Disturbance from pond management obscures local and regional drivers of assemblages of primary producers

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SUMMARY

1. Ponds have significant conservation value due to their potentially high contribution to local and regional diversity. However, most ponds are located in anthropogenically influenced areas, and their biodiversity is constantly threatened by human activities. Thus, knowledge of the effect of pond management on biodiversity is essential for designing effective conservation strategies.

2. Here, we study the main drivers of diversity of three functional groups of primary producers (phytoplankton, filamentous green algae and submerged macrophytes) in 87 ponds distributed across a large region (*c.* 90000 km^2) in Southern Spain. We hypothesised that spatial effects would increase with increasing propagule size. However, given the regional extent of the study, we anticipated that both spatial and environmental controls would be significant.

3. We determined α-, β- and γ-components of biodiversity for each functional group and pond type (embankment ponds, excavated ponds and artificial ponds) and assessed the influence of environmental and spatial drivers on diversity with generalised additive models (GAMs). Redundancy analyses (RDAs) with variation partitioning were used to determine the relative contribution of environmental and spatial predictors of the community assembly. Spatial variables were calculated by applying distance-based Moran's eigenvector maps (db-MEM).

4. Both α- and β-diversities of phytoplankton and filamentous green algae varied significantly with pond type. Generally, environmental predictors of diversity were more important than spatial variables. Assemblage structure was controlled by water chemistry and eutrophication, with a marked influence of pond type. Spatial variables included broad-scale variation for the three groups of primary producers, which were also strongly influenced by the management regime.

5. Limited management activities, as occurs at embankment ponds, promoted the local richness of phytoplankton and contributed importantly to the regional diversity of macrophytes. Moreover, the relative contribution of environmental and spatial variables was similar between embankment ponds and natural ecosystems, that is, dispersal limitation increasing with propagule size. Excavated and artificial ponds also contributed importantly to regional diversity by enhancing phytoplankton and filamentous green algal β-diversity. However, spatial patterns in the latter pond type did not meet our expectations, most likely due to the intensive disturbance from pond management hampering the development of macrophytes.

Keywords: dispersal limitation, filamentous algae, macrophytes, Moran's Eigenvector Map, phytoplankton

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Introduction

Protection of freshwater biodiversity often focuses on complex strategies that depend on the design of the protected areas (Dudgeon *et al.*, 2006). However, since most waterbodies are affected by human activities, conservation strategies ought to encompass anthropogenic areas (see review in Chester & Robson, 2013). The 'Reconciliation Ecology' concept (Dudgeon *et al.*, 2006) states that the paradoxical characteristics of anthropogenic ponds present a challenge to conservationists: Globally, the increase in the construction of ponds creates new aquatic habitats for flora and fauna (Knutson *et al.*, 2004; Abellán *et al.*, 2006; Mushtaq, Dawe & Hafeez, 2007), promoting biodiversity at both local and regional extents (Oertli *et al.*, 2002; Hazell *et al.*, 2004; Williams *et al.*, 2004; Abellán *et al.*, 2006; Céréghino *et al.*, 2008). Ponds can act as a refuge for species in the face of environmental disturbance, especially those that may be amplified by climatic change (Chester & Robson, 2013). However, as ponds are mainly situated in anthropogenic landscapes, they are adversely impacted by human activities (e.g. Dudgeon *et al.*, 2006). The influence of management practices on biodiversity has recently drawn the attention of conservationists, who attempt to understand the functioning of anthropogenically disturbed ecosystems (Lemmens *et al.*, 2013; Chester & Robson, 2013; Usio *et al.*, 2013). This is because the degree of manipulation and the management regime of ponds are both highly related to use and construction type (Casas *et al.*, 2011a,b; Juan *et al.*, 2012; Bonachela *et al.*, 2013), with strong implication for their α-, β- and γ-diversities (Fuentes-Rodríguez *et al.*, 2013).

In aquatic systems, drivers of α-diversity show dependency on organisms' trophic level and their interactions within the food web, as well as the habitat size (Dodson, Arnott & Cottingham, 2000). In the case of primary producers, strong and direct environmental dependencies are usual, since they occupy a low trophic level and nutrients and light are needed for their productivity (Dodson *et al.*, 2000; Reynolds, 2006; Soininen, Korhonen & Luoto, 2013). On the other hand, analyses of spatial variation (or non-directional β-diversity) in community structure have shown that the relative role of environmental and spatial fractions depends strongly on the spatial extent of the study (Heino, 2011 *and references herein*; Alahuhta & Heino, 2013). At a regional scale, organism dispersal rates may be of greater importance relative to species sorting along environmental gradients (Capers, Selsky & Bugbee, 2010). Meta-analyses have demonstrated that dispersal abilities are mediated by factors related to organism traits, such as body size (Finlay, Esteban & Fenchel, 1996; Allen *et al.*, 1999; Hillebrand *et al.*, 2001; Finlay, 2002), which in turn interacts with the mode of dispersion and dispersal strategies (Cottenie, 2005; De Bie *et al.*, 2012).

Although passive dispersion is common to all primary producers, differences in propagule size are crucial to understanding dispersal limitation and thus the role of spatial effects (e.g. Beisner *et al.*, 2006; Soininen *et al.*, 2007; Hájek *et al.*, 2011; De Bie *et al.*, 2012). Among primary producers, phytoplankton not only has the smallest cell sizes, but also demographic features (rapid growths, Reynolds, 2006) that implies large population sizes, high colonisation rates and almost 'ubiquity' (Finlay, 2002). By contrast, submerged macrophytes and filamentous green algae have larger propagules and slower life cycles (Paszkowski & Tonn, 2000; Gillooly *et al.*, 2002), limiting their dispersal to restricted extents, both in space and time (Allen *et al.*, 1999). Regarding dispersal strategies, hydrochorous dispersion should prevail over wind for submerged species (Johansson, Nilsson & Nilsson, 1996), but alternative modes of dispersion (e.g. zoochorous) are also common in isolated ecosystems such as ponds (Figuerola & Green, 2002). There have been several metacommunity studies including primary producers (e.g. Beisner *et al.*, 2006; Soininen *et al.*, 2007; Hájek *et al.*, 2011; De Bie *et al.*, 2012); however, metacommunity studies exclusively focused on primary producers are more scarce (e.g. Alahuhta & Heino, 2013). Indeed, studies have usually ignored filamentous green algae, a neglected group that can outcompete macrophytes (Trochine *et al.*, 2011) and have intermediate sized propagules, compared with macrophytes and phytoplankton.

In the present study, we set out to determine the most relevant drivers of α- and β-diversities and to assess the relative importance of environmental and spatial variables in structuring three primary producer assemblages (phytoplankton, filamentous green algae and submerged macrophytes) in a set of 87 ponds distributed across an area of 90 000 km^2 in Southern Spain. Furthermore, we sought to evaluate the influence of the management regime on diversity for the three most common pond types in the study area (Casas *et al.*, 2011b; Fuentes-Rodríguez *et al.*, 2013), with the aim to develop guidelines for best management practices for conservation purposes. We hypothesised that phytoplankton would have higher diversity than filamentous green algae and macrophytes, and that their differential dispersal abilities would also affect the relative contribution of environmental and spatial drivers. Indeed, we expected

that the pond type would influence patterns of α- and β-diversities of the three groups of primary producers studied.

Methods

Pond location and typology

We selected 87 permanent ponds using a stratified-random procedure covering the environmental and spatial heterogeneity of Andalusia in Southern Spain (90 000 km^2; Casas *et al.*, 2011b). The ponds were classified into three groups according to construction type and management regime in accordance with previous pond studies (Casas *et al.*, 2011b; Fuentes-Rodríguez *et al.*, 2013) resulting in a gradient of 'naturalness' (Table 1). The hydrology of all the ponds was, irrespective of construction and management type, anthropogenically modified to ensure the ponds did not dry out.

Embankment ponds (henceforth EMB) are natural hollows that retain mainly drainage water by means of small dams. The percentage of marginal vegetation in EMB is usually higher than in the other pond types as the pond substratum remains unaltered. Most EMB are managed only extensively, this is because they are mainly used for stockbreeding purposes, and are situated in extensive agro-silvo-pastoral systems with low flushing by natural processes (evaporation, precipitation), and their water levels are controlled by water pumping. EMB average size and age are higher than for the other pond types (Fuentes-Rodríguez *et al.*, 2013).

Excavated ponds (EXC) are man-made hollows that collect drained water or store channelised groundwater. Since no artificial waterproofing substratum is used, marginal vegetation development can be promoted as for EMB (Casas *et al.*, 2011b). However, since EXC are mainly used for irrigation purposes, water consumption is higher and fluctuations in water level are more pronounced than in EMB.

Artificial substrate ponds (ART) are small-sized ponds located above-ground level, which collect channelised groundwater and/or surface water from nearby rivers. The artificial substratum can be polyethylene or concrete, but in our study, the two subtypes were merged as no significant between-group difference emerged when analysing the diversity of primary producers (I. Gallego, *unpublished data*). Since most ART ponds are very small and located in intensively farmed areas, higher water renewal rates than in EMB and EXC ponds are expected. Interviews with the pond owners revealed that the average flushing rate was <22 days in ART ponds (Juan *et al.*, 2012). Intensive and destructive management practices such as periodic biocide treatment and dredging of submerged vegetation are common (Juan *et al.*, 2012; Bonachela *et al.*, 2013).

Sampling and analyses

Samples of primary producers were collected in early summer (June 2007) at the peak season of abundance and/or biomass of the organisms studied (De Meester *et al.*, 2005; Soininen *et al.*, 2007). Notwithstanding the fact that the study area was the Mediterranean region, which is characterised by a marked hydrological seasonality, our ponds had an artificial hydrology and thus their water levels were independent of the amount of rainfall (Casas *et al.*, 2011b; Juan *et al.*, 2012). Thus, seasonal and supraseasonal hydrologic variability lacks the relevance reported in natural Mediterranean ecosystems (Rodrigo, Rojo & Armengol, 2003; Casas *et al.*, 2011b; Del Pozo, Fernández-Aláez & Fernández-Aláez, 2011) and was omitted in this study. Fourteen litres of water were collected for phytoplankton and chemical analyses using a plexiglass tube sampler (ø 15 cm, length adjusted to pond depth). Water samples integrating the whole depth profile were gathered from two pelagic and two littoral randomly selected locations.

Table 1 Description of the three pond categories according to construction type and management regime

	Embankment ponds (EMB)	Excavated ponds (EXC)	Artificial ponds (ART)
Substratum	Natural	Natural	Artificial
Man-made infrastructure	Dam (occasionally)	Hollow	Hollow and concrete or PET lining
Water source	Drainage water	Drainage water	Surface water from nearby rivers
		Channelised groundwater	Channelised groundwater
Use	Stockbreeding	Irrigation	Irrigation (intensive farming)
Flushing	Low renewal	High renewal	Very high renewal
% of marginal vegetation	High	High	Scarce
Pond area	Large	Medium	Small
Pond management	None	Biocide treatment (occasionally)	Biocide treatment
			Dredging of SAV

Two phytoplankton replicates (0.25 L each) were immediately fixed with Lugol's solution (4% final concentration) and stored in the dark. Conductivity (Cond) and pH were measured *in situ* using a multiparameter probe (HANNA HI9828). Three 0.5-L subsamples were taken for chemical analyses. One subsample was filtered in the field through glass fibre filters (Whatman GF/F 0.7 μm, GE Whatman, Maidstone, Kent, U.K.) for chlorophyll *a* (Chl *a*) and total suspended solid (TSS) analyses. The remaining subsamples were preserved at 4 °C and processed within 24 h. The second subsample was filtered as above and used to measure alkalinity (Alk), soluble reactive phosphorous (SRP), soluble reactive silicate (SRSi), nitrate (NO_3-N), nitrite (NO_2-N) and ammonia (NH_4-N) following standard procedures described in Wetzel (2000) and APHA (2005). The non-filtered subsample was used to determine total phosphorus (TP) and total nitrogen (TN) following APHA (2005). Variables included in the study (mean ± SD) are listed per pond type in Table S1.

Phytoplankton samples were identified and counted with an inverted microscope (Carl Zeiss Axiovert 35) following the procedure described in Utermöhl (1958). Each phytoplankton sample was examined at various magnifications. Minimum 100 cells or setting units (colonies, filaments) of the most frequent species were identified, counting being continued until no more new species were encountered for 10 microscope fields. Phytoplankton species identification and biovolume calculation procedures are detailed in Gallego *et al.* (2012).

Submerged macrophytes and filamentous green algae were collected along two randomly selected transects from the shore to the centre of the pond (Casas *et al.*, 2011b). Identification was made to species level in most cases, or 'morphospecies' when the highest taxonomic resolution was not possible. Percentage cover of submerged aquatic vegetation (% SAV), including both filamentous green algae and macrophyte coverage, was estimated visually. Average belt width covered with hydrophytic marginal vegetation (MV) was measured using ortho-images (Casas *et al.*, 2012). The number of ponds with presence of filamentous green algae and/or macrophytes is summarised in Table S2.

Statistical analyses

Diversity of the total species pool (γ-diversity) and α- and β-diversities were calculated for phytoplankton, filamentous green algae and macrophytes. The total number and surface area of ponds differed by construction type. Thus, for comparison, we estimated γ-diversity

in a given construction type following the species richness index proposed by Margalef (1958) where sample size is divided by total pond surface area (ln-transformed) in a given group. α-diversity (local diversity) was measured as the average number of species per site for the whole set of ponds ($n = 87$), while β-diversity, representing the compositional dissimilarity among ponds within a given set of sites, was measured for each of the three construction types ($n_{EMB} = 37$, $n_{EXC} = 19$, $n_{ART} = 31$). Dissimilarity was calculated separately for the three functional groups using species abundances (phytoplankton) and presence/absence data (filamentous green algae and macrophytes). For this purpose, we used the Bray–Curtis dissimilarity ($1 - C_{BC}$), a common metric used in β-diversity studies (Anderson *et al.*, 2011). We employed a zero-adjusted Bray–Curtis coefficient to both FGA and macrophytes since it modulates the erratic behaviour of Bray–Curtis for near-denuded assemblages in the samples, that is, samples containing no species (Clarke, Somerfield & Chapman, 2006). Dissimilarity was calculated using PRIMER v6.1.12 (Clarke & Gorley, 2006). Non-metric multidimensional scaling ordinations (n-MDS) based on Bray–Curtis coefficients were used to summarise patterns in the community composition of the three groups of primary producers, for each pond type (see Figure S1). The individual contribution of each pond to β-diversity in a given group was calculated as the average value of all pairwise comparisons involving a particular pond.

The contribution of α- and β-diversities to γ-diversity was examined with additive diversity partitioning, where $\gamma = \beta + \alpha_{mean}$ allows objective comparison of diversity components (Wagner, Wildi & Ewald, 2000). Since β-diversity may reflect species replacement (i.e. turnover) and/or species loss (i.e. nestedness), we partitioned β-diversity into these components $\beta = \beta_{turnover} + \beta_{nestedness}$, based on multiple-site dissimilarity measures (Baselga, 2010, 2012).

Differences in α- and β-diversities of primary producers among pond types were tested using one-way ANOVA, and *post hoc* pairwise comparisons were carried out using Tukey HSD tests for unequal sample size when significant differences were detected. These analyses were performed in STATISTICA v7.1 (StatSoft, 2005). β-diversity was partitioned with the {betapart} library in the R package (R Development Core Team, 2012; Baselga, Orme & Villeger, 2013). We used Euclidean distances, obtained with PRIMER v6.1.12 (Clarke & Gorley, 2006), to calculate the mean geographical distance among pairs of ponds for each pond type. Similarly, environmental heterogeneity among pairs of

ponds per pond type was based on Euclidean distances, and data were standardised to zero mean and unit variance (Borcard, Gillet & Legendre, 2011). Differences among pond types were tested with Kruskal–Wallis, STATISTICA v7.1 (StatSoft, 2005).

Generalised Additive Models

We explored the influence of environmental and spatial drivers on the α- and β-diversities of phytoplankton, filamentous green algae and macrophytes using generalised additive models (GAM). GAMs are more flexible than generalised linear models (GLM) and can reveal complex relationships between diversity and explanatory variables, including skewed response patterns (Austin *et al.*, 2006). Quasi-Poisson error structure with log-linked function was used to accommodate α-diversity, while β-diversity response variables followed Gaussian and Gamma error distributions with identity and inverse link functions, respectively, for the three groups. We used REML smoothness estimation to select the most parsimonious model and a backward procedure to select variables to be retained in the final model. The significance of each variable in the model was assessed with *F*-test. For each model, we calculated the deviance explained (D_2), analogous to variance in linear regression analyses, and the adjusted R^2. The eigenfunctions generated with db-MEM analysis (detailed below) were included as spatial variables in the GAMs. We performed the analyses with the {mgcv} library in the R package (Wood, 2011; R Development Core Team, 2012). To test model assumptions, spatial autocorrelation in residuals was checked for each selected model. Further information is given in Data S1.

Spatial variables

Spatial variables were obtained by applying distance-based Moran's Eigenvector Maps (db-MEM) based on principal coordinates of neighbour matrices analysis (PCNM; Borcard *et al.*, 2011). This method produces orthogonal spatial variables that allow detection of spatial patterns over a wide range of scales (Borcard & Legendre, 2002). We obtained a connectivity matrix based on the Euclidean distance of the geographical coordinates of sites using the largest value of the minimum spanning tree (MST) distance linking all the sites as truncation distance (Legendre & Legendre, 1998). Straight-line distances among sites are appropriate for describing the dispersal paths of primary producers (Alahuhta & Heino, 2013), but may not be suitable for other aquatic organisms with limited dispersal abilities (Landeiro *et al.*, 2011). The resulting first eigenfunctions (or 'spatial filters') represent broad-scale variation, whereas eigenfunctions derived from small eigenvalues represent finer-scale variation in species composition.

Of the 51 generated db-MEM variables, we selected the 20 variables with positive spatial autocorrelation using the statistic Moran's *I* (Moran's *I* > Expected Moran's *I*). Prior to the spatial analyses, significant linear trends were removed from the species data and analysed separately since they can be considered a source of variation that may obscure the spatial patterns (Borcard *et al.*, 2011). The {PCNM} library from R was used to generate spatial variables.

Redundancy Analysis

We performed redundancy analysis (RDA) to explore relationships between community composition and both spatial and environmental data (McArdle & Anderson, 2001). RDAs were carried out for the complete set of ponds and for each pond type separately. We used forward selection of spatial and environmental variables with a double-stopping criterion (Blanchet, Legendre & Borcard, 2008). The contribution of each set of predictors was assessed with adjusted fractions of variation partitioning. Species data were Hellinger-transformed (Legendre & Gallagher, 2001) prior to analysis. This transformation provides unbiased estimates of variation partitioning based on RDA (Peres-Neto *et al.*, 2006). Hellinger transformation is also appropriate for binary data (filamentous green algae and macrophytes) because it is related to the Ochiai distance (Declerck *et al.*, 2011). We also tested for linear trends and, when significant, incorporated them explicitly (as X and Y coordinates) in the partitioning procedure, since linear trends constitute a source of variation and accordingly must be included in variation partitioning (Borcard *et al.*, 2011).

RDAs, forward selection and variation partitioning were performed in R using the {vegan} and {packfor} libraries (Oksanen *et al.*, 2008; Dray, Legendre & Blanchet, 2009).

Results

Diversity across functional groups and pond types

Overall, we registered 293, 20 and 19 species of phytoplankton, filamentous green algae and macrophytes, respectively. The γ-diversity index normalised to pond area (Margalef index) reached the highest value

for phytoplankton ($\gamma = 20.53$) followed by filamentous green algae and macrophytes ($\gamma = 1.34$ and $\gamma = 1.26$, respectively). Of the three functional groups, EMB had the highest taxon richness (Fig. 1a). Out of the total number of species registered in EMB, that is, 243, 119 occurred exclusively here (3.2 new taxa per pond). Twenty-one species occurred only in EXC and not in EMB and ART (1.1 taxa per pond), and 56 species occurred only in ART and not in EXC and EMB (1.8 taxa per pond). Only 54% of the ponds held submerged
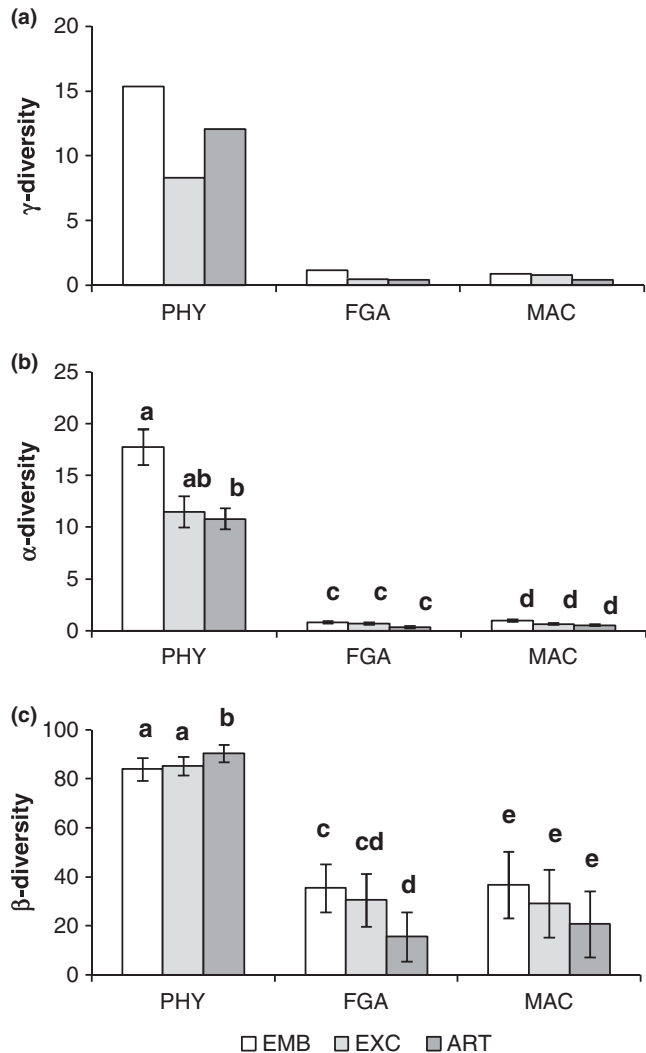
Fig. 1 Results of γ-diversity as an area-adapted Margalef Index, (a), α-diversity (b) and β-diversity (Bray–Curtis dissimilarity) as percentage (c) of each studied functional group for all pond types. For α- and β-diversities, significant differences among pond typology are expressed with different letters (ANOVA, HSD Tukey). Whiskers represent Standard Deviation (SD). PHY = Phytoplankton, FGA = Filamentous green algae, MAC = Submerged macrophytes, EMB = Embankment ponds, EXC = Excavated ponds, ART = Artificial ponds.

aquatic vegetation, either filamentous green algae or macrophytes. EMB had the highest presence of filamentous green algae or macrophytes (65%) and ART ponds the lowest (35%).

Both α- and β-diversities were highest for phytoplankton (Fig. 1b,c). The effect of pond type on α-diversity was statistically significant only for phytoplankton ($F = 4.59$, $P < 0.05$; Fig. 1b), being strongest in the EMB and weakest in the ART ponds (Tukey HSD test, $P < 0.05$).

Phytoplankton β-diversity varied significantly among pond types ($F = 8.76$, $P < 0.001$) and was highest in ART (Tukey HSD test, $P < 0.001$; Fig. 1c). Also filamentous green algae β-diversity varied significantly among pond types ($F = 3.23$, $P < 0.05$), being highest and lowest in EMB and ART, respectively (Tukey HSD test, $P < 0.05$; Fig. 1c). Macrophyte β-diversity did not differ significantly with pond type ($F = 2.16$, $P > 0.1$; Fig. 1c).

Additive diversity partitioning showed that the β-component was the main contributor to γ-diversity for all three primary producers (above 95% in all cases). EXC contributed most significantly to the α-component ($>10\%$), especially phytoplankton and filamentous green algae (see Fig. 2a), while ART exhibited the highest overall β-diversity ($>92\%$), mostly influenced by macrophytes (Fig. 2a). Partitioning of β-diversity showed that spatial turnover was most important irrespective of pond typology (Fig. 2b). The contribution of nestedness to β-diversity was very low (Fig. 2b), with the exception of ART where macrophytes showed a high species loss ($\beta_{nestedness} = 38.1\%$, Fig. 2b).

Environmental heterogeneity based on Euclidean distances demonstrated no significant differences among pond types (Kruskal–Wallis test, $H = 4.99$, $P > 0.1$; Fig. 3a). Mean geographical distance differed among pond types (Kruskal–Wallis test, $H = 7.39$, $P < 0.05$), ART having a higher average distance between pairs of ponds (Fig. 3b).

Spatial and environmental drivers of diversity

The optimal GAM model predicting phytoplankton α-diversity included five variables and explained 45.9% of total deviance (Table 2). Chl *a*, Cond and DIN were the selected environmental variables and exhibited maximum α-diversity at intermediate levels of Chl *a* and low values of Cond and DIN, respectively (Fig. 4a). Only one spatial filter representing an intermediate scale (V9; Table 2) was included in the final model. The pure environmental fraction was fourfold higher than the pure spatial component (Table 2).
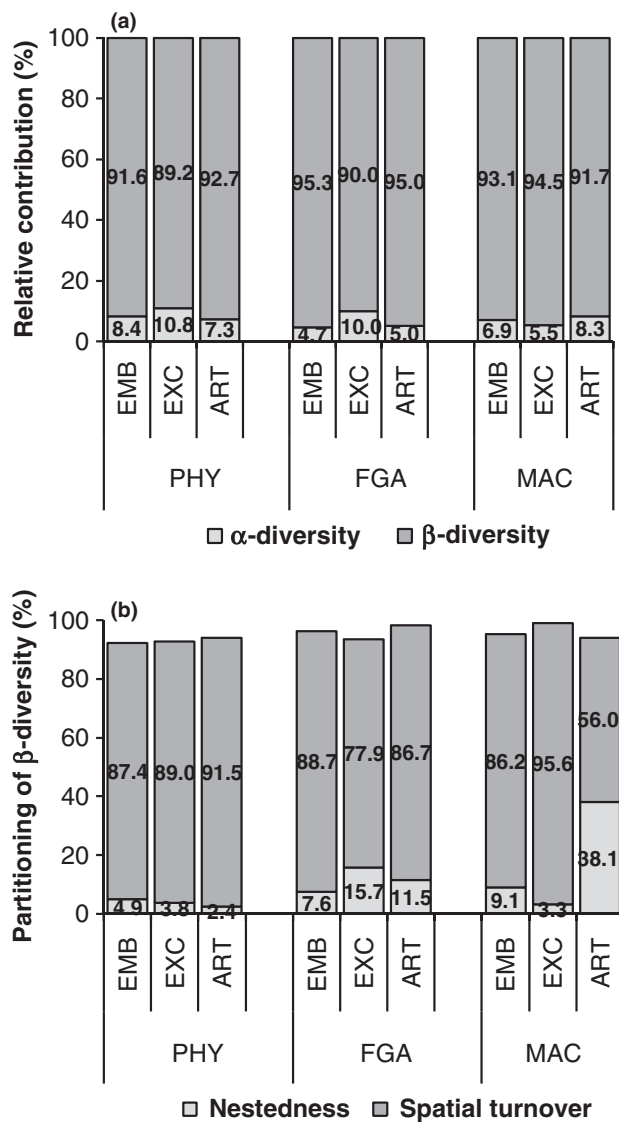
Fig. 2 Relative contribution (expressed as percentage) of α- and β-diversity (a) and partitioning of β-diversity (b) for each functional group of organisms according to pond type. PHY = Phytoplankton, FGA = Filamentous green algae, MAC = Submerged macrophytes, EMB = Embankment ponds, EXC = Excavated ponds, ART = Artificial ponds.
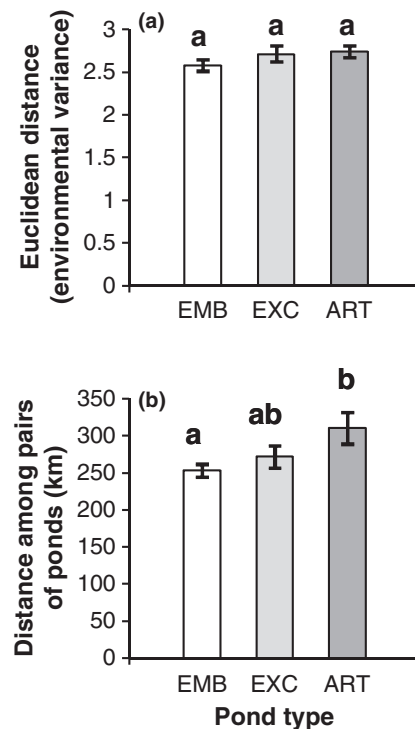

Fig. 3 Environmental heterogeneity (a) and average geographical distance between pairs of ponds (b) for each pond type. Significant differences among pond types are expressed with different letters (Kruskal–Wallis test). Whiskers represent Standard Deviation (SD). EMB = Embankment ponds, EXC = Excavated ponds, ART = Artificial ponds.

The α-diversity of filamentous green algae was best-predicted by a GAM model with two environmental variables (Chl *a*, DIN) and three spatial filters representing broad and intermediate scales (V1, V2, V12) with a total deviance of 35.9% (Table 2). Slightly negative relationships were observed for both environmental variables (Fig. 4a). The pure environmental fraction was found to be similar to the pure spatial fraction (Table 2).

The GAM model for α-diversity of macrophytes included only two variables (TP, Alk), explaining a total deviance of 19.1% (Table 2). α-diversity had a hump-shaped relationship with TP and was negatively correlated with Alk (Fig. 4a). None of the 20 significant spatial filters was included in the model (Table 2).

The β-diversity of phytoplankton was best-predicted by DIN, TP,%SAV and the spatial filters V3 and V13, explaining a total deviance of 38.8% (Table 2). The highest contribution to the model was provided by DIN (8.4%). β-diversity was positively related to TP, but negatively to%SAV (Fig. 4b). The pure environmental fraction was higher than the pure spatial fraction (Table 2).

Filamentous green algae β-diversity was predicted by the same environmental variables as used for α-diversity, but increased with increasing DIN and Chl *a* (Fig. 4b). Only one spatial variable was included in the model (V1), which explained nearly one-third of the 32.2% total deviance of the model (Table 2).

The β-diversity of macrophytes was best-predicted by a GAM model including as input variables: V10, Alk and SRSi (36.6% of total deviance explained; Table 2). Macrophyte β-diversity was promoted by increasing Alk and SRSi levels (Fig. 4b). The spatial variable, representing an intermediate scale, showed the highest drop contribution to the model (8.3%, Table 2).

Table 2 Explained deviance (D^2), adjusted fraction (R^2 Adj.) and variables included in the GAMs (drop contribution in brackets) predicting α- and β-diversity for phytoplankton (PHY), filamentous green algae (FGA) and macrophytes (MAC)

	α-diversity			β-diversity		
	PHY	FGA	MAC	PHY	FGA	MAC
D^2 (%)	45.9	35.9	19.1	38.8	32.2	36.6
R^2 Adj.	0.426	0.371	0.145	0.342	0.244	0.291
Variables included	Chl a (9.5%)	Chl *a* (9.7%)	TP (8.6%)	DIN (8.4%)	Chl *a* (15%)	V10 (8.3%)
	V9 (8.4%)	V12 (4.7%)	Alk (5.4%)	V13 (8.3%)	V1 (10.4%)	Alk (5.6%)
	Cond (7.2%)	V1 (3.8%)		V3 (7.2%)	DIN (3.7%)	Si (4.3%)
	DIN (5.6%)	V2 (3.5%)		TP (2.9%)		
		DIN (1.4%)		SAV (2.6%)		
[E] (%)	35.9	13.5	19.1	20.6	20	16.1
[S] (%)	8.4	14.2	–	13.9	10.4	8.3
[E+S] (%)	1.6	8.2	–	4.3	1.8	12.2

[E] = pure environmental fraction, [S] = pure spatial, [E+S] = shared environmental and spatial fraction.

Spatial and environmental variation partitioning in community composition

Variation partitioning revealed that both spatial and environmental fractions were significant for all three functional groups ($P > 0.05$, Table 3) in the all pond analysis. Linear trends were only significant for phytoplankton ($P < 0.05$). Phytoplankton assemblage composition was best-predicted by six spatial filters and five environmental variables, contributing equally to the explained variance (3.03 and 2.71%, respectively, Table 3). When dividing into pond type, the effect of the spatial component was higher than that of the environmental fraction for both ART and EXC, while environmental factors weighted higher for EMB (Fig. 5).

Overall, for filamentous green algae assemblages, a similar variance is explained for spatial and environmental fractions (3.3 and 2.1%, respectively, Table 3). However, when analysed separately, a higher contribution by local environmental factors was detected for EXC than for EMB and ART (Fig. 5).

Macrophyte assemblage composition was best-predicted by local environmental factors, including three variables (Cond, TP and %SAV) that explained 6.23% of the total variation (Table 3). When pond types were analysed separately, the spatial contribution was only significant for EMB (Fig. 5).

Discussion

Diversity across functional groups and pond types

As expected, our results revealed much higher α-, β- and γ-diversities for phytoplankton than for filamentous green algae and submerged macrophytes. The α-diversity of phytoplankton was similar to values recorded for other ponds in temperate climate regions (e.g. Rodrigo *et al.*, 2003; Vanormelingen *et al.*, 2008). However, the α-diversity of filamentous green algae and macrophytes in our ponds was much lower than in natural ponds (e.g. Søndergaard, Jeppesen & Jensen, 2005; Del Pozo *et al.*, 2011), suggesting that disturbance as a result of pond management is detrimental to the development of macrophytes and filamentous green algae. The ponds, however, hosted 65% of the macrophytes listed in the Andalusian Inventory of Wetlands, including some species catalogued as 'Vulnerable' in the Red List of this region (http://www.juntadeandalucia.es/medioambiente/site/rediam).

Notwithstanding the fact that all pond types contributed to γ-diversity, the number of taxa exclusively found in embankment ponds was higher than in the other two ponds types, suggesting that naturalness (and hence, less intensive pond management) could enhance diversity of primary producers. The high contribution to the regional pool of primary producer species in our study ponds mainly stemmed from the marked between-pond dissimilarity, attributable to the wide spectrum of environmental conditions and management. Thus, the high variety of different habitats significantly increased β-diversity, concurring with previous predictions for small and isolated ecosystems (De Meester *et al.*, 2005; Scheffer *et al.*, 2006; Chase, 2010).

A high proportion (about half) of the ponds lacked filamentous green algae or macrophytes, as observed in other studies (e.g. Akasaka *et al.*, 2010). Submerged vegetation is affected by alterations in the surrounding land use and may completely disappear at high nutrient concentrations (Søndergaard *et al.*, 2005; Declerck *et al.*, 2006; Akasaka *et al.*, 2010; Nielsen *et al.*, 2012). Also temporal factors may be involved, not least for macrophytes and filamentous green algae, which can both display

(a) α–diversity
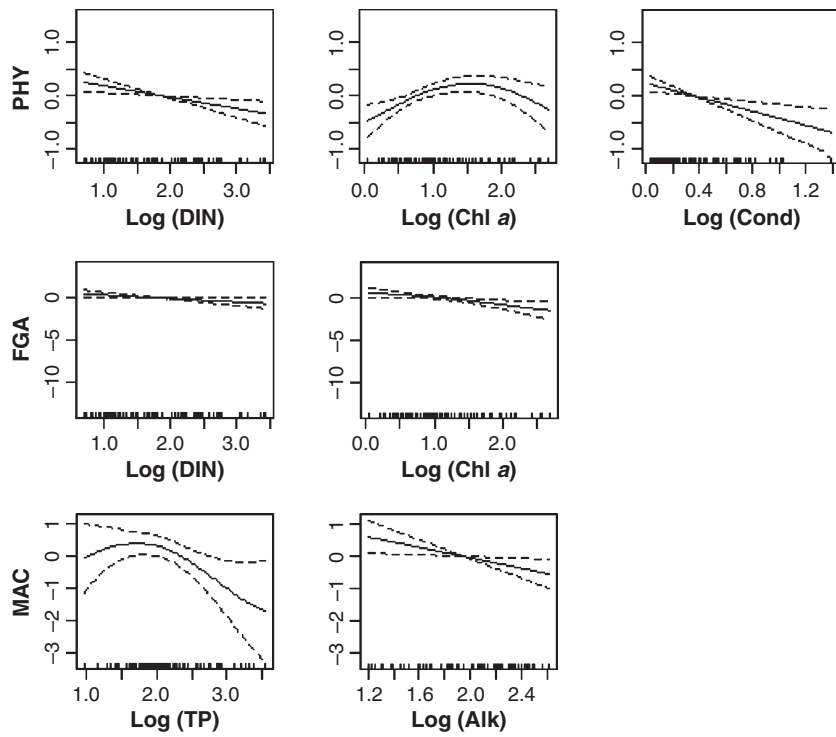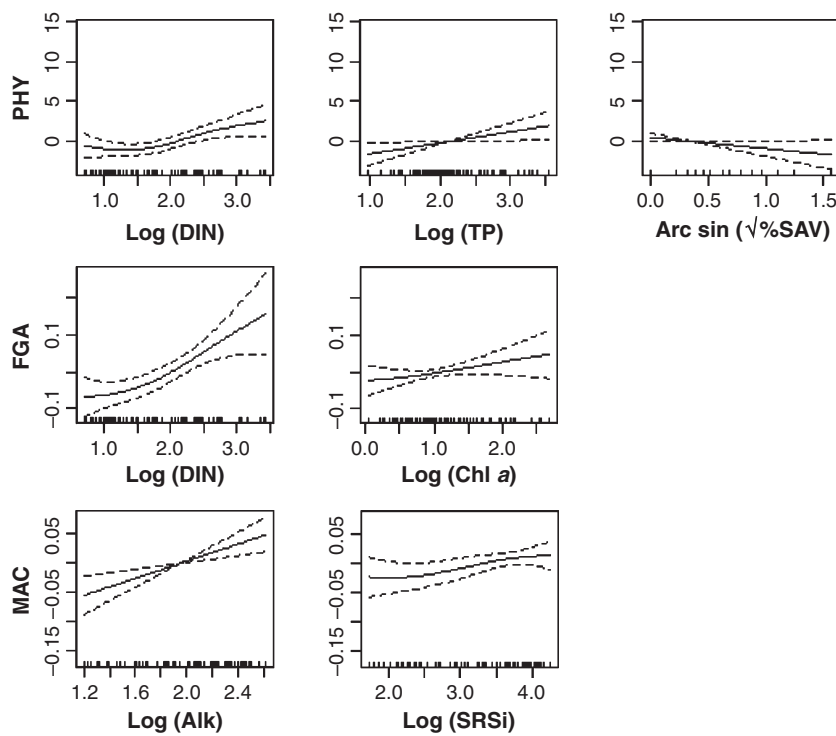

(b) β–diversity

Fig. 4 Responses of (a) α- and (b) β-diversity of phytoplankton (PHY), filamentous green algae (FGA) and macrophytes (MAC) to environmental variables selected by the generalised additive model (GAM). The dashed lines are *c.* 95% confidence intervals around the smooth function.

marked seasonality (Irfanullah & Moss, 2005; Sayer, Davidson & Jones, 2010). Moreover, disturbance as a result of pond management in the form of, for instance, free access of livestock, water level fluctuations, dredging and biocide treatment (Casas *et al.*, 2011a; Bonachela *et al.*, 2013) will negatively affect the development of

Table 3 Summary of spatial and environmental variables retained in RDAs showing the coefficient R^2 adjusted for each fraction as well as the residuals (Resid.) for the three functional groups studied

Functional group	Spatial var. retained	Environmental var. retained	R^2 adjusted				
			[E]	[S]	[T]	[E+S]	Resid.
PHY	1,2,3,5,12,16	Cond, TP, SRSi, MV, Chl *a*, %SAV	0.030***	0.027***	0.006*	0.006[nt]	0.925
FGA	2,7	%SAV, DIN	0.033***	0.021**	–	0.001[nt]	0.946
MAC	2	Cond, TP, %SAV	0.062*	0.014***	0.006[ns]	0.008[nt]	0.895

PHY = Phytoplankton, FGA = Filamentous green algae, MAC = Macrophytes, [E] = pure environmental fraction, [S] = pure spatial, [T] = linear trend, [E+S] = shared environmental and spatial fraction. Significance: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns = $P > 0.05$, nt = non-testable fraction.

macrophytes and perhaps filamentous algae. The fact that our ponds were sampled only once means our assessment of diversity lacks a seasonal perspective. This might contribute to the relatively small amount of variance explained by the models and underestimate the total diversity at the sites.

Several studies have pointed to the role of management as a predictor of aquatic diversity (e.g. Markwell & Fellows, 2008; Lutton, Sheldon & Bunn, 2010; Chester & Robson, 2013). In our study, pond management (~ pond type) played a pivotal role in the prediction of diversity of phytoplankton and filamentous green algae. Embankment ponds had the highest phytoplankton α-diversity and mainly hosted C- and S-strategists (colonisers and gleaners respectively; Reynolds, 2006), whose functional features (e.g. coenobial, low sinking rate) seem to be the result of the lenient management connected with the primary use of embankment ponds for stockbreeding purposes (Casas *et al.*, 2011b; Fuentes-

Fig. 5 Relative contribution of the pure spatial and the pure environmental fraction, expressed as a percentage, for each primary producer functional group and for pond typology. PHY = Phytoplankton, FGA = Filamentous green algae, MAC = Macrophytes, EMB = Embankment ponds, EXC = Excavated ponds, ART = Artificial ponds. *Spatial fraction non-significant ($P > 0.1$). **Detrended data.

Rodríguez *et al.*, 2013). Excavated ponds also exhibited a high α-diversity of phytoplankton, and their assemblages showed high similarity to those of the embankment ponds, that is, with a high proportion of gleaners. Although excavated ponds are more linked with agricultural use, management practices do not include heavy use of biocides and SAV dredging is uncommon (Casas *et al.*, 2011b). Artificial ponds had the lowest α-diversity of phytoplankton, which is most likely the result of the intensive management regime (Lemmens *et al.*, 2013). Since artificial ponds are mainly used for drip irrigation, periodical dredging, biocide application and high fluctuations in the water level are causes of frequent disturbances (Casas *et al.*, 2011a,b; Juan *et al.*, 2012; Bonachela *et al.*, 2013) that may maintain phytoplankton in its early successional stages, characterised by colonisers and low species richness (Reynolds, 2006).

Although no significant differences were identified in macrophyte diversity across pond types, embankment and excavated ponds contributed >50% to regional macrophyte diversity. Artificial ponds, for their part, showed a higher nestedness in the partitioning of macrophyte β-diversity, suggesting a smaller species pool than in the other two pond types.

Environmental drivers of diversity and influence of management regime

Primary producer diversity responded to water chemistry, including nutrients (e.g. nitrogen and phosphorous) and the aqueous mineral content (e.g. conductivity and alkalinity), as previously detected in the same set of ponds for zooplankton (León *et al.*, 2010) and benthic macroinvertebrates (Fuentes-Rodríguez *et al.*, 2013). Additionally, variables related to the nutrient content, such as Chl *a* and SAV coverage, were significant drivers of diversity for all the groups.

We obtained rather similar relationships between environmental variables for all three groups of primary
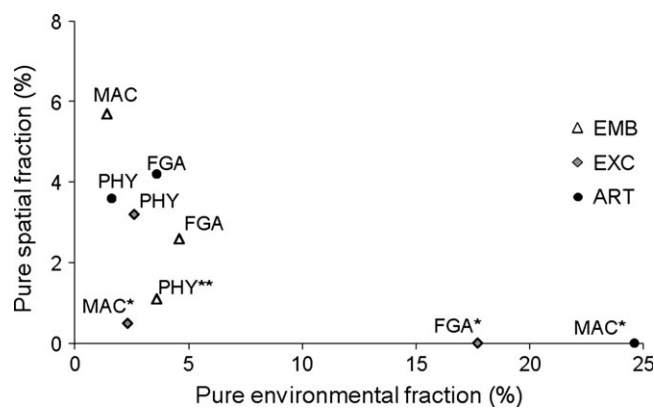
producers: α-diversity showed a negative correlation with nutrient level (N, P), while β-diversity increased with increasing concentrations of nutrients. In our ponds, N and P may be better predictors of productivity than Chl *a*, as demonstrated earlier for species richness (Tilman, 1993; Declerck *et al.*, 2005; Muylaert *et al.*, 2010) and studies on β-diversity in experimental ponds (Chase & Leibold, 2002; Chase, 2010). The key role of phosphorus as a driver of diversity has been extensively studied, and different responses have emerged (Dodson *et al.*, 2000; Jeppesen *et al.*, 2000; Mittelbach *et al.*, 2001; Declerck *et al.*, 2007; Korhonen, Wang & Soininen, 2011). As described for shallow ecosystems (Jeppesen *et al.*, 1998; Declerck *et al.*, 2005, 2007), TP in conjunction with SAV affect phytoplankton assemblage composition (Reynolds, 2006). The influence of pond management on the TP-SAV relationship is difficult to discern since SAV coverage was independent of pond type (Fuentes-Rodríguez *et al.*, 2013; *this study*). However, in our study area, the development of dense macrophyte meadows were hampered in the highly managed ponds (Casas *et al.*, 2011b; Juan *et al.*, 2012), suggesting that management practices usually modifies pond attributes, such as the presence of sediment, being linked with pond typology (Chester & Robson, 2013). The importance of nitrogen for planktonic richness has been observed in previous studies (e.g. Proulx *et al.*, 1996; Romo & Villena, 2005; Özkan *et al.*, 2013), with indirect effects on the abundance of submerged macrophytes (González-Sagrario *et al.*, 2005; James *et al.*, 2005; Moss *et al.*, 2012) or on filamentous green algae (Phillips, Eminson & Moss, 1978; Irfanullah & Moss, 2005; James *et al.*, 2005; Trochine *et al.*, 2011). The alkalinity–diversity relationships identified in our ponds were also indirectly linked with pond typology and management, as limestone soil is dominating at the central and eastern sites (where most artificial ponds are located) and siliceous substrata in the north-western part (where embankment ponds prevail).

Relative effect of spatial and environmental drivers on diversity patterns

The variation in primary producer assemblages was attributable to both environmental and spatial variables, suggesting that the assemblage structure was determined by neutral (Hubbell, 2001) and niche-based control (Leibold *et al.*, 2004) processes. This agrees with findings in previous studies on primary producers (Soininen *et al.*, 2007; Vanormelingen *et al.*, 2008; Capers *et al.*, 2010; Hájek *et al.*, 2011).

In other metacommunity studies, the relative importance of the local environment and spatial controls is determined by the geographical extent of the study. Thus, the role of dispersal limitation is presumably very relevant at a large regional scale (e.g. 10^5 km^2) and decreases in importance with diminishing spatial extent (Heino, 2011 and references therein), although some evidence against this has recently been found for macrophyte communities (Alahuhta & Heino, 2013). In our study (*c*. 90 000 km^2), the pure spatial fraction was significant, but lower than the pure environmental fraction of the three primary producer groups. Thus, environmental gradients, mainly in nutrients, were stronger than organism dispersal limitation in the shaping of species composition. Intense management may diminish the role of dispersal processes due to the abatement of production and/or dispersion of propagules, mainly for macrophytes. Moreover, the use of biocides, dredging and other management techniques may affect, not only the development of aquatic vegetation, but also the seed bank (Bonachela *et al.*, 2013) and thus enhance dispersal limitation.

An increased importance of the spatial component with increasing propagule size has been revealed for several autotrophic groups in previous studies (e.g. Beisner *et al.*, 2006; Soininen *et al.*, 2007; De Bie *et al.*, 2012). The highest dispersal rates are assumed for microscopic forms (Finlay *et al.*, 1996; Allen *et al.*, 1999; Finlay, 2002); thus, we expected that filamentous green algae and macrophyte assemblages would be more strongly spatially structured than phytoplankton and also that they would be highly related to broad-scale spatial variation due to their slower life cycles (Paszkowski & Tonn, 2000; Gillooly *et al.*, 2002). However, our results revealed not only a stronger spatial effect on phytoplankton assemblages than for macrophytes and filamentous algae, but also a linear trend, potentially indicative of dispersal limitation (Tilman, 1997; Bolker & Pacala, 1999). Linear trends imply processes operating at a scale larger than the sampling area (Borcard *et al.*, 2011). Indeed, the occurrence of specialist and singular planktonic species in our study area (Fanés, Sánchez & Comas, 2010) suggests restrictions on species distribution and hence limitations on dispersal abilities, which contrasts the 'ubiquity model' (Finlay, 2002), but supports the existence of clear geographical distribution patterns (Foissner, 2008).

The different disturbance levels varying with pond type may have caused the observed differences in the contribution of spatial and environmental predictors. A significant contribution of both environmental and spatial variables was found only for embankment ponds.

This suggests that minor management disturbances, as in embankment ponds, interfere only slightly with primary producer assemblages. Disturbance processes are apparently amplified in small, shallow and isolated ponds and lakes (Søndergaard *et al.*, 2005; Scheffer *et al.*, 2006), and this potentially plays a crucial role in our study sites. By contrast, the relative role of spatial contribution increased with the lower propagule size in artificial ponds, suggesting that the interference of management practices may alter the role of spatial contribution. Thus, disturbances may have affected the phytoplankton dissimilarity and overridden the dispersal processes of primary producers. Since we observed this only for phytoplankton, we suggest that disturbances *via* management are more harmful for primary producers with larger propagule sizes, that is, filamentous green algae and macrophytes.

The co-significance of environmental and spatial variables could also be indicative of mass effects (Cottenie, 2005), recently defined as a special case of species-sorting depending on the amount of dispersal within the metacommunity (Winegardner *et al.*, 2012; Heino, 2013). However, mass effect dynamics are described to occur at local rather than at broad scale and are less probable in isolated ecosystems (Declerck *et al.*, 2011; Hájek *et al.*, 2011; De Bie *et al.*, 2012). Perhaps mass effects were of importance for the phytoplankton assemblages, since low eigenvalues indicated fine spatial filters for this group.

The inclusion of other distance measures, for example watercourse distance, has improved the explanatory power of the models in other studies (e.g. Beisner *et al.*, 2006). However, our ponds were mostly isolated or not directly connected hydrologically by streams. Thus, the dispersal of the primary producers to and among our ponds likely occurs through other mechanisms such as wind (Kristiansen, 1996; Soomers *et al.*, 2010) or waterfowl (Figuerola & Green, 2002). This contrasts with most prior studies that have been performed in interconnected habitats (e.g. Beisner *et al.*, 2006; Akasaka & Takamura, 2012; O'Hare *et al.*, 2012) and in which the dispersal ability has been assumed to be strictly hydrochorous. Despite this, and unlike previous regional-scale studies (Beisner *et al.*, 2006; Nabout *et al.*, 2009), we obtained significant fractions of both environmental and spatial variables for phytoplankton.

The low variance explained by both environmental and spatial drivers in the primary producer assemblages was similar to the findings of several other studies (e.g. Beisner *et al.*, 2006; Hájek *et al.*, 2011; De Bie *et al.*, 2012; Alahuhta & Heino, 2013). It should be mentioned, how-

ever, that our results would have been weaker if we had excluded spatial variables. Low variances are attributable to the sampling procedure, disturbance history and intrinsic variability, that is, stochastic events, (Scheffer & Carpenter, 2003; Soininen *et al.*, 2007, 2013). The low temporal resolution of our study (ponds sampled only once) may also contribute to the low amount of variance explained (Soininen *et al.*, 2007; Lopes *et al.*, 2011). It could be argued that seasonal and interannual variability are important drivers of diversity in our study area, due to the Mediterranean climate. Thus, a caveat to our results is that our observations based on a single sample will have different numbers of taxa compared with a sampling strategy covering a full season. Furthermore, information on seasonal variation in management activities (including renewal rates as the main hydrologic source of the ponds, but also dredging and biocides treatment), may have elucidated variation in the impact of specific management strategies. Our findings are based on the assumption that the relationship between management, spatial and environmental drivers and the diversity patterns we found for a single sample hold in general. The cost of this assumption, however, should be balanced against the significant benefit gained from covering a broader gradient of environmental variables (covering a regional extent) and increasing the number of observations, per management type, which was crucial to providing data robust enough to statistically analyse the relative importance of space, environment and management strategy/disturbance levels on regional patterns of β-diversity. However, further research on the role of disturbance as a key driver of biodiversity will be needed to fully understand highly anthropogenic waterbodies (Fuentes-Rodríguez *et al.*, 2013; Lemmens *et al.*, 2013; Usio *et al.*, 2013).

In conclusion, the relative role of environmental and spatial factors determining species composition of primary producers in our study ponds depended on the management regime and other intrinsic properties of ponds determined by their typology (e.g. substratum type). Indeed, the spatial variation was not entirely determined by dispersal limitation and mass effects likely occur at local scale for the phytoplankton assemblages. However, management regime seemed to be the main constraint of variation since only the most naturalised ponds (embankment ponds) showed the expected pattern of a decreasing spatial fraction with increasing propagule size of primary producers. Despite the temporal limitation of our study, our conclusions concur with previous studies on freshwater ecosystems. Thus, from a conservation perspective, embankment

ponds are preferable to artificial ponds; this is because they show patterns similar to those of lakes and other natural ponds as well as promote the α-diversity of phytoplankton. The construction of excavated and artificial ponds contributes to the regional species pool by enhancing the β-diversity of both phytoplankton and filamentous green algae.

Acknowledgments

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Non-metric multidimensional scaling ordinations (n-MDS) of phytoplankton (PHY), filamentous green algae (FGA) and macrophytes (MAC).

Table S1. Summary of the main environmental and spatial drivers of primary producer diversity and community structure expressed as mean values and standard deviations according to pond typology.

Table S2. Number of ponds with presence of benthic primary producers, such as either filamentous green algae (FGA) or/and macrophytes (MAC) per pond type and in total.

Data S1. Detailed procedure to test the absence of spatial autocorrelation in the selected GAM models.

Data S2. Classification of phytoplankton species according to survival strategies (C, S, R) per pond type (Reynolds, 2006).

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