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Carbon dioxide efflux during the flooding phase of temporary ponds

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ABSTRACT

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Small water bodies, such as temporary ponds, have a high carbon processing potential. Nevertheless, despite the global occurrence of these systems, the carbon effluxes from such water bodies have been largely overlooked. In this study, we examined the intra- and intersystem variability of carbon dioxide (CO_2) effluxes from a set of Mediterranean temporary ponds during the flooding phase, a hot-spot for biogeochemical cycling in temporary systems. The CO_2 effluxes showed higher variability among the various sections of each pond (i.e., inundated, emerged-unvegetated and emerged-vegetated) than among the ponds. The emerged-vegetated sections showed the highest CO_2 effluxes per unit area and tended to drive the total effluxes at the whole-ecosystem scale. The mean CO_2 efflux (121.3 ± 138.1 mmol m^{-2} d^{-1}) was in the upper range for freshwater ecosystems. The CO_2 effluxes were not related to catchment properties but rather to the organic content of the sediments, especially in the emerged sections of the ponds. Our results indicate that temporary ponds, especially their emerged sections, are important sources of CO_2 to the atmosphere, highlighting the need to include the dry phases of these and other temporary aquatic systems in regional carbon budgets.

Key words: Carbon fluxes, CO_2 emissions, temporary ecosystems, temporary ponds.

RESUMEN

Flujos de dióxido de carbono durante la fase de inundación de estanques temporales

Los pequeños cuerpos de agua como los estanques temporales tienen un elevado potencial para procesar carbono. Sin embargo, a pesar de su presencia global, los flujos de carbono procedentes de estos sistemas han sido muy poco estudiados. En el presente trabajo, se estudió la variabilidad intra- e inter-sistémica de los flujos de dióxido de carbono (CO_2) en un conjunto de estanques temporales mediterráneos durante su fase de inundación, un momento en que los ciclos biogeoquímicos en sistemas temporales se intensifican. Las emisiones de CO_2 presentaron una mayor variabilidad entre las diferentes secciones dentro de cada estanque (es decir, inundada, emergida-sin vegetación y emergida-vegetada) que entre los diferentes estanques. Las secciones emergidas-vegetadas mostraron las mayores emisiones de CO_2 por unidad de superficie, siendo las principales responsables de las emisiones totales a escala ecosistémica. Las emisiones de CO_2 (media 121.3 ± 138.1 mmol m^{-2} d^{-1}) corresponden al rango superior para ecosistemas de agua dulce. Las emisiones no mostraron relación con las características de la cuenca de captación de cada estanque, sino más bien con el contenido en materia orgánica de los sedimentos, especialmente en las secciones emergidas de los estanques. Nuestros resultados indican que los estanques temporales, especialmente sus secciones emergidas, son importantes fuentes de CO_2 hacia la atmósfera, poniendo de manifiesto la necesidad de incluir las fases secas de éstos y otros sistemas acuáticos temporales en los balances regionales de carbono.

Palabras clave: *Flujos de carbono, emisiones de CO_2, ecosistemas temporales, estanques temporales.*

INTRODUCTION

Ecological processes in small aquatic ecosystems have been poorly studied to date because it has been assumed that small systems make a minor contribution to global processes (Downing, 2010). However, recent studies have drawn attention to these systems, arguing that small lakes and ponds not only dominate the areal extent of inland waters but also support disproportionately intense processes compared with larger ecosystems (Downing, 2009; Downing *et al.*, 2006). For example, it has been shown that areal rates of carbon burial, oxygen depletion, and CO_2 efflux are much higher in smaller than in larger water bodies (Dean & Gorham, 1998; Downing *et al.*, 2008; Kortelainen *et al.*, 2006).

Temporary ponds are small inland water bodies that experience periodic emerged (no surface water) phases (Williams, 1997). They are well known to host a large number of rare and endemic species and are recognised as key ecosystems for biodiversity conservation (Miracle *et al.*, 2010). Contrastingly, little is known about their biogeochemical functioning. Indeed, temporary ponds represent a particular case of a neglected ecosystem for biogeochemists, primarily because their temporary nature poses a challenge for the study of biogeochemical processes. In particular, although studies in Arctic landscapes have demonstrated that carbon effluxes to the atmosphere from temporary ponds can represent up to one-half of the regional emissions (Abnizova *et al.*, 2012), little is known about the rates of carbon processing and the drivers of such processes in other regions (Downing, 2010). Such a lack of knowledge is particularly critical in arid and semi-arid areas of the world such as the Mediterranean, where temporary ponds are one of the most frequent types of inland water (Sánchez-Carrillo, 2009). A proper characterisation of the carbon fluxes mediated by temporary ponds and other temporary ecosystems in both their emerged and inundated phases is thus a necessary step for detailed regional carbon budgeting in these areas. In particular, carbon effluxes from the water body are a key component of carbon cycling in systems such as temporary ponds, where transport fluxes along aquatic conduits have a minor role in the fate of carbon.

In this study, we examined the intra- and intersystem variability of CO_2 effluxes from a set of Mediterranean temporary ponds during the flooding phase, a hot-spot for biogeochemical cycling in temporary systems (Huxman *et al.*, 2004; Valett *et al.*, 2005; Jenerette *et al.*, 2008). We expected the areal CO_2 effluxes to be comparable to or even higher than typical effluxes from other Mediterranean stagnant aquatic ecosystems. Finally, we investigated whether the CO_2 effluxes in the ponds were determined by properties of the surrounding catchment or dominated by the intrinsic properties of each pond.

MATERIALS AND METHODS

Study sites

We studied a total of 12 temporary ponds located on the island of Menorca (39°56′N, 4°6′E, Balearic Islands, Western Mediterranean). The climate is Mediterranean, with a dry and hot summer period. The mean monthly temperatures range from 10 °C in January to 25 °C in August. The mean annual precipitation is 549 mm and is typically concentrated in autumn and winter, with November the most humid month and July the driest. The ponds were selected from a detailed inventory of these systems on the island (Fraga *et al.*, 2010) to cover the widest possible spectrum of physicochemical (Pretus *et al.*, 2010), geomorphologic (Cardona *et al.*, 2010) and hydrological properties (Estaún *et al.*, 2010). Thus, the selected ponds range widely in terms of environmental properties (Table 1).

Field and laboratory methods

The study was conducted during the flooding phase of the ponds in November 2013. A cumulative rainfall of 130 mm was recorded from the end of the dry phase (September) until the sampling campaign. The CO_2 efflux or exchange of CO_2 with the atmosphere (F_{CO_2}) was measured in both the inundated and emerged sections of

Table 1. Morphometric and physicochemical characteristics of the studied ponds and their catchments. *Propiedades morfométricas y físicoquímicas de los estanques temporales estudiados y sus cuencas.*

Pond	Morphological features						Physico-chemistry	Main land uses	Main lithology
	Max. Depth (cm)	Max. flooding area (m^2)	Area frequently flooded (m^2)	Area ephemerally flooded (m^2)	Area flooded during sampling (m^2)	Surface catchment (ha)			
Son Morell	20	580	201	380	85	2.1	Turbid (inorg. particles), lowly mineralized	Urbanization and pine forests†	Limestones and conglomerates
Curniola	150	769	545	225	0.0	173	Turbid (inorg and org. particles), lowly mineralized	Dry croplands	Sandstones and limestones
Binigafull	48	357	357	0.0	0.0	0.3	Transparent, strongly vegetated	Irrigated croplands	Conglomerates
Bassa verda	140	863	208	655	208	1.1	Extensively vegetated with strongly coloured (DOC) water.	Pine forests	Sandstones and conglomerates
Torrellafuda	165	2448	916	1533	340	107	Turbid (inorg. particles), intermediate DOC.	Dry and irrigated croplands	Limestones (calcarenite)
Mal lloc	155	832	481	351	322	12.3	Extensively vegetated, dystrophic, strongly coloured (DOC) water.	Dry croplands and med. forests§	Limestones (calcarenite)
Pallisses	36	340	144	197	0.0	2.4	Strongly mineralized and antropogenically influenced (nutrients)	Dry croplands and shrublands	Pelites and sandstones
Bassa verda des compte	91	1045	1045	0.0	0.0	1.2	Turbid (inorg. particles), lowly mineralized	Shrublands and pine forests	Marl and limestones
Ets armaris	58	4369	1945	2424	0.0	6.1	Turbid (inorg. particles), dystrophic, intermediate DOC.	Dry croplands and coastal vegetation	Turbidites
Sa Mesquida	103	313	242	71	242	0.2	Extensively vegetated and strongly mineralized	Urbanization	Turbidites
Cap Negre	49	351	98	253	98	0.3	Transparent, intermediate DOC	Shrublands	Turbidites
Marina Curniola	55	149	44	36	0.0	3.1	Transparent, low DOC	Shrublands	Dolomites, limestones and marlstones

† *Pinus halepensis* forests, § *Quercus ilex* and *olea europaea* forests.

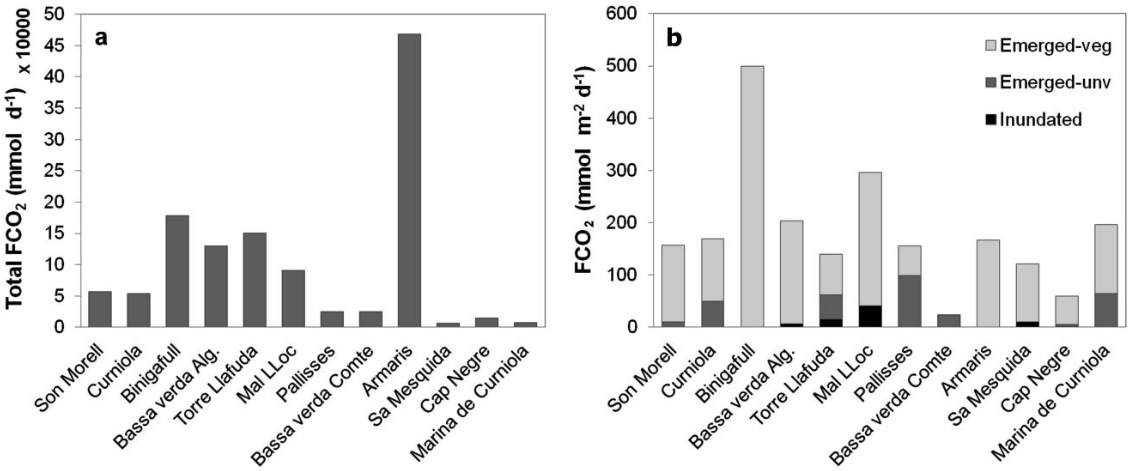

Figure 1. CO_2 effluxes from the studied temporary ponds. a) total flux, b) areal flux by sections. *Flujos de CO_2 desde los estanques temporales. a) flujo total, b) flujo por unidad de superficie para cada sección.*

each pond. In the emerged section, the measurements distinguished between vegetated and non-vegetated areas. This nomenclature will be used throughout the text to refer to the different sections of the ponds.

Characterisation of the ponds

At each pond, the surface area of each section was measured *in situ* both manually and using a GPS and afterwards digitised with the help of aerial photography and based on the cartographic data in Fraga *et al*. (2010). The organic content of emerged and inundated sediments was determined by loss on ignition (Dean, 1974) on triplicate samples. Plant biomass as small roots was included in the organic content determination. Mean altitude, mean slope, lithologies, soil types, land cover and total area in the catchment of each pond as well as in a 500 m buffer around the pond were determined by geographic information systems (GIS) data layers obtained from Fraga *et al.* (2010). The layers were combined using QGIS (Quantum GIS Development Team, 2014).

CO_2 effluxes

The F_{CO_2} was measured *in situ* at the inundated, emerged-unvegetated and emerged-vegetated sections of each pond. Three replicate flux measurements were performed at each section using an opaque enclosed chamber connected to an infrared gas analyser (IRGA model EGM-4, PP-Systems, Amesbury, USA). The chamber method allows accurate direct measurements of CO_2 emissions from either water or terrestrial surfaces. The floating chamber for air-water flux measurements (inundated section) had a surface area of 0.194 m^2 and a volume of 27.1 L. The chamber for flux measurements in emerged sediments (vegetated and unvegetated sections) had a surface area of 0.0078 m^2 and a volume of 1.171 L (model SRC-1, PP-Systems, Amesbury, USA). Flux measurements in emerged sediments corresponded to CO_2 emissions including both soil and root respiration. In all cases, the CO_2 concentration in the closed air volume of the chambers was monitored every 4.8 s, with an accuracy of 1 %. The flux measurements lasted until at least 10 µatm of change in CO_2 were reached, with a maximum duration of 600 s in water (minimum of 300 s) and of 300 s in emerged sediments (minimum of 120 s). The triplicate measurements in the vegetated and unvegetated sections were randomly distributed within each section. At each chamber location, sediment temperature and humidity were measured with portable sensors (ECH2O 10HS, Decagon, USA and Hi93500, Hannah, USA). During water flux measurements, air temperature and wind speed at 2 m were monitored continuously with an anemometer (Kestrel 4500, Nielsen-Kellerman Boothwyn, USA) mounted on a tripod.

The gas flux for each chamber measurement was calculated from the slope of the linear regression between the CO_2 concentration in the chamber and time ($R^2 > 0.9$), correcting for temperature and atmospheric pressure (Lambert & Fréchette, 2005). The gas flux for each section was expressed in mmol m^{-2} d^{-1}, with the convention that positive fluxes correspond to CO_2 effluxes to the atmosphere.

The total CO_2 efflux for each pond (mmol d^{-1}) was calculated by multiplying the mean specific areal flux of each section by the surface area of each section. The mean whole-ecosystem flux of CO_2 (E-F_{CO_2} in mmol m^{-2} d^{-1}) was obtained by dividing the total CO_2 flux by the maximum flooding area of each pond (Table 1).

Statistical analyses

To assess the changes in CO_2 fluxes depending on the pond or on the section within each pond, an analysis of variance (ANOVA) was performed. Due to the sensitivity of ANOVA to unbalanced and incomplete designs, we applied the ANOVA to two linear mixed models of the log-transformed data. In the first, we considered the section of the pond as a fixed effect and the ponds as blocks of design (random effects). In the section, we only considered the random effect. To identify differences in effluxes between sections, multiple comparison *post-hoc* tests (Tukey) of the mixed model were performed.

To examine the influence of the surrounding environment on CO_2 fluxes, we performed a principal component analysis (PCA) on the correlation matrix of the main land cover types (% urban, % agricultural, % forest, % shrubland and % water bodies), lithologies (calcareous, sandstones and turbidites) and hydromorphology (total area and slope of the catchment). All variables were normalised prior to analysis by log 10 or arcsine $\sqrt{(x)}$ (for percentage data) transformation. The relationship between the catchment variables and CO_2 effluxes was then examined using a simple linear regression with the scores of the components of the PCA as the independent variables and the areal flux of CO_2 as the dependent variable. Secondarily, an RDA with the catchment properties and the CO_2 effluxes in emerged sediment or water as independent sets of variables was performed to further confirm the results obtained with the PCA.

All the statistical analyses were performed in R software 3.0.2 (R Core Team, 2013) using the packages *nlme* (Pinheiro *et al.*, 2013), *multcomp* (Hothorn *et al.*, 2008) and *vegan* (Oksanen *et al.*, 2013).

RESULTS

CO_2 effluxes in the ponds

All the ponds were net emitters of CO_2 to the atmosphere. The mean (± standard deviation, SD) ecosystem F_{CO_2} (E-F_{CO_2}) was 121.3 ± 138.1 mmol m^{-2} d^{-1}, ranging from 20.1 to 526.1 mmol m^{-2} d^{-1} (Fig. 1). Although some ponds contributed substantially to the variability of E-F_{CO_2} among ponds, most ponds had fluxes around the mean value (Fig. 1). The main driver of the contribution to the total pond efflux was the area of the pond, with the largest pond (Armaris) showing the highest effluxes (Fig. 1a). If the values were expressed as areal flux, the differences between ponds diminished (Fig. 1b). Only six of the studied ponds were inundated during the field campaign. However, no significant differences in the areal efflux (mmol m^{-2} d^{-1}; $F = 1.3, p > 0.05$) or in the total efflux per pond (mmol d^{-1}; $F = 0.7$, $p > 0.05$) were found between ponds independently of whether they were flooded.

The ANOVA for the mixed model indicated significant differences in the CO_2 flux among the three sections of each pond ($F = 45$; $p < 0.001$). *Post-hoc* tests showed that the efflux was significantly higher in the emerged sections than in the inundated sections of the ponds (Fig. 2; $p < 0.001$). Within the emerged sections, the efflux was higher from vegetated sediments than from unvegetated sediments (Fig. 2; $p < 0.001$). Vegetated areas not only had higher relative effluxes (Fig. 1b) but also represented the largest areas within the ponds (64 % on average). No

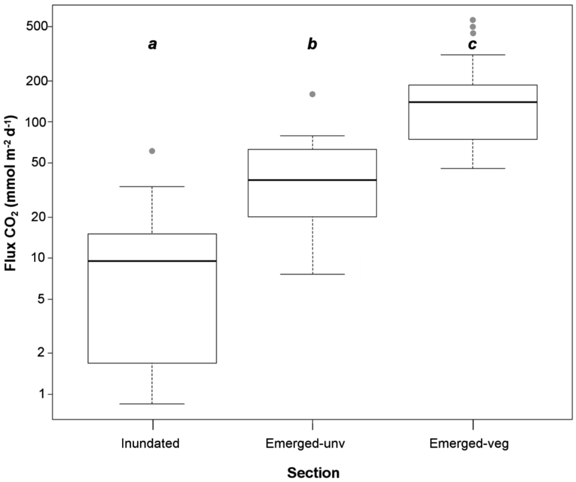

Figure 2. CO_2 effluxes from the different sections of the ponds. Data are given in Tukey boxplots. Significant differences between groups ($p < 0.001$, *post-hoc* tests) are marked with different letters. *Flujos de CO_2 desde las distintas secciones de los estanques. Boxplots de Tukey, las letras indican diferencias significativas (tests* post-hoc*,* p < *0.001) entre secciones.*

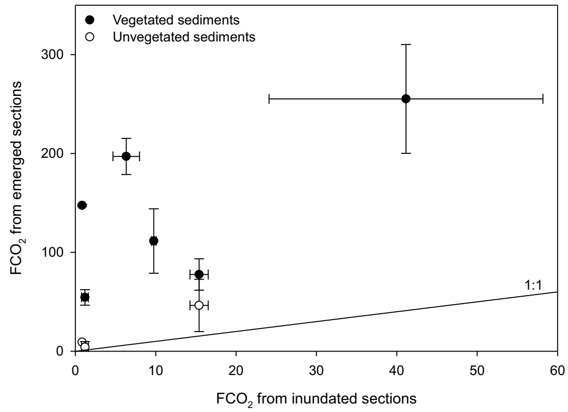

Figure 3. Relationship between the CO_2 efflux (in mmol m^{-2} d^{-1}) from the emerged and inundated sections of the ponds. The 1:1 line is shown for reference. *Relación entre el flujo de CO_2 (en mmol m^{-2} d^{-1}) desde las secciones emergidas y inundadas de los estanques. Se muestra la línea 1:1 como referencia.*

significant relationship was found between the fluxes in the inundated and the emerged sections of the ponds (Fig. 3).

Relationship with the environmental variables

The two first axes of the PCA with the catchment variables explained 53.2 % of the variance (Fig. 4a), grouping the ponds in three sets. A first set was positively correlated with the first axis: agricultural soil uses, calcareous lithologies and large catchment areas. A second group was positively correlated with the second axis: turbidites lithology and higher percentage of urban areas. Finally, a third group was negatively correlated with both axes: a higher percentage of forested lands, stronger slopes and sandstone lithologies.

The main axes of this PCA were not correlated with the E-F_{CO_2} of the ponds (mmol m^{-2} d^{-1}; Fig. 4b,c). Complementarily, the RDA confirmed that the CO_2 fluxes from emerged sediments or water were not significantly correlated with the set of catchment landscape variables because no environmental variables were significantly correlated with the CO_2 effluxes of the ecosystem or the different sections.

The E-F_{CO_2} showed a significant relationship with the mean organic content of sediments (Fig, 5a; $R^2 = 0.42$; $p < 0.05$). Whereas the efflux from the inundated sections was not significantly related to the sediment organic content (Fig. 5b), the efflux from the emerged sections showed a marked relationship with the organic content (Fig. 5c; $R^2 = 0.71$; $p < 0.01$). No significant relationship was found between the efflux from the emerged sections and the humidity of the emerged sediments ($p > 0.05$).

DISCUSSION

Our study confirms temporary ponds to be effective carbon processors in the landscape. During their flooding phase, the studied ponds were net emitters of CO_2 to the atmosphere, and these efflux rates of CO_2 were, moreover, in the upper range for effluxes from freshwater ecosystems (Raymond *et al.*, 2013). Such high fluxes occurred primarily in the extensive emerged sections of the ponds (Fig. 1, Fig. 2). These emerged sediments represented the largest section in the ponds (88 % of the area on average) and also presented the highest fluxes of CO_2 per area (Fig. 1b). This property explains the much higher ecosystem CO_2 fluxes observed here than previously reported for Mediterranean temporary wetlands, where only the aquatic phase was considered (Morris *et al.*, 2013). Thus, the relevance of temporary ponds in the carbon fluxes in Mediterranean landscapes will be highly driven by the emerged sections of these environments. Nevertheless, it should be kept in mind that the estimates presented here do not represent the annual net ecosystem exchange of the emerged sediments. During the period of study, the emerged sediments were relatively humid (just rewetted), influenced by the recent precipitation events which may have exacerbated CO_2 emissions (hot moment *sensu* Gallo *et al.*, 2013). Interestingly, the CO_2 efflux from these temporary ponds was comparable to the CO_2 efflux from Mediterranean soils (median, range = 188, 44–371 mmol m^{-2} d^{-1}; $n = 42$; Global soil respiration database (Bond-Lamberty & Thomson, 2010)). Our results are in line with re-

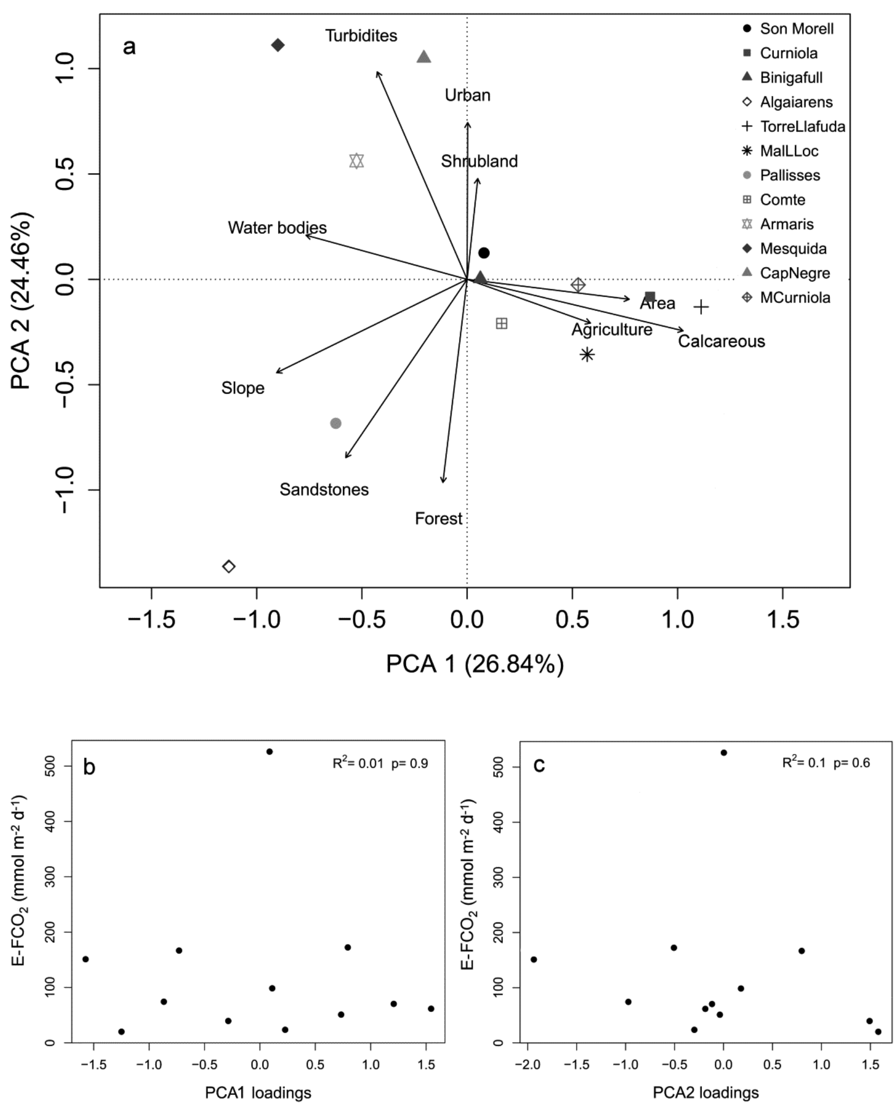

Figure 4. a) Multivariate ordination (principal component analysis) of the catchment properties of the studied ponds. b) Relationship between the first and c) second PCA axis and the ecosystem flux of CO_2. *a) Ordenación multivariante (análisis de componentes principales) de las propiedades de la cuenca de captación de los estanques estudiados. b) Relación entre el primer y c) segundo componentes principales y el flujo ecosistémico de CO_2.*

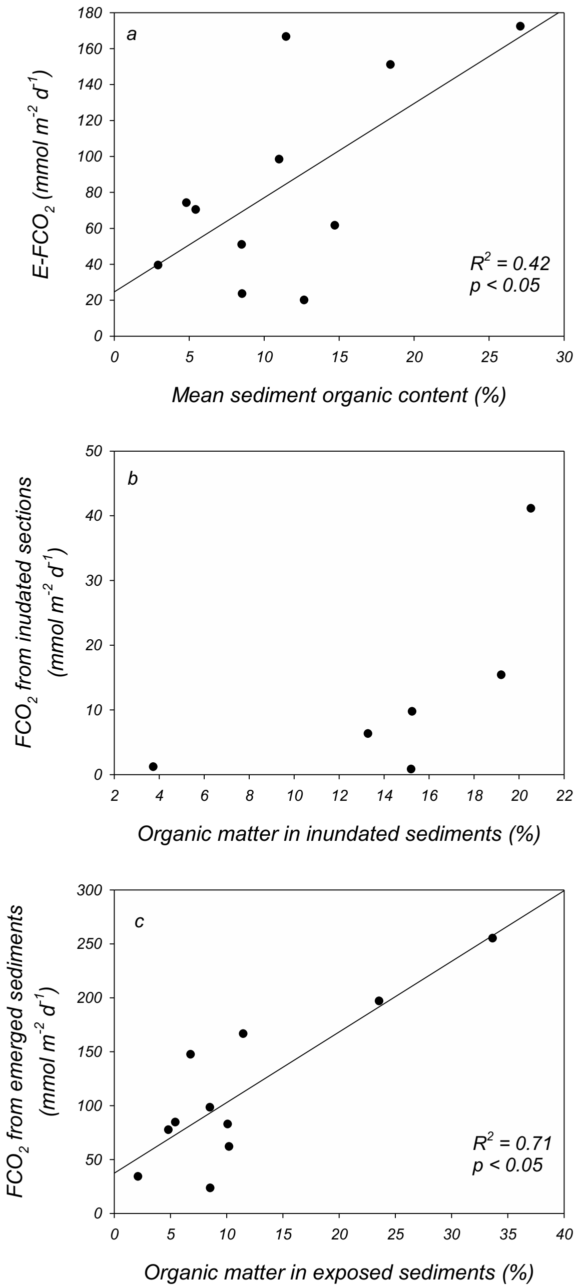

Figure 5. Relationship between CO_2 efflux and sediment organic content at an ecosystem scale (a), and for the gas flux from the inundated (b) and emerged sections (c). In a), the organic content is weighted by the surface area of each section. The lines correspond to the significant ($p < 0.05$) linear least-squares regressions. *Relación entre el flujo de CO_2 y el contenido orgánico sedimentario a escala ecosistémica (a), y para las secciones inundadas (b) y emergidas (c) de los estanques. En a), el contenido orgánico está ponderado por la superficie de cada sección. Las líneas corresponden a las regresiones lineales (mínimos cuadrados) significativas (* p *< 0.05).*

sults from inundated wetlands, where increases in CO_2 effluxes after drying have been widely reported (Moore & Knowles, 1989, Freeman *et al.*, 1993, Fenner & Freeman, 2011). Moreover, our results agree with recent observations on CO_2 effluxes from dry river beds (von Schiller *et al.*, 2014). Overall, these results emphasise the overlooked importance of the emerged sections of temporary freshwater ecosystems in terms of CO_2 effluxes.

The variability in the F_{CO_2} among sections of the ponds was higher than the variability among ponds. The higher F_{CO_2} observed in the emerged sections compared with that from the inundated sections might be related to a physical limitation of gas diffusion in the latter. In the inundated sections, the CO_2 must diffuse through the water column to reach the atmosphere, and gas efflux is finally determined by wind-driven turbulence in the boundary layer (Bade, 2009). On the contrary, in emerged sediments, gas diffusion is not limited by the existence of a water column.

The higher fluxes observed in the vegetated than in the unvegetated sections of emerged sediments might be related to root respiration. Root respiration can reach up to half of the total soil respiration in vegetated soils (Andrews *et al.*, 1999; del Grosso *et al.*, 2005). Additionally, other root-linked processes such as microbial respiration in the rhizosphere could also play an important role on enhancing the CO_2 efflux from vegetated soils (Luo & Zhou, 2006).

The lack of relationship between the effluxes from inundated and emerged sections indicates that the drivers of fluxes in the different sections of the ponds are not necessarily the same (Fig. 3) and, accordingly, that the magnitude of the fluxes in the different sections of the pond will not necessarily follow the same direction spatially or temporally.

Can the F_{CO_2} at the system level be defined by watershed properties?

Small aquatic systems with high watershed-to-system area ratios are expected to be highly dependent on external drivers (Álvarez-Cobelas *et al.*, 2005). We found that catchment characteristics, such as land use or lithology, were not related to the E-F_{CO_2} fluxes from the studied ponds. This apparently poor influence of the catchment characteristics on the CO_2 effluxes persisted when the effluxes were considered separately by emerged and inundated sections. On the contrary, the differences in CO_2 effluxes between ponds were most likely related to intrinsic properties of the pond. Among these, organic matter quality and quantity and nutrient availability will most likely play a key role in determining the system's heterotrophic metabolism. In the studied ponds, the efflux at a system level was significantly correlated with the organic content of the sediments (Fig. 5a), representing 40 % of the variance in the fluxes. The sedimentary organic content was in accordance with mean values in wetlands, temporary ponds and lagoons (Mitsch & Gosselink, 2007; Florencio *et al.*, 2009, Obrador & Pretus, 2013). Interestingly, only the emerged sections maintained the relationship between CO_2 flux and sediment organic content, whereas the fluxes from the inundated sections were independent of this. The lack of relationship for the inundated sections might be due to a different gas exchange between the water and the atmosphere but also to the respiration of dissolved organic carbon in the water column. Thus, effluxes from inundated sections would more likely be related to the dissolved organic matter than to the sediment organic matter. The characterisation of the organic matter component, either dissolved or particulate, in these systems might furnish an insight into the links between mineralisation and consequent flux and the organic matter present, especially in the inundated sections of the ponds. Further work on the quality and concentration of DOM in the water column of the ponds is needed to assess this relationship.

CONCLUSIONS

The temporary ponds exhibited high CO_2 fluxes per unit area during the flooding phase. Most of these effluxes occurred in the emerged sections, especially in those areas with vegetation. This finding demonstrates the need to include the emerged sections when incorporating the effects of temporary systems on CO_2 effluxes, a pattern to recognise not only in temporary ponds but in other fluctuating systems such as dry river beds, dry reservoir belts or wetlands.

Although the fluxes from the ponds were not related to the properties of their catchments at an ecosystem scale or by sections, the significant relationship between the organic content of sediments and these effluxes highlights the need for a deep characterisation of the organic matter in these environments. This characterisation would be a fundamental step in determining the main drivers of carbon efflux from temporary ponds at a local scale and for upscaling to regional carbon budgets.

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