

Watershed land use types as drivers of freshwater phytoplankton structure

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Abstract The potential importance of watershed land use types, lake/watershed morphometry/topography and geographic distance as drivers of phytoplankton community composition was evaluated by using data collected from 18 freshwaters (lakes and reservoirs) distributed around Greece. In all freshwaters, phytoplankton species composition showed a strong correlation with the composition of land uses within their watersheds but no correlation with morphometry/topography and geographic distance. Cyanobacteria were found to be associated with artificial and agricultural land use types. Chrysophytes were closely associated to forested areas whereas euglenophytes to industrial, commercial, and transport units. Phytoplankton total biomass was significantly higher in freshwaters with a cover of agricultural and artificial land use >30% in their watersheds. This rather low

threshold of agricultural and artificial land use cover might be indicative of the higher sensitivity of Mediterranean freshwaters to eutrophication process. Analysis performed separately for lakes and reservoirs revealed some diverse patterns with lake morphometric/topographic variables significantly affecting similarity in species occurrence. The results demonstrate that land use types reflecting anthropogenic pressures could act as critical drivers explaining phytoplankton structure. Our research suggests that Mediterranean freshwaters could be highly sensitive to land use types within their watersheds, thus landscape structure and configuration should be taken into account toward effective conservation and management plans.

Keywords Land use types · Drivers · Freshwater phytoplankton · Lakes and reservoirs · Mediterranean

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Introduction

Agriculture has been acknowledged as one of the most important drivers of land transformation in global scale (Lambin et al., 2006), whereas many global studies have shown that a big percentage of cultivated land has been created against forests and wetlands (Millennium Ecosystem Assessment, 2005). Freshwaters are important life resources. Whereas good water quality of these systems is a prerequisite for numerous ecosystem services (Meybeck & Helmer, 1996), in most parts of the world freshwater ecosystems have

suffered severe degradation (Carpenter et al., 2011). The causes of degradation of these ecosystems are strongly related to the surrounding land use types reflecting undergoing activities (Perry & Vanderklein, 1996). As a result, studies on the potential factors driving changes in water conditions and aquatic communities have become increasingly popular during the last decades, with our knowledge about individual drivers accumulating rapidly (Stomp et al., 2011).

Understanding the relationships between ecological lake functionality and watershed changes is an essential step for the selection and application of effective, long-term conservation and management strategies (Silva et al., 2011). Toward this direction, scientists have used biological indicators of water quality for detecting potential changes of biotic communities structure over spatial and temporal scales (Burns & Galbraith, 2007; Van Egeren et al., 2011). Phytoplankton is a primary biotic community indicating changes in ecological water quality due to its sensitivity and dynamic responses to the surrounding environment (Padisák et al., 2006). Shifts in the taxonomic composition of phytoplankton as a result of changes in nutrient conditions have been widely documented, with more clear evidence arising from studies on summer phytoplankton communities (Sommer, 1989; Watson et al., 1997). Phytoplankton groups are suggested to reflect trophic conditions (Rojo et al., 2000). For instance, in eutrophic freshwaters the relative importance of chrysophytes to community structure (biodiversity, biomass) decreases whereas that of cyanobacteria increases (Watson et al., 1997). Moreover, in stressed and heavily degraded ecosystems, a decrease in biodiversity is associated with an increase in biomass of few species (Perry & Vanderklein, 1996; Michaloudi et al., 2009).

Agricultural and urban land type uses are recognized as the main sources of nutrient input and various contaminants in lakes and reservoirs (Carpenter et al., 1998; Carney, 2009). When exceeding 40 and 15% of the watershed area, respectively, they are considered as significant morphological alterations and pressures in freshwaters (LAWA, 2003). The transformation of natural catchment into agricultural land, industry or urban areas and the associated eutrophication of the water are also considered a major threat to freshwater species diversity (Weijters et al., 2009). The role of land use and watershed development as descriptors of aquatic

biodiversity is highlighted in a limited number of studies dealing with phytoplankton (Burns & Galbraith, 2007; Stomp et al., 2011) and other components of the aquatic biota such as bacteria, protozoa (Burns & Galbraith, 2007), and zooplankton (Van Egeren et al., 2011). Hoffmann & Dodson (2005) showed that watershed development was the best single descriptor of zooplankton richness for all lakes describing biodiversity patterns better than productivity or lake area alone. On the other hand, lake morphometry is considered as the best index of phytoplankton structure and productivity, reflecting climate and watershed conditions (Wetzel, 2001; Mazaris et al., 2010). For reservoirs it is well-known that hydraulic regime, size, and depth changes due to operational use have clear implications on their biotic communities (Kennedy, 1999). Still the limited studies that investigate phytoplankton composition and biomass changes in relation to freshwater/watershed morphology or land use (e.g., Maberly et al., 2003; Carney, 2009; Liu et al., 2011) provide information on a local rather than a broad spatial scale (Stomp et al., 2011). Furthermore, this information concerns mainly temperate areas whereas limnosystems of other regions such as the Mediterranean are quite distinct from the contemporary limnological paradigm; further raising the need for additional research (Alvarez Cobelas et al., 2005).

Clearly, there are a number of reasons why phytoplankton community structure can be used for assessing water quality. Notably, there is evidence to suggest that environmental heterogeneity could drive the observed compositional patterns. While occurrence of specific phytoplankton species could primarily be limited by abiotic conditions (lake depth, water retention time) and biotic interactions (Reynolds et al., 1993), recent evidence from biogeographical studies have raised the issue of distance decay patterns in microorganism community composition (Whitaker et al., 2003; Soininen et al., 2007). Considering these results, it is critical that before using phytoplankton community structure as an indicator of water quality and environmental conditions, we should improve our understanding on whether compositional structure and properties are driven by geographical distance limitations, by pure environmental factors or their combination. Only recently, studies on determinants of phytoplankton metacommunity structure across freshwaters have received great interest (Soininen et al., 2007).

This article aims to show the potential importance of pressures that human activities pose on phytoplankton structure of lakes and reservoirs contributing (i) to the limited number of papers linking land use types and phytoplankton and (ii) to the knowledge on phytoplankton metacommunity structure determinants. Therefore, phytoplankton structure of 11 lakes and 7 reservoirs in Greece was examined in relation to watershed land use types, morphometric/topographic variables, and geographical distance. Three were the basic objectives: (1) to assess the potential influence of watershed land use types and lake/watershed morphometry/topography on phytoplankton community descriptors (species, taxonomic groups, and total biomass) of a wide range of freshwaters, (2) to test whether compositional patterns of phytoplankton are driven also by geographical distance, and (3) to investigate if the relative importance of watershed land use types, lake/watershed morphometry/topography and/or geographical distance vary between the natural lakes and reservoirs.

Materials and methods

Study area

A total of 18 freshwaters (11 lakes and 7 reservoirs) of different trophic status and hydrological regimes were included in this study (Fig. 1). The freshwaters ranged in surface area from 1.3 to 65 km² and had a maximum depth from 1.1 to 120 m. They were located across an altitudinal gradient ranging from 25 to 850 m a.s.l. extending at a longitude from 20°53'E to 26°1'E and latitude from 38°10'N to 40°59'N. Their watersheds ranged in area from 76 to 11763 km² (Table 1).

Phytoplankton data

Phytoplankton data were obtained during the warm period (June–October) of the years 2007–2010. At least three samplings were performed during this period at each freshwater. Depth-integrated samples were collected from the euphotic zone near or at the deepest part of each freshwater. Live and preserved samples were examined in sedimentation chambers using an inverted microscope with phase contrast (Nikon SE 2000). Phytoplankton individuals were identified to species level using taxonomic keys. Cyanobacteria were

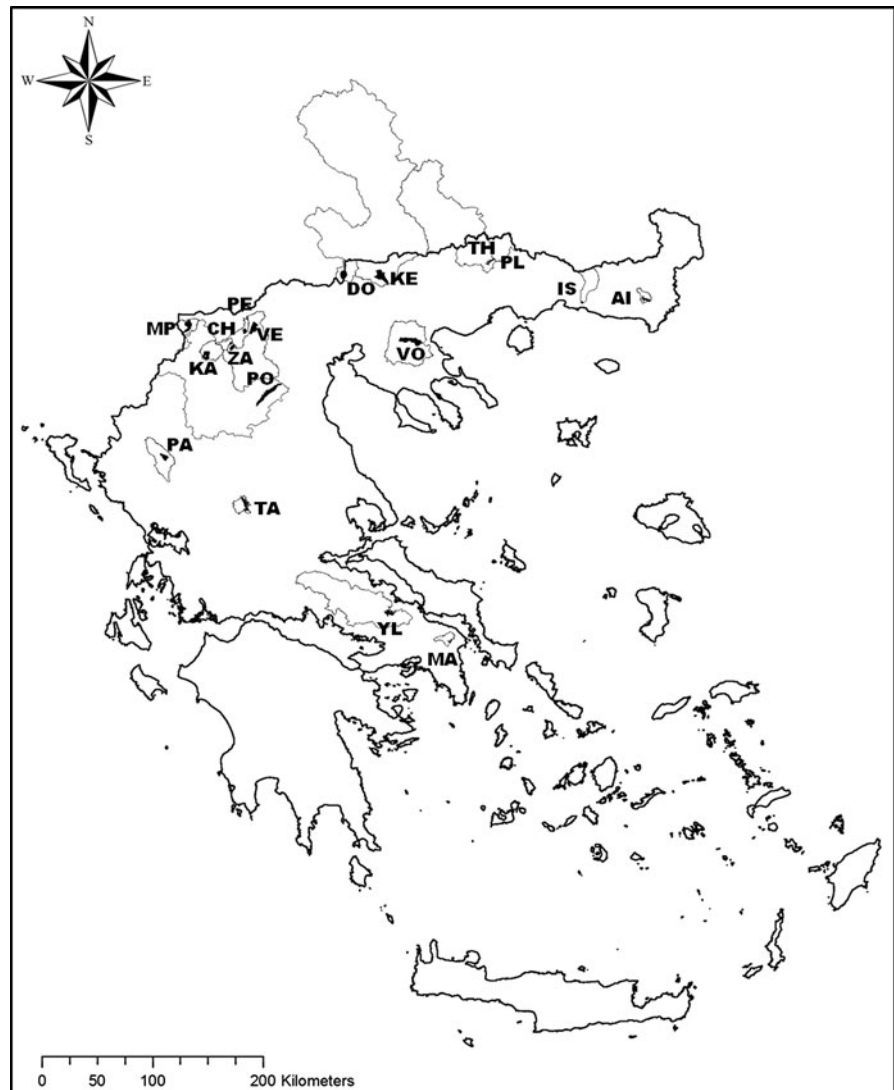
evaluated by polyphasic approach (e.g., Moustaka-Gouni et al., 2010). Phytoplankton counts (cells, colonies, and filaments) were performed using Utermöhl's sedimentation method (Utermöhl, 1958). At least 400 individuals in total and 100 individuals of the most abundant taxa were counted per sample in sedimentation chambers of 50, 25, 10, 5, and 2 ml, depending on the density of the phytoplankters in the samples. For biomass estimation, the dimensions of 30 individuals (cells, colonies, or filaments) of each species were measured using tools of a digital microscope camera (Nikon DS-L1). Mean cell or filament volume estimates were calculated using appropriate geometric formulae (Hillebrand et al., 1999).

Freshwaters morphometric/topographic data and watersheds land use types

In the present analysis, we used a number of morphometric and topographic variables [surface area (km²), mean and maximum depth (m), watershed area (km²), and altitude (m)] as potential drivers of phytoplankton changes. ArcGis software (GIS, 1994) was employed to draw lake/reservoir and watershed areas based on physical barriers and topographical features. Mean and maximum depths were available from various sources (i.e., research programs, the Hellenic Ministry of Agriculture). Geographical distance between two freshwater systems, was estimated as the Euclidean distance between their centers.

The database of CORINE Land Cover 2000 for Greece (EEA, 1993) was used in order to identify land use types of watersheds. The CORINE Land Cover 2000 database represents the only land use type database validated at national level. Land use types are grouped into three levels, with increasing details on the spatial elements of the land use types presented; in this study we used the second and third levels of land use data for our analysis. Land-use cover proportions were calculated at the scale of the entire watershed using analytical tools of ArcInfo (ArcGIS 10.x software). Basic land use types recognized within our study areas include: agricultural (arable land/permanent crops/pastures/heterogeneous areas), artificial (urban fabric/industrial, commercial and transport/mine, dump and construction/artificial non-agricultural vegetated areas), wetland (inland, maritime), forest and semi-natural (forests/scrubs and herbaceous vegetation/open spaces) land use categories.

Fig. 1 Map of Greece indicating the location of the studied freshwaters and their watersheds (*MP* Mikri Prespa, *KA* Kastoria, *CH* Chimaditis, *ZA* Zazari, *PE* Petron, *VE* Vegoritis, *PA* Pamvotis, *DO* Doirani, *KE* Kerkini, *VO* Volvi, *TH* Thisavros, *PL* Platanovrisi, *IS* Ismarida, *AI* Aisimis, *PO* Polyphytos, *TA* Tavropos, *YL* Yliki, *MA* Marathonas)



Data analysis

In order to examine any potential difference in phytoplankton biomass between freshwaters with a high and a low cover of artificial and agricultural land use we performed non-parametric Mann–Whitney test. To proceed with the pairwise comparisons in phytoplankton biomass, we grouped freshwaters by applying different thresholds of % cover in artificial and agricultural land use ranging from 15 to 45%.

To examine the influence of land use types, morphometry/topography and geographic distance on phytoplankton species composition we used standard Mantel and partial Mantel permutation tests

(Green et al., 2004; Reche et al., 2005; Sommaruga & Casamayor, 2009). Mantel correlation coefficient (r_s) ranges from -1 to 1 , with the significance of the tests determined based on 999 permutations (Clarke & Warwick, 2001, Rosenberg, 2001).

The standard Mantel test is used in order to compare two independent similarity matrices that describe the same set of entities (Quinn & Keough, 2002). In our study, the entities were the different freshwaters and standard Mantel tests were used to test whether the associations between phytoplankton occurrence data (presence/absence per freshwater) and morphometric/topographic variables (per site) or percentage of land use types cover (per freshwater) or geographical distances

Table 1 Morphometric/topographic features of the studied freshwaters and percentage (%) of land use cover in their watersheds (WA:LA Watershed Area:Lake Area)

Code	Freshwater	Morphometric/topographic features					Land use cover (%)				
		Altitude	Area (km ²)	Watershed area (km ²)	WA:LA	Mean depth (m)	Artificial	Agricultural	Forests & Semi-natural	Wetlands	Freshwaters
MP	Mikri Prespa	850	39.15	197.83	5	4.1	0.26	13.89	4.85	4.85	19.84
KA	Kastoria	625	28.97	271.63	9	4.1	1.58	33.69	53.29	0.77	10.67
ZA	Zazari	600	2.04	75.73	37	1.7	1.55	40.17	55.58	0.00	2.69
CH	Chimaditis	590	10.56	112.58	11	1.2	1.16	35.54	52.11	0.00	11.19
PE	Petron	575	10.10	346.43	34	2.6	5.89	47.90	38.85	0.81	6.55
VE	Vegorit	510	40.62	2108.53	52	20	6.96	40.08	49.82	0.13	3.02
DO	Doirani	150	34.83	299.42	9	3	1.94	34.79	49.16	2.48	11.63
IS	Ismarida	25	1.31	320.54	245	0.5	4.19	48.42	45.36	1.58	0.44
VO	Volvi	40	68.41	1281.67	19	13.8	1.08	44.14	49.07	0.37	5.34
PA	Pamvotis	500	20.07	479.94	24	4.3	8.17	44.85	42.07	0.73	4.18
YL	Yliki	100	20.65	2436.44	118	28	1.67	47.92	49.38	0.00	1.03
KE	Kerkini	50	65.16	11762.85	181	3.1	2.59	31.31	65.04	0.24	0.82
AI	Aisimis	200	8.73	93.99	11	15	0.00	10.88	79.84	0.00	9.29
PO	Polyphytos	300	64.37	5577.85	87	26.2	0.93	36.25	61.93	0.17	0.72
TA	Tavropos	800	21.62	163.077	8	47	0.00	14.74	72.00	0.00	13.26
MA	Marathonas	230	1.71	118.86	70	15	10.28	48.18	40.10	0.00	1.44
TH	Thisavros	400	6.93	4233.84	611	40	1.30	17.96	79.75	0.00	0.99
PL	Platanovrisi	250	2.03	4630.55	2281	15	1.22	16.42	81.38	0.00	0.98

between freshwater, were stronger than expected from chance. In addition, partial Mantel tests were used to examine the relationships between any two matrices while holding another one constant (Legendre, 2000). Phytoplankton composition refers either to species composition or to taxonomic groups composition. Species composition is based on the species occurrence data. The species occurrence data were used for the species presence/absence matrices of analysis.

We used Bray Curtis index to produce similarity matrices for every pair of freshwaters based on phytoplankton occurrence data. Similarity matrices were also produced separately for the morphometric/topographic variables and percentage of land use types cover by using Euclidian distance as a measure through multivariate space between the data points. Morphometric/topographic variables were standardized prior the production of the similarity matrix. An inter-lake/reservoir distance matrix was also produced based on Euclidian distances between the center of each freshwater.

Single matrices (morphometric/topographic variables, land use types, and geographic distance) were used to examine independently their potential influence upon phytoplankton similarity by mean of Mantel permutation tests. Partial Mantel tests were employed to examine for plausible correlation between phytoplankton species composition and each one of the above groups of variables by gradually keeping constant the remaining matrices. For example, we addressed the plausible correlation between geographic distance and phytoplankton species composition by initially holding the morphometric/topographic matrix constant; next we kept constant the land use matrix and finally both matrices were hold constant. This process was repeated for all three groups of parameters, resulting in a total of nine separated analyses.

To investigate whether patterns of phytoplankton community structure are influenced by the same groups of parameters we repeated the above analysis after grouping freshwaters as lakes or reservoirs.

Canonical Correspondence Analysis (CCA) (Quinn & Keough, 2002) was used to assess the relationship between land use types with (a) phytoplankton species composition and (b) phytoplankton taxonomic groups composition. In order to achieve a better interpretation of the results, land use types were grouped according the second scheme of Corine Land Cover data set which actually divides detailed land use types into 999 broader categories. Following this procedure, a total of 15 land use types were recognized in our study areas and maintained for the analysis.

Single Mantel tests and partial Mantel tests were run by Passage software (Rosenberg, 2001); CCA and the Mann–Whitney test were performed by Past software Version 2.09 (Hammer et al., 2001).

Results

The majority (72%) of the studied freshwaters belonged to watershed basins with artificial and agricultural land types covering more than 30% of their area (Table 1). According to the different land use cover types retrieved from Corine 2000, catchment modification is more intense around lowland lakes and reservoirs.

A total of 300 phytoplankton species were identified in the 18 freshwaters during the warm period of 2007–2010. These species belonged to nine taxonomic groups (Fig. 2). The most diverse taxonomic group was chlorophytes (138 species) followed by cyanobacteria (65) and euglenophytes (41). Mean phytoplankton biomass ranged from $0.6 \pm 0.75 \text{ mg l}^{-1}$ to $236.6 \pm 2.7 \text{ mg l}^{-1}$ (Fig. 3). Pairwise correlation analysis demonstrated that significantly higher values were recorded in those freshwaters with an agricultural and artificial land use cover $>30\%$ in their watersheds (Higher cover $167.76 \pm 82.13 \text{ mg l}^{-1}$; lower $6.63 \pm 4.02 \text{ mg l}^{-1}$) (Mann–Whitney $U = 7.01$; $P = 0.01$).

Phytoplankton composition (presence/absence matrix) was significantly related to the composition of land use types within their watershed ($r_s = 0.378$, $P < 0.01$). In contrast, we found no significant relationship between phytoplankton composition and morphometry/topography similarity matrix or the geographic distance matrix of the freshwaters ($P > 0.05$). The significant relationship between phytoplankton species composition and land use type matrix was maintained even after we removed the effect of morphometry/

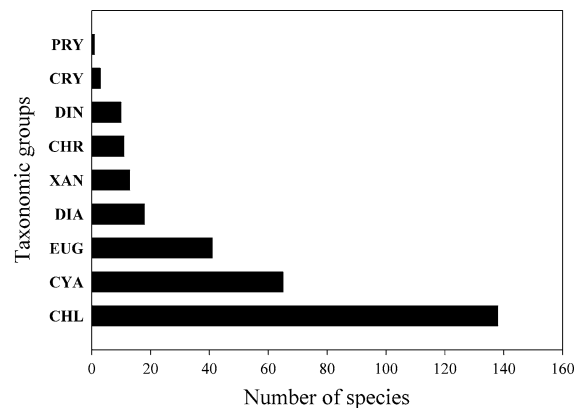


Fig. 2 Total number of species belonging to taxonomic groups (*DIN* Dinophytes, *CYA* Cyanobacteria, *CHR* Chrysophytes, *CRY* Cryptophytes, *DIA* Diatoms, *EUG* Euglenophytes, *CHL* Chlorophytes, *PRY* Prymnesiophytes, *XAN* Xanthophytes) in the studied freshwaters during the period 2007–2010

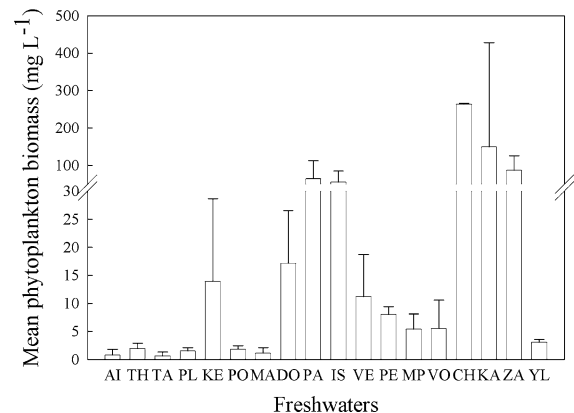


Fig. 3 Mean phytoplankton biomass values recorded in the studied freshwaters during the period 2007–2010. Error bars represent standard deviation

topography ($r_s = 0.32$, $P < 0.01$) and geographic distance ($r_s = 0.367$, $P < 0.01$) but also their combined effect ($r_s = 0.31$, $P < 0.01$). Partial Mantel test revealed no other statistical significant relationship.

Different results were obtained when analyzing separately lakes and reservoirs. Phytoplankton species composition of lakes showed a significant correlation with morphometric/topographic variables ($r_s = 0.39$, $P < 0.05$). Still, partial Mantel tests showed no significant correlation for any of the studied matrices. Standard Mantel tests revealed the lack of similarity between phytoplankton species composition of reservoirs and any of the explanatory matrices. However,

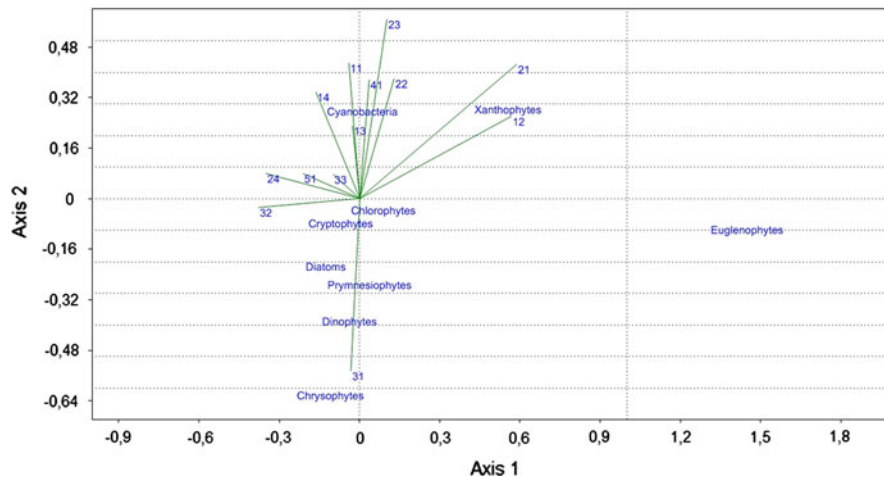


Fig. 4 Ordination diagram for the Canonical Correspondence Analysis of phytoplankton taxonomic groups present in the studied freshwaters and the land use types in the corresponding watersheds (11–14 artificial: 11 urban fabric, 12 industrial commercial and transport units, 13 mine dump and construction

sites, 14 artificial non-agricultural vegetated areas; 21–24 agricultural: 21 arable land, 22 permanent crops, 23 pastures, 24 heterogeneous agricultural areas; 31–33 forests: 31 forests, 32 scrub and/or herbaceous vegetation associations, 33 open spaces with little or no vegetation; 41 wetlands; 51 water bodies)

once the effect of land use types and geographic distance were removed, morphometry/topography was highly correlated with species composition matrix.

The results of the CCA for phytoplankton taxonomic groups (Fig. 4) showed that the first axis of the plot conditional model explained 58.4% of the variance in the species data. This axis represented a gradient from arable lands (Corine type 21) and industrial, commercial and transport units (Corine type 12) to natural shrub and/or herbaceous vegetation associations (Corine type 32). The second axis explained 22.04% of the variance in the species data and represented a gradient of pastures (23) to forests (31). The locations of the taxonomic groups in the biplot indicate the plot level conditions to which they were most closely associated. Cyanobacteria were more closely associated with artificial and agricultural land use types such as urban (Corine type 11) and artificial (Corine type 13, 14) sites and permanent crops (Corine type 22). Chrysophytes, dinophytes, prymnesiophytes, and diatoms were closely associated to forests (Corine type 31) and xanthophytes to arable land (Corine type 22) and industrial, commercial and transport units (Corine type 12). Chlorophytes were located very close to the axes cross point. In contrast, euglenophytes formed a separate group apart from the rest taxonomic groups with a location in the biplot more close to artificial and agricultural land types.

CCA analysis did not reveal a clear pattern between phytoplankton species composition and land use types.

Discussion

The results of our analysis highlighted the importance of land use types as potential drivers shaping phytoplankton community structure. Despite the differences in hydrological regime and morphometric/topographic variables characterizing the 18 studied freshwaters, land use types were strongly correlated with phytoplankton community structure of all freshwaters even after controlling for geographical distance and morphometric/topographic heterogeneity. Among the most important land use types recognized to better distinguish phytoplankton community structure were agricultural and artificial areas.

According to the German Working Group on water issues (LAWA, 2003), agricultural and artificial (e.g., urban) land use types exceeding a 40 and 15% of the catchment area, respectively, are considered as important morphological alterations and pressures on freshwaters water quality. In our study, phytoplankton biomass was significantly higher in freshwaters with watersheds cover of agricultural and artificial land use >30%, thus revealing lower thresholds of agricultural

and artificial land use cover for changes in phytoplankton biomass. It is most likely that the lower values obtained in this study might show the critical transition threshold in eutrophication process from mesotrophic to highly eutrophic freshwaters under anthropogenic pressures in the Mediterranean landscape. In this region, due to the higher watershed area : lake area ratio of freshwaters compared to those of cold temperate ones, lakes and reservoirs should experience stronger watershed effects (Alvarez Cobelas et al., 2005) and might be more vulnerable to lower percentage of agriculture land use. In our study, most lakes and reservoirs had a quite higher watershed area:lake area ratio than the cold temperate ones, comparable to the ratio of other Mediterranean freshwaters (Alvarez Cobelas et al., 2005). Another plausible explanation could be the rather small number of sites used in our study in comparison to the sites used by LAWA.

Land use was also recognized as the most important remote driver of phytoplankton species composition for all freshwaters. Evidence from recent studies performed at the same region demonstrated that phytoplankton species occurrence and diversity is largely affected by environmental heterogeneity (Mazaris et al., 2010). At the long-term, land use types are likely to affect morphological and biochemical features of freshwaters; for example agricultural and urban land type uses are recognized as the main sources of nutrient input in lakes and reservoirs (Carpenter et al., 1998; Carney, 2009). Excessive input of nutrients, particularly phosphorus, regardless of the type of freshwater can result in implications for its phytoplankton community structure by increasing primary production, reducing water transparency and oxygen, reducing diversity and inducing the occurrence of phytoplankton algal blooms often dominated by toxin-producing species (Lampert & Sommer, 2007).

In this study, land use types were also found to be strongly correlated with phytoplankton composition at a higher taxonomic level. Cyanobacteria species were found to be associated with artificial and agricultural land use types such as urban and artificial sites and permanent crops. The high contribution of cyanobacteria species to phytoplankton diversity has been commonly observed in eutrophic lakes in Greece (e.g., Moustaka-Gouni, 1993; Mazaris et al., 2010) and worldwide (e.g., Reynolds, 1998). Chrysophytes, dinophytes, prymnesiophytes, and diatoms were closely associated to forests. These groups generally

predominate at a lower nutrient status (Reynolds, 1984; Sommer, 1989; Padisák et al., 2009). The most species-diverse group of freshwater phytoplankton, chlorophytes, was located at the axes cross and, this may indicate their ubiquitous distribution in freshwaters, dominance in airborne phytoplankton and their role as pioneer colonists in aquatic systems (Chrysostomou et al., 2009; Genitsaris et al., 2011). In contrast, the location of euglenophytes in the biplot clearly separated this group apart from the rest taxonomic groups with them being closer to artificial (industrial, commercial, and transport units) and agricultural land types. A high number of euglenophytes species is reported in water bodies with a high content of organic substances (Borics et al., 2003). In our case, high species richness and similarity of euglenophytes were observed in four shallow lakes. The highest number of euglenophyte species along with the highest number of phytoplankton species was observed in the very shallow lake Ismarida (IS) which has a high watershed area: lake area ratio and a high percentage of water column occupied by macrophytes. An increase in phytoplankton species richness with percentage of the water column occupied with submerged macrophytes is also reported in subtropical shallow lakes (Kruk et al., 2009).

The distribution of phytoplankton species in the studied freshwaters was not related to geographical distance thus not exhibiting any spatially predictable occurrence pattern. The lack of distance decay phytoplankton pattern in our study does not clearly imply a random or cosmopolitan phytoplankton distribution. There is known evidence to support that both local environmental factors and geographical distance could drive microorganism community composition (Martiny et al., 2006). Soininen et al. (2007) found that plankton community composition may be jointly regulated by neutral and niche-based processes by examining determinants of plankton metacommunity structure across small spatial scale in boreal wetland ponds. Recently, large-scale biodiversity patterns in freshwater phytoplankton have been presented by Stomp et al. (2011) who showed that biodiversity gradients in phytoplankton were driven by local environmental factors, implying land use effects.

Our analysis performed separately for lakes and reservoirs revealed some different patterns. Lakes sharing similar morphometric/topographic variables (depth, surface, watershed area, and altitude) showed

significantly higher similarity in species composition (e.g., Mazaris et al., 2010). In reservoirs a strong effect of morphometry was only found after removing the direct effect of land use and geographic distance. It is well-known that reservoir hydraulic changes due to operational use have clear implications on the biotic communities of these highly dynamic systems (Kennedy, 1999). The lack of correlation between the community matrix and land use does not necessarily imply the lack of effect of the latter on the reservoir's phytoplankton composition. Actually, one could argue that the land use effect on phytoplankton community composition might be greater in reservoirs since nutrient loads to these systems are usually greater than for lakes located in drainage basins with similar land uses (Jørgensen et al., 2005). Reservoirs generally have higher watershed area:lake area ratios than lakes. In our study, the average watershed area:lake area ratio of the reservoirs (464.1) was considerably higher than that of lakes (51.2). A possible explanation for the lack of correlation between the community matrix and land use in reservoirs, considering also that the strong relationship between morphometry and community composition only appears when removing the effect of land use and geographic distance, is that drivers and responses interact (Carpenter et al., 2011). Consequently, a certain phytoplankton community composition is typically the result of multiple causes (drivers) which often interact and vary geographically. Therefore, it is not always feasible to disentangle these interactions so as to understand and moreover to explain separately the causes and consequences of a given state (Carpenter et al., 2011). Furthermore, the most striking feature of reservoirs, the shorter water retention time compared to lakes with profound effects on phytoplankton structure (Katsiapi et al., 2011) might suppress the correlation between the community matrix and land use types.

Overall, our study suggests that agricultural and urban land uses within a freshwater's watershed represent an important driver of phytoplankton community structure, (composition and diversity). Tracing the links between remote variables such as land use types and phytoplankton structure at different spatial and temporal scales provides a unifying approach toward understanding how biotic communities of lakes and reservoirs are shaped under anthropogenic pressures. This is rather important for water management in regions such as the Mediterranean, where

freshwaters are insufficiently studied, different from the cold temperate ones and highly vulnerable to anthropogenic pressures and climate change.

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