



# Interplay between productivity and regional species pool determines community assembly in aquatic microcosms

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## Abstract

The relative importance of deterministic and neutral processes in shaping assembly of communities remains controversial, partly due to inconsistencies between theoretical, empirical, and experimental studies. We investigate the interplay between local (productivity) and regional (size of species pool) assembly mechanisms in communities of phytoplankton and zooplankton in 72 experimental microcosms. Local environmental conditions were manipulated by varying the level of nutrients in the water (ambient, low, high). The size of regional species pool colonizing each microcosm was manipulated by mixing phytoplankton and zooplankton species from different numbers of source ponds ( $n = 2, 4, 8$  and  $16$ ). Our results show that local communities assembled differently depending on the numbers of sources available for colonization. Microcosms with larger species pools supported greater numbers of species. In contrast, the effects of productivity led to different results across trophic groups. Phytoplankton communities were, on average, more diverse on more productive treatments, while zooplankton communities were more diverse under less productive treatments. Phytoplankton and zooplankton communities responded to both sources of variation, although the size of species pool was a better predictor of communities' composition than the local effects of productivity. These results reinforce the view that community assembly is influenced by the interplay of both local and regional drivers but that the relative importance of these factors varies with trophic groups.

**Keywords** Deterministic processes · Phytoplankton · Stochastic processes · Trophic group · Zooplankton

## Introduction

Multiple processes operate simultaneously to influence patterns of species diversity at different scales (Ricklefs 1987; Chase 2003; Cadotte 2006; Östman et al. 2006; Márquez and Kolasa 2013; Cornell and Harrison 2014). Community assembly—the construction and maintenance of local communities through sequential arrival of potential colonists from an external species pool (Warren et al. 2003; Fukami

2004)—provides a conceptual foundation for understanding the processes that determine which species and how many can co-occur in any particular locality (Chase 2003). Conceptually, the assembly of a local community can be visualised as species passing through a series of filters, which represent historical (e.g., dispersal, speciation) and ecological (e.g., competition, predation, disturbance, abiotic environmental factors) constraints in the arrival and survival of organisms at a certain locality (Zobel 1997; Lawton 1999; Hillebrand and Blenckner 2002). Much of the discussion on community assembly has focused on the relative importance of environmental determinism versus stochastic processes (e.g., Strong et al. 1984; Diamond and Case 1986; Hubbell 2001). There is a growing evidence that both deterministic processes, such as environmental filtering, biotic interactions, and interspecific trade-offs, and stochastic processes, such as dispersal limitation, colonization, extinction, and speciation, simultaneously affect the diversity and composition of local communities (Leibold et al. 2004; Cottenie 2005; Gravel et al. 2006; Chase and Myers 2011; Márquez and Kolasa 2013).

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Although the assembly of communities from the available species pool—the set of species that could disperse and potentially colonize and establish within a community (Lessard et al. 2012)—is likely to be outcome of both stochastic and deterministic processes (Ricklefs 1987; Chase 2003; Leibold et al. 2004; Chase and Myers 2011; Márquez and Kolasa 2013), the relative importance of deterministic versus stochastic factors on community assembly remains undetermined in a general sense (Chase 2007, 2010; Chase et al. 2009; Chase and Myers 2011), since they act on different temporal and spatial scales (Hillebrand and Blenckner 2002). If communities are strongly controlled by deterministic processes, assembling under similar environmental regimes should follow a common path and converge in composition and abundance (Chase 2003, 2007; Chase et al. 2009; Márquez and Kolasa 2013). If true, local communities under particular environmental constraints should be fairly predictable (Chase 2007). In contrast, if regional processes are more important, local community structure should appear to be shaped predominantly by stochastic processes, such as immigration, colonization and extinction, all of which depend on the processes operating at much coarser scales of resolution and extent; and community composition should be unpredictable relative to the species pool (Chase 2007).

One key issue hindering progress in understanding the relative contributions of deterministic and stochastic processes on community assembly is the nature of existing evidence, mainly coming from observational studies in natural communities (e.g., Hill et al. 2017; Matias et al. 2017). In such studies, community assembly patterns can be confounded by the assembly history of the communities, i.e., the sequence and timing in which species join the ecological community (Chase 2003; Fukami et al. 2010). We addressed these issues by using a microcosm experimental system conducted with freshwater ponds at regional scale. Microcosms, small experimental enclosures intended to simulate natural communities (Stewart et al. 2013; Altermatt et al. 2015), are particularly useful as they allow studying whole ecosystems, from bacteria to animals (Altermatt et al. 2015). Advantages of microcosms include ease of replication and repetition, precise control over environmental variables, and the flexibility to manipulate the parameters and treatments under investigation (Jessup et al. 2004; Srivastava et al. 2004; Stewart et al. 2013; Altermatt et al. 2015), which enables the detection of very subtle effects with reasonable power (Srivastava et al. 2004). Experimental microcosms have been used extensively as model systems to test a variety of hypothesis about species diversity and habitat disturbance, species diversity and productivity (e.g., Kassen et al. 2000; Matias et al. 2013), habitat connectivity (e.g., Forbes and Chase 2002), trade-offs in community ecology (e.g., Kneitel and Chase 2004; Livingston et al. 2012), metacommunity

richness (e.g., Cadotte 2006), species interactions (e.g., Petchey 2000), climate change (e.g., Woodward et al. 2010).

Most experimental studies have investigated either local or regional processes separately (but see Kneitel and Chase 2004), often revealing inconsistent responses to similar processes (Östman et al. 2006). Here, we examined how community assembly (phytoplankton and zooplankton) was affected by initial community composition (as a function of the size of the regional species pool) and productivity. Productivity is often considered a primary determinant of species composition, coexistence and diversity (Dodson et al. 2000; Chase 2003). It is suggested that increases in productivity would be analogous to increases in area thereby resulting in increases in species richness and abundance (e.g., Wright 1983), which means that more productive sites support greater numbers of species (Srivastava and Lawton 1998). It has been also argued that variations in size of the species pools influence greatly community composition, implicating factors that vary at broad spatial scales and trickle down to local scales (Ricklefs 1987; Kraft et al. 2011; Karger et al. 2015). Here we tested the hypothesis that (1) local communities with higher levels of productivity should support more diverse communities, suggesting that local processes are more important than regional processes in the assembly of communities; and (2) local communities exposed to larger pools of potential colonists should have greater numbers of species, suggesting that regional processes are more important than local processes in the assembly of communities.

## Methods

### Experimental setup

The experiment was setup at the “El Ventorrillo” Biological Station (Madrid, Spain), managed by the National Museum of Natural Science (CSIC) in Madrid. We used two twin walk-in climatic chambers (Ibercex V-450-D) with ventilation to establish 72 microcosms (10 L white plastic tanks; 30 cm high x 30 cm diameter). Within each chamber, microcosms were setup uncovered in groups of 12, each group with dedicated light sources. All microcosms were exposed to a photoperiod of 12 h/12 h (light/dark) and to a constant air temperature of 15 °C. Temperature was checked using TidbitV2 waterproof temperature data loggers (Onset HOBO). Each microcosm was initiated with approximately 500 g of topsoil (approximately 5% of total volume) collected locally and filled with well water with nutrient concentrations below the detection limits. No additional water was added during the experiment, since loss of water through evaporation was minimal.

## Manipulation of productivity

We manipulated the productivity of the microcosms by varying the level of nutrients, nitrogen (N) and phosphorous (P), according to nutrient levels found in natural ponds in the sampling region: ambient (no nutrients added), low ( $N = 0.55 \text{ mg L}^{-1}$ ;  $P = 0.02 \text{ } \mu\text{g L}^{-1}$ ) and high ( $N = 1.2 \text{ mg L}^{-1}$ ;  $P = 0.1 \text{ } \mu\text{g/L}$ ). The level of nutrients was manipulated using Seachem Flourish Nitrogen<sup>TM</sup> and Seachem Flourish Phosphorous<sup>TM</sup>. Seachem Flourish Nitrogen<sup>TM</sup> provides nitrogen in both nitrate ( $\text{NO}_3^-$ ) and ammonium form ( $\text{NH}_4^+$ ), and Seachem Flourish Phosphorous<sup>TM</sup> provides phosphorous in potassium phosphate form ( $\text{K}_3\text{PO}_4$ ). After the manipulation of productivity, the nutrient levels were measured once at the beginning of the experiment using Sera® Nitrat-Test and Sera® Phosphat-Test.

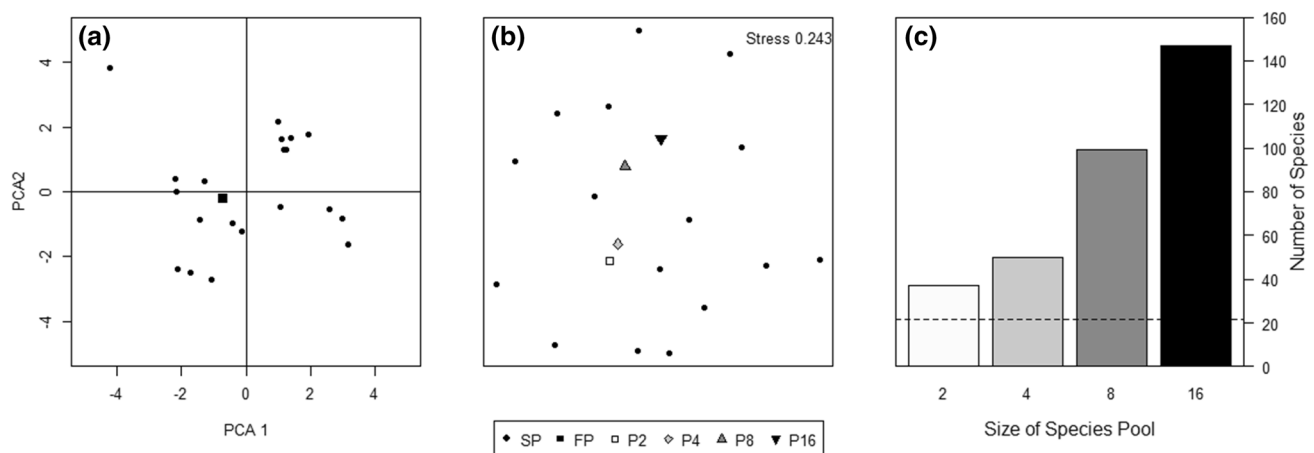
## Manipulation of species pools

Studies examining the relationship between the size of species pool and local species richness have manipulated the species pool by combining species obtained from different local-scale surveys (e.g., Chase and Myers 2011; Kraft et al. 2011), by using all species known to occur in a given region (e.g., White and Hurlbert 2010), or by a combination of both approaches (e.g., Ricklefs 2000). Here, we manipulated the size of species pool colonizing microcosms by mixing water samples from different source ponds ( $n = 2, 4, 8$  and 16 source ponds) with increasing environmental variability.

We surveyed a total of 24 freshwater bodies in the region north to Madrid, from which we chose 16 source ponds according to accessibility and environmental conditions

(see Online Resource 1 in Electronic Supplementary Material). Five horizontal hauls (1-m-long) were carried out with plankton nets (25  $\mu\text{m}$  mesh size) to collect phytoplankton and zooplankton samples; additionally, we collected 5 L of water in each location. Environmental parameters, such as pH, temperature, conductivity, and dissolved oxygen, were measured in each pond using a multiparametric probe (Hach), turbidity and chlorophyll *a* concentration were measured using a handheld fluorometer (AquaFluor<sup>TM</sup>, Turner Designs). Water samples were collected on the day of the experiment and kept inside the climatic chambers (see above) upon arrival to the laboratory. We mixed the different water samples into planned combinations just before the inoculation of the microcosm. Based on the environmental variables (see Online Resource 2 in Electronic Supplementary Material), we analysed the variability between source ponds using a Principal Components Analysis (Fig. 1 a) and selected the source pond that had the most “average environmental conditions” as our focal pond. We then calculated the environmental distances from the focal pond to all other ponds and ranked them. The different source ponds were assigned to each species pool based on their distance ranking to ensure that smaller species pools include closely related ponds; conversely, larger species pools included ponds with increasing environmental dissimilarity (Fig. 1 a, b).

Each microcosm was inoculated once at the beginning of the experiment with 200 mL of the corresponding simulated species pool (2, 4, 8 and 16 ponds). The final combinations ensured that each source pond had the same relative contribution within each species pool; meaning, for species pool 2, 4, 8 and 16 each source pond contributed with 100 mL, 50 mL, 25 mL, and 12.5 mL, respectively. The inoculum



**Fig. 1** Decomposing regional species pools. **a** Environmental distances calculated using principal components analysis (PCA) of all 16 source ponds using all environmental variables. Symbols indicate source ponds; square symbol indicates the focal pond (source pond that had the closest to “average environmental conditions”); **b** NMDS

ordinations based on the combination of phytoplankton and zooplankton communities. *SP* source ponds, *FP* focal pond, *P2* species pool size 2, *P8* species pool size 8, *P16* species pool size 16. **c** Number of species in each species pool. Dashed line indicates the mean number of species present in the source ponds

included a range of producers, i.e. phytoplankton (e.g., green microalgae, diatoms, cyanobacteria, etc.), and consumers. i.e. zooplankton (e.g., rotifers and microcrustaceans) to the microcosms. The number of species varied between the manipulated species pools; species pools with larger size had more species (P2=37—Phyto=23, Zoo=14; P4=50—Phyto=35, Zoo=15; P8=99—Phyto=74, Zoo=25; and, P16=147—Phyto=115, Zoo=32; Fig. 1c). Phytoplankton communities were dominated by green microalgae, which presented higher number of taxa (Chlorophyta; P2=12, P4=16, P8=39, P16=50) and by diatoms (Bacillariophyta; P2=6, P4=10, P8=15, P16=39). Other groups were also represented, such as blue-green algae (Cyanobacteria; P2=2, P4=4, P8=8, P16=9), cryptophytes (Cryptophyta; P2=1, P4=2, P8=4, P16=8), and dinoflagellates (Miozoa; P2=1, P4=2, P8=7, P16=7). As expected, rotifers were the group with more identified taxa on zooplankton communities (Rotifera; P2=8, P4=9, P8=12, P16=18), followed by microcrustaceans (Cladocera; P2=2, P4=2, P8=6, P16=7; and, Copepoda; P2=3, P4=3, P8=6, P16=6). The number of species present in the source ponds ranged between 9 and 42 (mean=21.81 species per pond). At the end of the experiment, the number of species present in the microcosms ranged between 12 and 41, with a mean number of 20.36 species per microcosm, which indicates that the level of species diversity in each microcosm was analogous to the diversity found in natural source ponds.

### Sampling

At the end of the experiment, 60 days after the inoculation, aquatic communities were sampled from each microcosm. 0.2 L of water was collected and preserved with lugol solution (5%) for phytoplankton, and 2 L were filtered through a 53 µm mesh and preserved with ethanol 96% (sample final concentration approximately 50%) for zooplankton. Identification and enumeration of all collected specimens were done using an optical microscope (Olympus BX43), and the identification was made at the lowest taxonomic level possible. The abundances were calculated as number of cells per litre (cell L<sup>-1</sup>) for phytoplankton and number of individuals per litre (individuals L<sup>-1</sup>) for zooplankton.

### Data analysis

We tested for differences in community composition within each trophic group by comparing composition and abundance of species along three levels of productivity and different sizes of species pool. We tested for differences in community composition (number of species) using two-way ANOVA, ‘aov’ function in R package stats (R Core Team 2016), with ‘productivity’ and ‘size of species pool’ as main factors.

Differences in community abundance were tested using PERMANOVA, ‘adonis’ function in R package vegan (Oksanen et al. 2016), with Bray-Curtis dissimilarity measures and productivity’ and ‘size of species pool’ as main factors. Phytoplankton and zooplankton total abundances were log (x + 1) transformed prior data analyses. A *posteriori* pairwise comparisons were undertaken to test for differences between productivity groups and between species pool groups, using the function ‘permanova’ in R package vegan (Oksanen et al. 2016).

Strong positive relationships between algal biomass and nutrient loading have been observed in most lakes (Smith et al. 1998; Bergström et al. 2005), thus phytoplankton biomass can be used as a *proxy* of the system productivity. Phytoplankton biomass (mg L<sup>-1</sup>) was estimated based on measurements of the size of species and the adaptation of cells’ shapes to geometrical shapes according to Sun and Liu (2003) and Olenina et al. (2006). The individual biovolumes (µm<sup>3</sup> × 10<sup>-9</sup>) of different species were multiplied by each species’ abundance (cell L<sup>-1</sup>). From the biovolume data, the biomass (wet weight) was derived by a rough assumption of a plasma density of 1 g cm<sup>-3</sup>:

$$\begin{aligned} 1 \text{ mm}^3 \text{L}^{-1}(\text{biovolume}) &= 1 \text{ cm}^3 \text{m}^{-3}(\text{biovolume}) \\ &= 1 \text{ mg L}^{-1}(\text{wet weight}) : \\ 1 \text{ mm}^3 \text{m}^{-3}(\text{biovolume}) &= 10^6 \mu\text{m}^3 \text{L}^{-1}(\text{biovolume}) \\ &= 1 \mu\text{g L}^{-1}(\text{wet weight}) \\ &= 0.001 \text{ mg L}^{-1}. \end{aligned}$$

We tested for differences in phytoplankton biomass using two-way ANOVA with ‘productivity’ and ‘size of species pool’ as main factors. As expected, phytoplankton responded strongly to productivity (F=7.890, P=0.008; Table 1), showing an increase in biomass production with high productivity (see Online Resource 3 in Electronic Supplementary Material).

Finally, we tested the effects of the productivity and size of species pool on community variability using Jaccard, calculated with presence-absence data and Bray-Curtis dissimilarities, calculated using log (x + 1) transformed species abundance data. We used ‘metaMDS’ function in the R package vegan to perform non-metric multidimensional scaling (NMDS) on distance matrixes calculated using ‘vegdist’ function in R package vegan (Oksanen et al. 2016).

To identify the relative contribution of local and regional processes to compositional variation in phytoplankton and zooplankton communities, we partitioned the variation in community composition matrices of each trophic group with respect to matrices of productivity or size of species pool using the function “varpart” in R package vegan (Anderson

**Table 1** Variation in community composition and phytoplankton biomass using two-way ANOVA with “size of species pool” and “productivity” as main factors

Variable			Df	Mean Sq	F value	P
Phytoplankton	Number of species	Productivity = P	2	109.60	6.218	0.0035**
		Size of species pool = SP	3	98.94	5.614	0.0019**
		P × SP	6	21.47	1.218	0.3098
		Residuals	60	17.62		
		Tukey HSD P: Amb = Low < High; SP: 2 = 4 = 8 = 16				
	Biomass	Productivity = P	2	20,921	5.692	0.0052**
		Size of species pool = SP	1	55,473	15.092	0.0002***
		P × SP	2	5789	1.575	0.2147
		Residuals	66	3676		
		Tukey HSD P: Amb = Low < High; SP: 2 = 4 = 8 = 16				
Zooplankton	Number of species	Productivity = P	2	11.85	3.485	0.0364*
		Size of species pool = SP	1	25.89	7.616	0.0075**
		P × SP	2	4.03	1.184	0.3125
		Residuals	66	3.40		
		Tukey HSD P: Amb = Low = High; SP: 2 = 4 = 8 = 16				

Pairwise comparisons, done using the function ‘TukeyHSD’ in R package stats (R core Team 2014), showed significant differences only between productivity levels for phytoplankton at  $P < 0.05$ . Significance levels: \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$

et al. 2011; Chase et al. 2011). We used the distance-based Redundancy Analysis (dbRDA) outputs adjusted R-squared values that correspond to unbiased estimates of the proportion of variation explained by each of the three fractions: productivity, size of species pool, and unexplained variance (Oksanen et al. 2016).

## Results

Overall, green microalgae (Chlorophyta = 41 taxa) dominated the phytoplankton communities, both in number of taxa and abundances, followed by diatoms (Bacillariophyta = 20 taxa) and blue-green microalgae (Cyanobacteria = 5 taxa). Zooplankton communities were dominated by rotifers (Rotifera = 22 taxa), copepods and cladocerans were present but in lower numbers and abundances (Copepoda = 10 taxa, Cladocera = 5 taxa). The numbers of species and numbers of individuals found in local communities differed depending on the numbers of sources of colonists (i.e., size of species pool), and depending on the productivity level (ambient, low or high). Local communities had overall more species (Fig. 2a, c) and greater abundances (Fig. 2b, c) when they were colonized from a greater number of source pools.

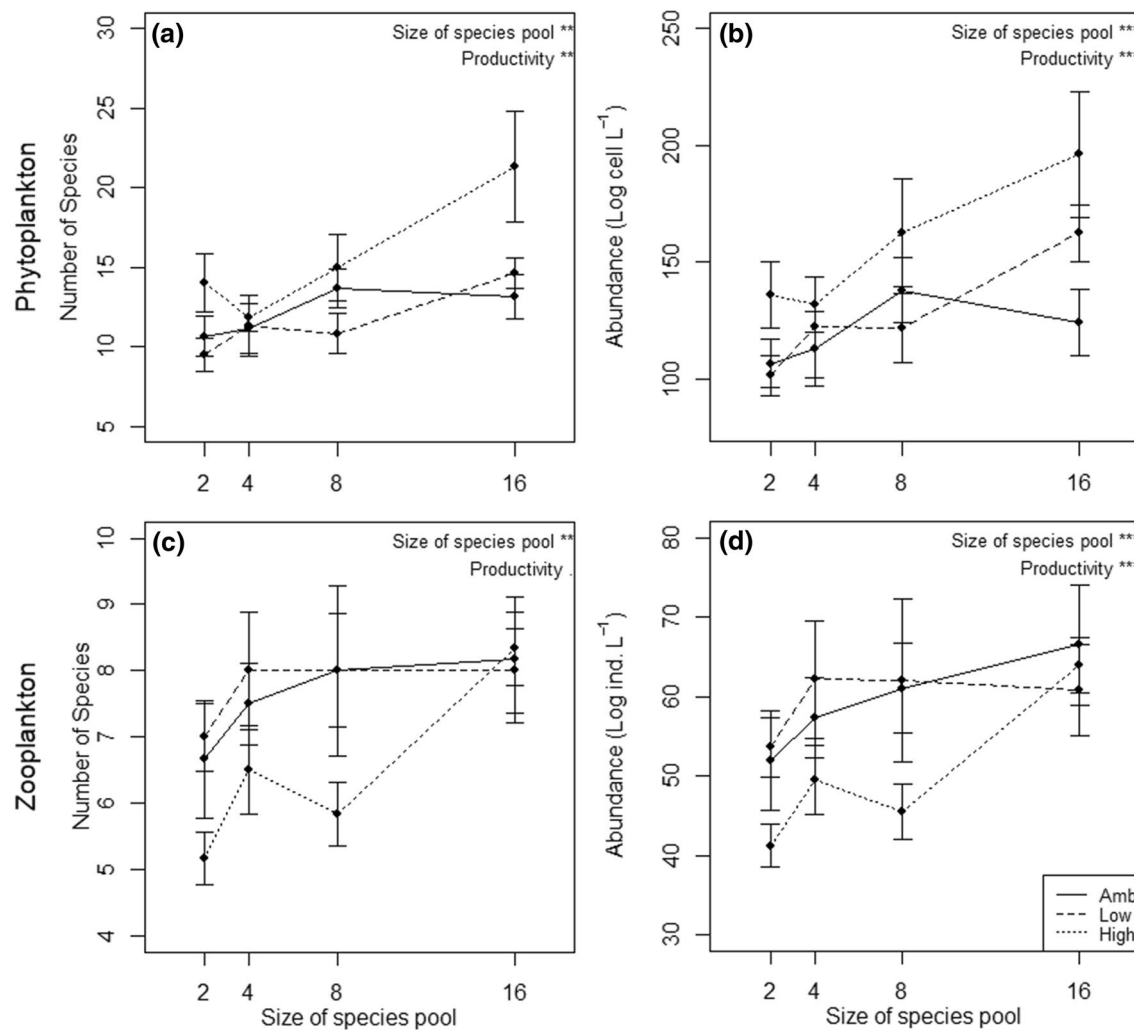
The size of the species pool had a strong effect on the number of species of phytoplankton ( $F = 5.6$ ,  $P < 0.05$ ; Table 1) and zooplankton ( $F = 7.6$ ,  $P < 0.05$ ), as well as on their abundances regardless of the measure of dissimilarity used (Phytoplankton—Bray–Curtis:  $F = 4.7537$ ,  $P < 0.005$ ; Jaccard:  $F = 3.2$ ,  $P < 0.005$ ; Zooplankton—Bray–Curtis:

$F = 5.0$ ,  $P < 0.005$ ; Jaccard:  $F = 5.2$ ,  $P < 0.005$ ; Table 2). Phytoplankton communities showed also more species ( $F = 6.2$ ,  $P < 0.05$ ) and higher abundances (Bray–Curtis:  $F = 3.5$ ,  $P < 0.005$ ; Jaccard:  $F = 2.7$ ,  $P < 0.005$ ; Table 2) on the more productive treatments. However, zooplankton had a reverse pattern (Fig. 2c, d) being, on average, more species rich ( $F = 3.5$ ,  $P < 0.05$ ; Table 1) and abundant (Bray–Curtis:  $F = 4.3$ ,  $P < 0.005$ ; Jaccard:  $F = 3.6$ ,  $P < 0.005$ ; Table 2) under less productive treatments (ambient and low). A posteriori pairwise comparison, using Tukey’s test, showed no significant differences between species pool levels (at  $P < 0.05$ ) for both communities’ composition. However, it showed that phytoplankton composition from microcosms with higher productivity was significantly different from those in less productive sites (Table 1). Finally, it showed no significant differences between treatments with different sizes of species pool and different levels of productivity ( $P < 0.05$ ) for both phytoplankton and zooplankton abundances.

The species pool size and productivity affected phytoplankton and zooplankton communities’ variability in different ways. There was a significant correlation in the variation of composition between the two trophic groups (Jaccard dissimilarities; Pearson  $r = 0.21$ ;  $P < 0.001$ ; see Online Resource 4 in Electronic Supplementary Material). Similarly, when we compared communities taking in account their relative abundances (Bray–Curtis dissimilarities) within each trophic level, we also found significant but weaker correlation between the two groups (Pearson  $r = 0.09$ ;  $P < 0.001$ ).

Both local and regional processes explained small amounts of compositional variation in phytoplankton and





**Fig. 2** Effects of species pool size and productivity on local communities. Numbers of species of **a** phytoplankton and **c** zooplankton; abundances of **b** phytoplankton and **d** zooplankton. Lines indicate the

mean values, and error bars indicate standard error. Significance levels: \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$

zooplankton communities (Fig. 3). However, size of species pool had a slightly higher contribution to compositional variation in phytoplankton and zooplankton communities (3.89%  $P < 0.01$ , and 11.18%  $P < 0.001$ , respectively; Fig. 3) then productivity (2.79%, 0.001 and 4.73%  $P < 0.001$  respectively).

## Discussion

Changes in species richness and abundances of species were best explained by an interaction between local productivity and the size of regional species pool in our microcosm experiment. Local communities assembled differently depending on the numbers of sources available for colonization but, overall, microcosms with larger species pools

supported greater numbers of species (which supports hypothesis two). However, each trophic level responded differently to productivity: phytoplankton communities were, on average, more diverse on more productive treatments, while zooplankton communities were more diverse under less productive treatments (supporting partially hypothesis one). Several studies have reported divergent responses by different trophic groups to different drivers and processes influencing communities' assembly (e.g., Declerck et al. 2007; Korhonen et al. 2011; Matias et al. 2017). For example, Matias et al. (2017) found that producers (phytoplankton and benthic diatoms) responded more to changes in the environment (mainly to phosphorous concentrations), while zooplankton did not show correlations with the environment but it did covary consistently with pairwise geographical distances between lakes.

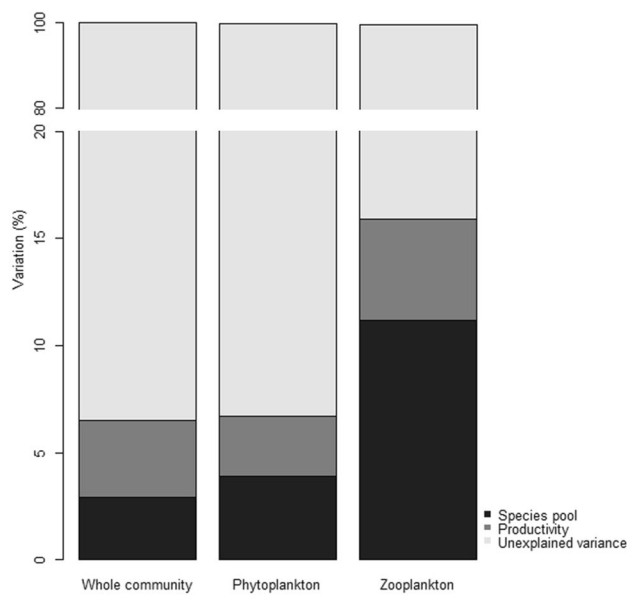
**Table 2** Permutational multivariate analysis of variance (PERMANOVA) among microcosms for phytoplankton and zooplankton abundances, using Bray–Curtis log (x + 1) transformed and Jaccard dissimilarities

			Df	MeanSqs	F. model	R <sup>2</sup>	Pr (> F)
Phytoplankton	Bray–Curtis log (x + 1) trans- formed	Productivity = P	2	0.21	3.548	0.0847	0.0001***
		Size of species pool = SP	1	0.28	4.754	0.0567	0.0003***
		P × SP	2	0.17	2.964	0.0708	0.0003***
		Residuals	66	0.06		0.7878	
		Total	71			1	
	Permutest P: Amb = Low = High; SP: 2 = 4 = 8 = 16						
	Jaccard	Productivity = P	2	0.70	2.706	0.0684	0.0001***
		Size of species pool = SP	1	0.81	3.160	0.039	0.0006***
		P × SP	2	0.60	2.295	0.0580	0.0012**
		Residuals	66	0.26		0.8337	
		Total	71			1	
	Permutest P: Amb = Low = High; SP: 2 = 4 = 8 = 16						
Zooplankton	Bray–Curtis log (x + 1) trans- formed	Size of species pool = SP	1	0.78	4.963	0.0617	0.0008***
		Productivity = P	2	0.67	4.254	0.1057	0.0001***
		P × SP	2	0.08	0.517	0.0128	0.8568
		Residuals	66	0.16		0.8198	
		Total	71			1	
	Permutest P: Amb = Low = High; SP: 2 = 4 = 8 = 16						
	Jaccard	Size of species pool = SP	1	1.34	5.222	0.0640	0.0002***
		Productivity = P	2	0.92	3.587	0.0879	0.0002***
		P × SP	2	0.42	1.627	0.0398	0.0572
		Residuals	66	0.26		0.8084	
		Total	71			1	
	Permutest P: Amb = Low = High; SP: 2 = 4 = 8 = 16						

A significant PERMANOVA indicates that the multivariate composition of the community differs between species pool size and/or productivity (or their interaction). Pairwise comparisons calculated using 'permat-est' in R package vegan (Oksanen et al. 2016), showed no significant differences between species pool levels and between productivity levels at  $P < 0.05$ . Significance levels: \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $P < 0.05$

Productivity is often considered a primary determinant of species composition, coexistence and diversity (Dodson et al. 2000; Chase 2003). It is argued that increases in productivity would be analogous to increases in area thereby resulting in proportional increases in total number of species and numbers of individuals (e.g., Wright 1983). The productivity begets diversity hypothesis proposes that more productive sites support greater numbers of species because they contain more individuals and thus have faster population recovery times from disturbance (Srivastava and Lawton 1998). In our experiment, this was true for phytoplankton communities; however, zooplankton communities showed lower diversity in more productive microcosms. The diversity-productivity relationship can be attributed to habitat variability, predator–prey dynamics, relative rates of supply of alternative resources, the outcome of competitive interactions (e.g., Leibold 1999), that we did not account for, and several other possible mechanisms that remain to be identified (Barnett and Beisner 2007). Earlier works (e.g., Dodson et al. 2000; Hessen et al. 2006; Ptacnik et al. 2010) have shown that there may be predictable large-scale patterns in plankton richness mediated by productivity. However, the

diversity-productivity relationship is often studied using small-scale field experiments, or studies are conducted in laboratory microcosms and, at smaller scales it seems that there is no obvious pattern. Several studies (e.g., Chase and Leibold 2002; Hoffmann and Dodson 2005; Declerck et al. 2007; Korhonen et al. 2011) showed that productivity-diversity relationship presents variable patterns in different trophic groups ranging from positive linear and unimodal to negative linear relationships. Using natural systems, Hoffmann and Dodson (2005) found that zooplankton diversity was positive linear for pristine lakes (typically with low productivity) and negative linear for developed lakes (typically with high productivity); and, Korhonen et al. (2011) observed productivity-zooplankton diversity relationship ranging from positive linear and unimodal to negative linear. In an outdoor mesocosms experiment, Declerck et al. (2007) also showed a linear decrease in zooplankton diversity with increasing productivity. Caution should be used when comparing results between local and regional mechanisms of community assembly in studies of differing spatial scales (Heino et al. 2012; Hill et al. 2017). This is because environmental controls on communities are likely to be dominant



**Fig. 3** Partitioning of the variation in community structure in response to size of species pool or productivity across two trophic groups. Variation is partitioned in three fractions: size of species pool (black), productivity (dark grey) and unexplained variance (light grey)

at smaller spatial scales compared to larger regions, while regional mechanisms will have a greater influence on community structure at larger spatial scales (Heino et al. 2015a). A few mechanisms for diversity decline along a productivity gradient have been proposed: resource heterogeneity, competitive displacement, and habitat quality (Kassen et al. 2000; Declerck et al. 2007). The small dimensions of our containers make it improbable that changes in resources heterogeneity influenced diversity, but we lack appropriate data to confirm this assertion. Competitive displacement of a consumer species by one or a small set of dominant species is often referred to as a possible explanation for a negative response of consumer diversity at the high end of a productivity gradient (e.g., Declerck et al. 2007). However, in our experiment productivity was not associated with the dominance of a particular species in microcosms with higher levels of productivity. One explanation for the lower zooplankton diversity in high productivity treatments might be explained by changes in phytoplankton community. There was a significant correlation between both trophic groups which may indicate that changes in phytoplankton community could be affecting zooplankton communities. Algal bloom events develop often with increases on nutrient levels, which can interrupt the flow of energy through trophic levels. Cyanobacteria can reach very high abundances in higher levels of nutrients, and they are more capable of producing secondary metabolites (e.g., toxins), structural or other defences (e.g., mucus) that render them less palatable

to zooplankton (Mitra and Flynn 2006). However, our microcosms were dominated by small cells or colonies of green microalgae and diatoms, which are generally more palatable to zooplankton (Tönno et al. 2016). Lower zooplankton diversity and abundance in highly productive sites may be also due to the fact that high productivity may lead to a deterioration of abiotic conditions (Hoffmann and Dodson 2005), and the decreased zooplankton diversity with productivity may reflect the distribution of fundamental niches in the regional species pool, with fewer species adapted to conditions associated with high productivity. Also, the productivity range we used in this experiment was not very high. In other nutrient enrichment experiments (e.g., Wang et al. 2016) the levels of nutrients used are much higher (around  $30\times$  higher) than the ones we used. However, nutrient levels in our low and high productivity treatments were chosen to represent levels close to low and high levels found in natural ponds in the region.

It has been proposed that community composition is also strongly influenced by differences in size of the species pools (the number of species in the species pool) and hence by factors that vary at broad spatial scales and trickle down to local scales (Ricklefs 1987; Kraft et al. 2011; Karger et al. 2015). The species pool concept holds that local variation in community patterns is dependent on the availability of species (Zobel 2016) and, in our study, as expected, microcosms with larger species pools presented, on average, larger numbers of species. While there might not be one single acceptable definition of species pool, it should be defined explicitly rather than arbitrarily (Lessard et al. 2016). As mentioned before, studies have defined their species pools by pooling species from local-scale surveys, by using all species known in the region, or by a combination of both (Ricklefs 2000; White and Hurlbert 2010; Chase and Myers 2011; Kraft et al. 2011; Karger et al. 2015). Here, we manipulated the size of the species pools based on environmental affinities, the different source ponds were assigned to each species pool based on their environmental distance ranking. This approach ensures that smaller species pools include closely related ponds; while larger species pools included ponds with increasing environmental dissimilarity. We followed this environmental distance approach because the altitudinal gradient in the sampling area (region north of Madrid; Online Resource 1 in Electronic Supplementary Material) is very important. But by explicitly accounting for the influence of environmental filtering in the construction of our species pools, we could be strengthening the inference of local processes in shaping the communities' structure and composition (Zobel 1997; Lessard et al. 2016). However, it should be acknowledged that a combination of mass effects, dispersal limitation and species sorting (local environmental variables) has been reported to most effectively explain variation among freshwater communities (Cottenie 2005; Hill



et al. 2017). An ideal approach would allow for comparing different types of filters, e.g., environmental (as we used here) and dispersal filters, on the same scale, by separating the spatial, environmental and dispersal components of the species pool. Hill et al. 2017 found that, when the entire community was considered, local environmental variables were dominant drivers of variation; however, their results also clearly indicated that spatial factors should not be overlooked and can, individually or in combination with local environmental variables, have a significant effect in diversity. The purely environmental component could be separated from the geographical component by manipulating dispersal, i.e., by manipulating the contribution of the inoculum depending on their origin. A pool could be defined on the basis of distance (as a proxy for dispersal probability), where only species within a certain distance would be included, and the filter would be the actual distance. For example, instead of dividing the inoculum from the 16 source ponds in equal parts, as we did in this experiment, we could have made the inoculum from the closer source ponds more concentrated and dilute the ones from the most distant source ponds, which may be closer to reality. The role of species pools in generating local diversity and compositional patterns is widely accepted in theory, but empirical investigation remains quite limited (Zobel 2016). One of the main difficulties in explaining community patterns has been our weak ability to apply the species pool concept to investigations of real communities. Consequently, the concept has not had as great an impact as it might on theory related to the mechanisms underlying diversity patterns and community assembly (Zobel 2016). The fact that the influence of the size of species pool was greater than the local effects of productivity is interesting, since most meta-community studies using field data (e.g., Cañedo-Argüelles et al. 2015; Kärnä et al. 2015; Hill et al. 2017) have reported a greater influence of the environment (i.e., species sorting) than of dispersal (i.e., mass effects). This could be related with the chosen treatment magnitudes mentioned before. The low total proportion of variance explained in this experiment is typical of that recorded across recent freshwater metacommunity studies and suggests that the complete structure of freshwater metacommunities is inherently difficult to model or predict (Heino et al. 2015b). Ponds are often characterised by stochastic processes both in terms of flora or fauna and environmental conditions (Chase 2007), which may provide some justification for the very large proportion of unexplained variation observed and lead to a less definitive explanation of community variance by environmental variables (Heino et al. 2015a).

Experimental microcosms offer the possibility to test this and other concepts in ecology and evolution (Fukami 2004; Jessup et al. 2004; Srivastava et al. 2004; Cadotte et al. 2005; Livingston et al. 2012; Altermatt et al. 2015). Microcosms

provide a link between theory and nature (Stewart et al. 2013; Altermatt et al. 2015), by simplifying the complexities of natural systems. This characteristic has been argued as the strength (e.g., Jessup et al. 2004; Srivastava et al. 2004; Altermatt et al. 2015) as well as the weakness (e.g., Carpenter 1996) of microcosms. Carpenter (1996) suggested that, by minimizing ecosystem complexity and the multidimensionality of natural conditions, experimental microcosms are disconnected from natural systems and concluded that microcosms have limited relevance for community and ecosystem ecology. Even though natural communities have had centuries to approach an equilibrium between environment and species composition and experience seasonal and annual variation in environmental conditions as well as interactions with other trophic groups (Ejrnæs et al. 2006), the number of species present in the microcosms at the end of our experiment support the assertion that communities of phyto- and zooplankton that were assembled and persisted in the microcosms were analogous to those in natural ponds (see “Manipulation of species pools”). In the case of most microscopic organisms (< 1 mm), the fast generation time enables experiments to run for many generations, allowing us to test theory about short- and long-term effects of manipulations with experiments that last only weeks or months (Srivastava et al. 2004), which could be impossible to measure in nature during a span of a human life (Jessup et al. 2004).

Our study has demonstrated that community assembly in aquatic microcosms was determined by both local (productivity) and regional drivers (size of the species pool). Results lend support to the contemporary view that both local and regional processes are important to explain community structure and composition (Gravel et al. 2006; Chase and Myers 2011; Márquez and Kolasa 2013). However, the relative importance of local and regional processes can vary within the food web, which might be a result of different traits within each trophic group (Leibold et al. 2004; Ricklefs 2004; Matias et al. 2017). The study of community assembly in natural systems remains challenging, and work on how to bridge microcosm experiments to natural systems is a worthy direction of future research. Outdoor mesocosm experiments form a necessary link between small-scale laboratory experiments (microcosms) and comparative field studies (see Stewart et al. 2013). With climate change already affecting a wide variety of ecosystems, including aquatic ones, experimental approaches are of importance to help us to understand how communities will assemble in a changing world. That trophic groups are responding differently to changes in their environment also reveals the potential importance of measuring responses using functional groups.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics** The surveys performed comply with the current laws of Spain.

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