *mgcv* (Wood 2017).

Results

GAMs explained higher proportions of metacommunity variation than RDAs, both for pure environmental and spatial components, as well as higher explained fractions of total variation (Figure 2). GAM was therefore more efficient in explaining metacommunity structure, even though results highly diverged between methods for particular groups of organisms. Nevertheless, considering their highest explanatory power, only results from GAMs will be shown and discussed hereafter.

The total proportion of explained variation by environmental and spatial components (E+S) (Figure 3) ranged between 0.05 for molluscs and 0.61 for amphibians in the tropical ponds (average 0.36, SD 0.16). In the Mediterranean ponds, the explained variation varied from 0.18 for sediment Archaea to 0.85 for rotifers (average 0.51, SD 0.19). The total explained variation for all groups were significantly higher in the Mediterranean metacommunity (Wilcoxon signed-rank test, $p = 0.008$). However, some major groups, in particular prokaryotic organisms and amphibians, showed a higher proportion of explained metacommunity variation in the tropical setting.

Pure environmental effects were higher than pure spatial effects in both regions (Fig. 4), although significant differences were only found in the Mediterranean ponds (Wilcoxon signed-rank test; $p = 0.262$ in tropical ponds, $p = 0.002$ in Mediterranean ponds; Figure 4). We also found higher pure environmental effects in Mediterranean than in tropical metacommunities (Fig. 3, Fig. 4) (Wilcoxon signed-rank test, $p < 0.001$), whereas the pure spatial component was not significantly different between regions (Wilcoxon signed rank test, $p = 0.658$). The total environmental component (pure and overlapped fraction) was also higher in Mediterranean ponds (Wilcoxon signed rank test, $p = 0.049$), but the overlap between spatial and

environmental components (i.e. spatialized environment) was higher in tropical ponds (Wilcoxon signed rank test, p = 0.035).

Environmental and spatial components show differences between regions when analysing active and passive dispersers separately (Figure 4). Regarding passive dispersers, we only found significant differences between regions on pure environmental effects (p = 0.005), but not in the total environmental component, pure spatial effects or total explained variation. In addition, Mediterranean passive dispersers experienced significantly stronger pure environmental than spatial effects (p = 0.005). As for active dispersers, both total explained variation and the pure environmental component were found significantly higher in Mediterranean ponds (p = 0.008 and p = 0.039, respectively). We did not find significant differences in any component between tropical active and tropical passive dispersers. Contrarily, GAMs provided a significantly higher proportion explained in active than in passive Mediterranean dispersers (Kruskal-Wallis test, p = 0.019). Purely spatial effects were not found to significantly differ in any comparison between regions or dispersal modes. In addition, results of betadisper analysis showed higher significant environmental heterogeneity in Mediterranean ponds than in the tropical region (P = 0.018; 4.889 average distance to centroid in tropical ponds, 5.747 in Mediterranean ponds).

When compared the pure environmental and spatial components for each group between biogeographic regions (Figure 5), no clear patterns emerged except for the environmental component in passive dispersers. In this case there was a seemingly concordant increase in the proportion of pure environmental effects between tropical and Mediterranean communities. This increase was observed for all groups but ostracods. Indeed, when we excluded this group, there was a positive correlation (Pearson r=0.6, p=0.02) between regional values of (E|S)/(E+S), which was not significant if we included Ostracoda. In particular, it is remarkable the case of Rotifera and Diatomea, which showed very high and very low pure environmental effects

respectively in both settings. In active dispersers, there was not such pattern for the proportion of pure environmental effects, neither in the interregional comparison of (S|E)/(E+S) for passive or active dispersers, even if the former seemed to be more spatially controlled in the tropical region than in the Mediterranean ponds, but the differences were not significant. Relationship between pure spatial and pure environmental components among biogeographic regions and organisms is shown in Appendix S1: Fig. S2.

Discussion

Overall, we found a higher proportion of explained variation in Mediterranean than in tropical pond metacommunities, considering both environmental and spatial effects and the mean values of the diverse array of analysed organisms. This is consistent with the expectation that more productive environments in the tropics might show more stochasticity than less productive ones in temperate areas, where metacommunities might be modulated more tightly by environmental determinism (Chase 2010).

Our results show that both environmental filtering and dispersal processes played an important role in the assembly of pond metacommunities in both regions, despite the abovementioned differences in explanatory power. However, pure environmental effects were stronger in Mediterranean compared to tropical pond metacommunities (Myers et al. 2013; Souffreau et al. 2015), as expected from the classical view of tropical environments as more homogeneous than temperate ones, at least in terms of climatic variation and its effects on community organization (Wallace, 1878; MacArthur 1972; Hubbell & Foster 1986). Given the higher environmental heterogeneity across the Mediterranean water bodies, also supported by our analyses, these results were therefore not unexpected (Ai et al. 2013), as larger gradients can provide environmental space for divergently specialized organisms. So, even if there are more species in the tropical ponds, given their shorter environmental gradient and reduced species sorting, we expect to find a higher degree of ecological redundancy and stochasticity in

these habitats, although unmeasured important environmental factors such as biotic interactions could be playing a hidden major role (Roslin et al. 2017; Leibold & Chase 2018).

We hypothesized spatial effects to be lower in the tropical metacommunity, due to the shift in connectivity during the rainy season, which leads to community homogenisation (Thomaz et al. 2007; Rojo et al. 2016; Brasil et al. 2020), in comparison to the reduced precipitation over Mediterranean waterbodies, which are expected to be more isolated. However, for most organisms, this pattern was not observed. This might be partly explained by the sampling time at the early stage of the hydroperiod, when connectivity is not yet at its maximum. At least during this initial period, it seems therefore that dispersal constraints are apparently equally strong for aquatic organisms in both regions. As Janzen (1967) suggested, we might also expect that orography could strongly limit dispersal due to sharp altitudinal climate shifts, more effective as barriers in the tropics than in temperate zones, as tropical species may not be adapted due to the temporal homogeneity of temperature regimes. The sampled tropical ponds are distributed in two watersheds separated by the Continental Divide, with wide differences in rainfall amount and seasonality, which can be crucial for the distributions of some species (Chandler and King 2011). This orographic barrier and abrupt climatic transition are probably showing their combined effects in the overlap between environmental and spatial components (E∩S), which was found to be higher in the tropical ponds. Anyway, the observed stronger role of species sorting in temperate ecosystems and important spatial effects in tropical habitats are compatible with previous studies on vegetation (Myers et al¸ 2013) or even bacterioplankton in shallow lakes (Souffreau et al. 2015). The unexpected low spatial effects in Mediterranean ponds might also be related with historical connectivity due to transhumance (Incagnone et al. 2014), or to intense between-ponds movements of potential vectors including birds and mammals (Frisch et al. 2007; Vanschoenwinkel et al. 2008; Valls et al. 2016 ,2017).

The intensity of the influence of spatial vs. environmental effects on metacommunity organization strongly depends on the group of organisms (De Bie et al. 2012; Heino et al. 2015), but we found it to be very variable for the same group between geographical settings, with the exception of pure environmental effects on some passively dispersing planktonic groups. A significant spatial effect was found even in the smallest studied organisms, including prokaryotes, planktonic protists and small metazoans. Although organisms smaller than 1 mm have traditionally been considered ubiquitous, with no biogeography (Finlay 2002), we found significant spatial effects in both active and small passive dispersers, including prokaryotic organisms, supporting the view that microorganisms are subjected to basically the same processes as those affecting macroorganims (Hortal 2011). Indeed, we did not find the expected differences in spatial and environmental effects between different body-sized, active or passive dispersers (De Bie et al. 2012; Padial et al. 2014) from the same region, as neither did Heino et al. (2012) or Schulz et al. (2012). The relation between dispersal ability and species sorting proposed by De Bie et al. (2012) do not hold here as a general trend. Passive and active dispersers of the same region barely differ between them (only Mediterranean active and passive dispersers with respect to total explained proportion), suggesting that spatial and environmental constraints are similar for organisms with different dispersal abilities (Schulz et al. 2012). Hydrology plays a key role in aquatic freshwater tropical ecosystems. Annual floods during the wet season drive connectivity changes, homogenizing environmental conditions and biological communities (Thomaz et al. 2007; Brasil et al. 2020). Thus, early-hydroperiod spatial patterns in small tropical organisms can be the result of historical contingencies (Castillo-Escrivà et al. 2017b), such as consecutive homogenising flooding events (or heavy rain periods) that shifted connectivity at regional scale, thus spatially structuring more connected areas in their passively dispersed organisms compared to others further away. These results suggest that space plays a more meaningful role, compared to environment, in tropical than in

Mediterranean metacommunities, maybe not only by the reduced environmental gradients but also because of dispersal limitation (Janzen 1967) or because of higher connectivity and dispersal surplus (Thomaz et al. 2007, Heino et al. 2015; Brasil et al. 2020).

Large fractions of the metacommunities variation remain however unexplained, what suggests an important role for the 'elements of chance' or randomness (Jeffries 1988). Stochastic processes and priority effects are expected to be strong at the beginning of the hydroperiod due to egg-bank hatching, before abiotic and biotic sorting of species can effectively filter local communities (Antón-Pardo et al. 2016; Castillo-Escrivà et al. 2017c; Mahaut et al. 2018). These residuals represent a higher proportion in the tropical metacommunity, probably related to the higher species richness, but also because of the lower environmental heterogeneity (Leibol and Chase 2018), as shown by the betadisper analysis. Habitat heterogeneity positively correlates with the influence of species sorting processes, and therefore we may also expect a stronger influence of ecological redundancy in the richer tropical communities, under shorter environmental gradients. Also, biotic interactions are supposed to be stronger in the tropics (Roslin et al. 2017). Unmeasured biotic variables, which have been neglected for years in metacommunity studies, can give rise to misleadingly high proportions of unexplained residual variation.

To conclude, niche and dispersal-related processes played an important role in structuring metacommunities of tropical and temperate temporary ponds. However, environmental effects dominated both settings, and especially in the most variable habitats of the Mediterranean ponds. Additionally, the type of dispersal ability of the analysed organisms (active or passive) did not seem to relate to the proportion of spatial and environmental control on their metacommunities, unlike expected from metacommunity theory and dispersal processes. We found no general pattern among taxonomic groups between regions, with very variable and idiosyncratic responses, although passive dispersers seem to be more consistent in

their response to environmental factors. Organisms are generally more environmentally than spatially controlled, except for some groups of tropical passive dispersers and a few insects in the Mediterranean setting. This is however, a snapshot study at a period of time characterised by high stochasticity. To disentangle the actual role of each process shaping metacommunities, we need more effort across time using the same methods and an assortment of taxonomic groups in different settings to quantify better not only the relative role of environmental and spatial components along a temporal series but also of time *per se* in structuring metacommunities in highly dynamic ecosystems.

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Figure legends

Figure 1: Map of the study area with the location of the ponds in each biogeographic region: tropical in Costa Rica (a) and Mediterranean in eastern Spain (b).

Figure 2: Visualization of the proportion of variation explained by space, environment, and the unexplained variation, according to the statistical method used (Generalized Linear Model or Redundancy Analysis). The variation attributable to joint environment and space ([E ∩ S]) was allocated to environment and space in proportion to their pure forms ([E|S] and [S|E]). Point sizes represent the proportion explained by joint environment and space (ranging from 0 to 0.49). Colors represent biogeographic regions (Green=tropical, yellow=Mediterranean). Triangles and circles represent active and passive dispersers, respectively.

Figure 3: Results of variation partitioning analysis for each group of organisms in tropical and Mediterranean metacommunities. The proportion of variation explained by each component is represented with a different colour. Taxa in bold type include species from the following groups enclosed in the corresponding line. Red dashed line represents average total explained variation. Number of identified species (Tropical | Mediterranean species) are shown next to each group label.

Figure 4: Proportion of variation explained by both environment and space (E+S), pure environmental component (E|S), spatialized environmental component (E∩S), and pure spatial component (S|E) for the whole dataset (a), and separately for passive (b) and active (c) dispersers. Green and yellow colours represent tropical and Mediterranean ponds, respectively.

Figure 5: Pure environmental (a) and spatial (b) effects as a proportion of the total variation explained by space and environment and their overlap (E+S), for each group of organism, and according to biogeographic region and dispersal mode. SA: sediment Archaea, WA: water Archaea, SB: sediment Bacteria, WB: water Bacteria, PH: phytoplankton, CY: Cyanobacteria, CH: Chlorophyceae, MP: mixotrophic phytoplankton, DT: Diatomea, RO: Rotifera, CR: microcrustaceans, CP: Copepoda, OS: Ostracoda, MA: macroinvertebrates, IN: Insecta, PA: Paleoptera, HE: Heteroptera, CL: Coleoptera, DI: Diptera, CH: Chironomidae, MO: Mollusca, AM: Amphibia, AV: Aves.

FIGURES

Figure 1

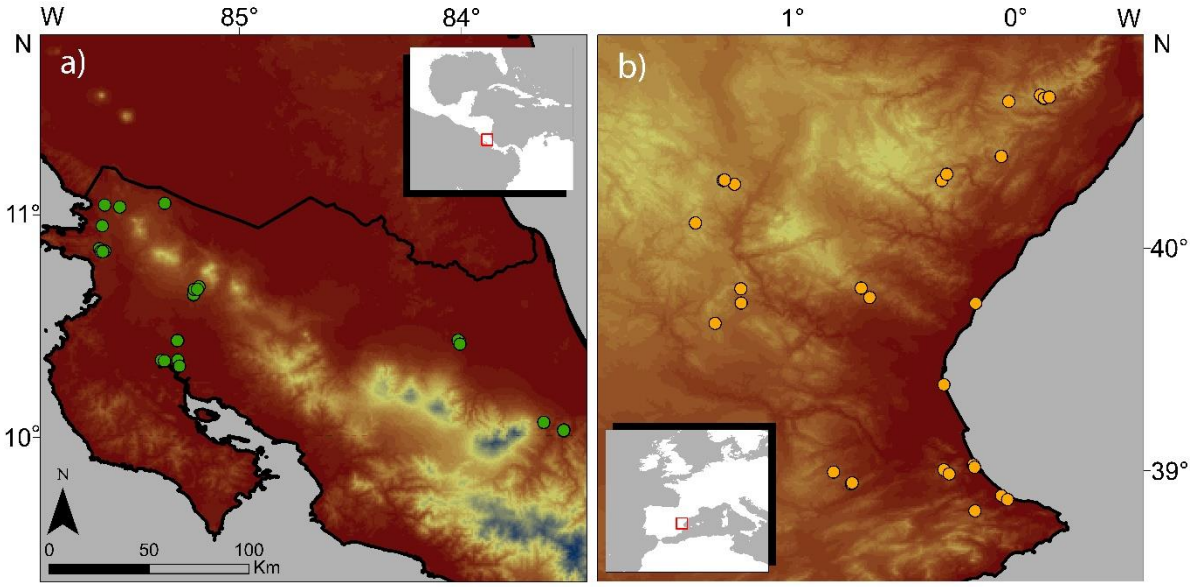

Figure 2

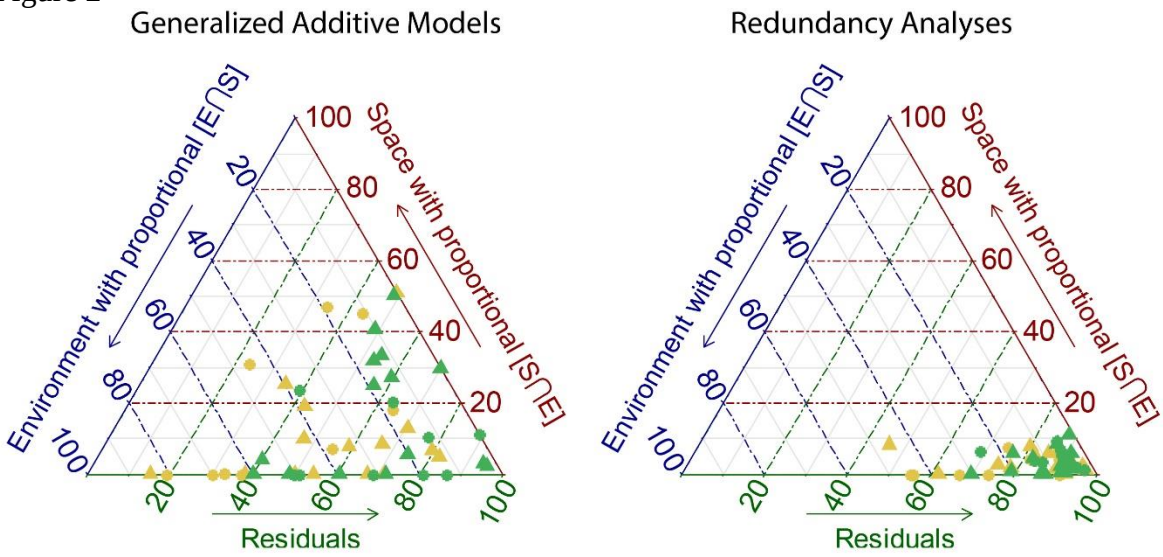
Generalized Additive Models
Redundancy Analyses
Environment with proportional [E∩S]
Space with proportional [S∩E]
Residuals
100
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Figure 3

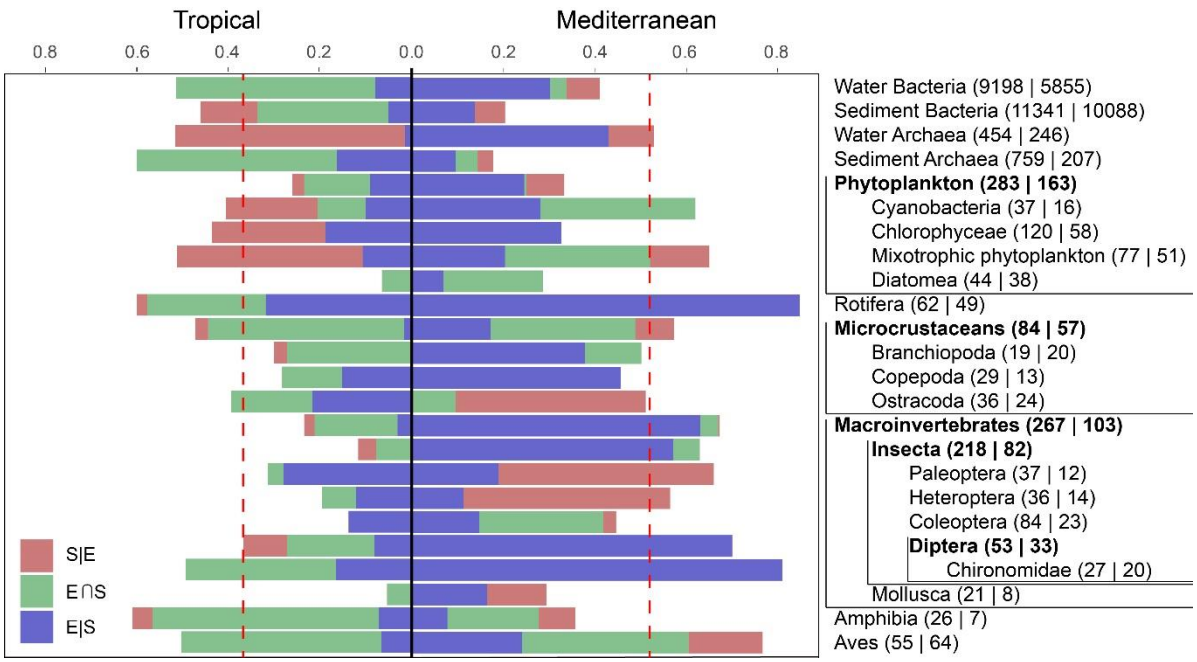
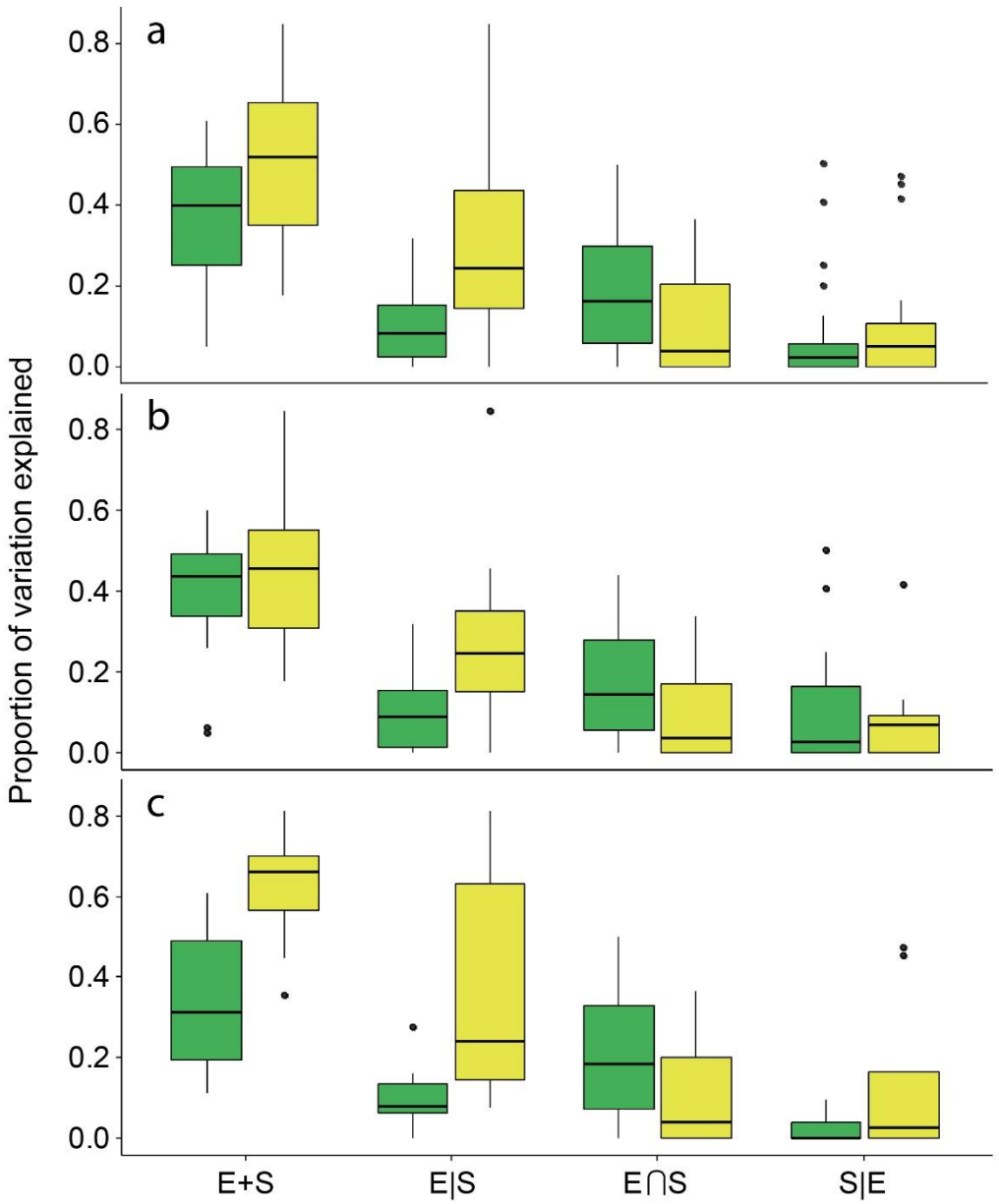

Tropical
Mediterranean
0.8
0.6
0.4
0.2
0.0
0.2
0.4
0.6
0.8
S|E
E∩S
E|S
Water Bacteria (9198 | 5855)
Sediment Bacteria (11341 | 10088)
Water Archaea (454 | 246)
Sediment Archaea (759 | 207)
Phytoplankton (283 | 163)
Cyanobacteria (37 | 16)
Chlorophyceae (120 | 58)
Mixotrophic phytoplankton (77 | 51)
Diatomea (44 | 38)
Rotifera (62 | 49)
Microcrustaceans (84 | 57)
Branchiopoda (19 | 20)
Copepoda (29 | 13)
Ostracoda (36 | 24)
Macroinvertebrates (267 | 103)
Insecta (218 | 82)
Paleoptera (37 | 12)
Heteroptera (36 | 14)
Coleoptera (84 | 23)
Diptera (53 | 33)
Chironomidae (27 | 20)
Mollusca (21 | 8)
Amphibia (26 | 7)
Aves (55 | 64)

Figure 4


a
b
c
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0.2
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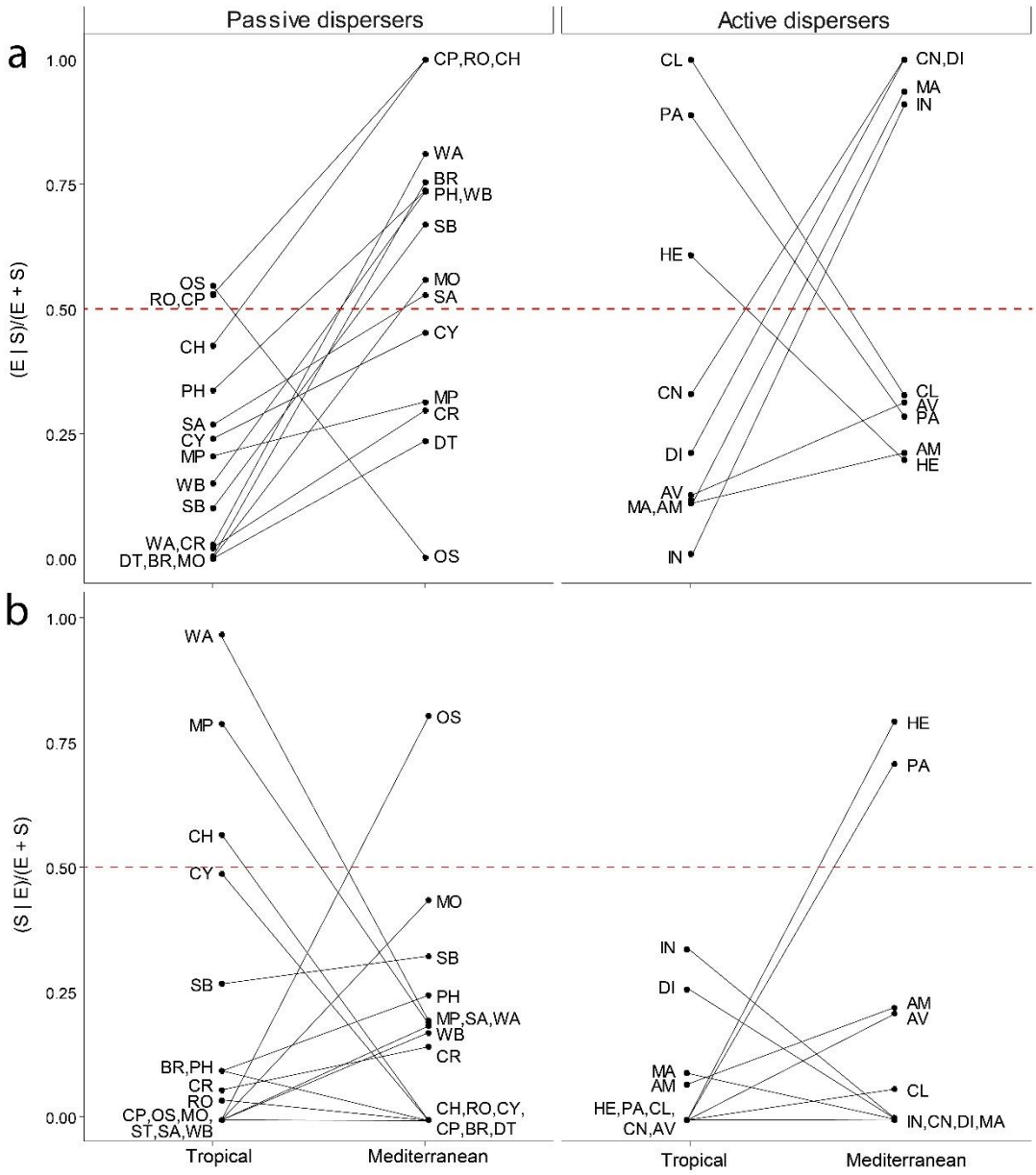
0.6
0.8
Proportion of variation explained
E+S
E|S
E∩S
S|E

Figure 5


Passive dispersers
Active dispersers
a
b
(E | S)/(E + S)
(S | E)/(E + S)
1.00
0.75
0.50
0.25
0.00
OS
RO,CP
CH
PH
SA
CY
MP
WB
SB
WA,CR
DT,BR,MO
CP,RO,CH
WA
BR
PH,WB
SB
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CN
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AV
MA,AM
IN
CN,DI
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BR,PH
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IN,CN,DI,MA
Tropical
Mediterranean
Tropical
Mediterranean