Quantifying rapid spatial and temporal variations of CO_2 fluxes from small, lowland freshwater ponds

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Abstract Small ponds comprise a substantial portion of the total area of the Earth's inland waters. They can be powerful carbon sinks or sources, potentially significant processors of organic carbon. Our understanding of their role is constrained by the absence of information regarding their CO_2 fluxes ($F\ CO_2$) and how these change with wet or dry phases and across distinct pond plant communities. We monitored the $F\ CO_2$ from 26 neighbouring small ponds over a 2-week drying period in late summer in 2014. The mean $F\ CO_2$ on day 1 (-641 ± 1490 mg m^{-2} day^{-1}) represented a net intake across the site. As ponds dried they switched to becoming CO_2 sources resulting in a net site emission of CO_2 by day 12 (3792 ± 2755 mg m^{-2} day^{-1}) although flux rates did not vary systematically between plant communities. Significant variability in the $F\ CO_2$ was observed amongst adjacent ponds on individual sampling days, resulting in marked spatial heterogeneity in CO_2 processing. This large degree of temporal and spatial heterogeneity across short time periods and small distances highlights the variability in the $F\ CO_2$ from temporary systems, making it hard to generalize their role in carbon cycle models.

Keywords Carbon flux · Temporary pond · Small wetland

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Introduction

In recent years, the role that small ponds play in global geochemical processes has received increasing interest (Cole et al., 2007; Battin et al., 2009; Downing, 2010). Estimations of their cumulative global coverage have suggested that they are comparable in area to the Earth's largest lakes (Downing et al., 2006), although more recent estimates have been more conservative (Seekell & Pace, 2011; Verpoorter et al., 2014). Equally these systems support disproportionately intense processes for their size, when compared to larger water bodies (Torgersen & Branco, 2008; Downing, 2010; Catalán et al., 2014). This makes them ideal cyclers of atmospheric carbon (here after C), accounting for a substantial portion of the missing C budget from which small ponds and wetlands are frequently omitted.

The absence of small ponds from C budgets is in part due to a lack of robust data quantifying their rates and processes. Biogeochemical processing in ponds remained relatively understudied until the late twentieth century as limnological research focused on

larger lakes and river systems, where it was assumed that the dominant inland aquatic processing of C occurred (Downing, 2010). However, just as ponds were once overlooked as wildlife habitats but are now known to be disproportionately rich in species and rarities compared to streams, rivers and lakes (Williams et al., 2004; Davies et al., 2008), their potential significance for ecosystem services, such as C sequestration, is being increasingly recognized (Cole et al., 2007; Tranvik et al., 2009; Downing, 2010; Cereghino et al., 2014; Gilbert et al., 2014). The number of studies on C cycling within ponds is rapidly increasing (Downing, 2010; Boix et al., 2012; Ewald et al., 2012). Within this overall biome of ponds, temporary systems are receiving increasing interest (Torgersen & Branco, 2008; Fromin et al., 2010; Catalán et al. 2014; von Schiller et al., 2014).

Temporary ponds are known by a range of diverse regional names or technical definitions: e.g. seasonal, ephemeral, playa or vernal (Keeley & Zedler, 1998). Recognized as ecologically valuable they support a specialist flora and fauna, which adds a significant contribution to γ biodiversity on the landscape scale, that is able to withstand drought through resistant propagules or by rapid re-colonization (Collinson et al., 1995; Jeffries, 1998, 2010). They are internationally important terrestrial habitats, ubiquitous in all climatic zones across the globe including extreme desert and polar environments, including thaw ponds in Arctic Tundra (Gallagher & Huissteden, 2011), temporal pools in Mediterranean and desert biomes (Catalán et al., 2014), constructed rice paddies in equatorial tropics (Jonai & Takeuchi, 2014), to melt pools in Antarctica (Allende & Mataloni, 2013). They are also typical of temperate biomes such as south American grasslands (e.g. *mallines*, Kutschker et al., 2014), prairie potholes and woodland vernal ponds in North America (Batzer et al., 2005; Gala & Melesse, 2012), across the riverine plains of Europe (e.g. tributaries of the Danube in Hungary; Boven et al., 2008), through into the Asian steppes (Mozley, 1937; an unusual example of a rare early appreciation of their value). Temporary habitats can also be historically long-lived features in the landscape, for example the pingo ponds of East England (Foster, 1993; Williams et al., 2001), so that their geochemical impact will also play out over many years. However, their presence is frequently overlooked both in natural landscapes such as grassland or temperate forest, and in intensively modified landscapes such as arable or grazing agriculture (Williams et al., 2001).

The key feature that unifies such systems is that they exhibit seasonal changes in their hydrological regimes resulting in periodic dry phases, exposure of the base substrate and often desiccation of sediment layers. Typically in temperate climates, including the ponds in this study, recharge is rainfall dependent, and as such this change in hydro-period is dependent on the balance between evaporation rates and net rainfall over short periods. In the UK unreliable summer rainfall (Fowler & Kilsby, 2002) often results in several drying and rewetting cycles over short periods of time, with rainfall variations from year to year further complicating the quantification and modelling of their ecosystem processes. This problem is compounded by the likely increase in climate variability caused by climate change. A particular uncertainty arises from new extremes of rainfall or temperature, which will subject ponds and their wildlife, to novel stresses which may alter existing rates of geochemical processing and species' distributions (Jeffries, 2010; Jones, 2013).

Whilst C burial rates in ponds are amongst the highest of all ecosystems (Downing, 2010), ironically it is the low water volume of temporary ponds that renders them vulnerable to drying and sediment desiccation during periods of low rainfall, greatly impacting sediment C stability. Sediment conditions quickly change from anoxic to oxic, permitting aerobic microbial activity in the surface substrate, resulting in higher mineralization rates of organic matter and subsequent CO_2 efflux (Fromin et al., 2010). Furthermore, in exposed sediments, CO_2 release is no longer hindered by the water column, through which CO_2 will usually diffuse before release to the atmosphere at the surface boundary layer (Catalán et al., 2014). Assessing CO_2 effluxes of temporary ponds in response to rapid changes in seasonal drying cycles is crucial to quantifying their role in the global C cycle.

In this study we begin to address this by monitoring the temporal and spatial heterogeneity of CO_2 fluxes amongst 26 small experimental ponds in Northeast England in response to desiccation during a summer dry period. The study was intentionally designed to capture changes over relatively fine-grained spatial and temporal scales; ponds just metres apart, and over a period of days within a two-week summer drying phase.

Site description

This study took place on a set of 26 experimental ponds. Constructed in 1994, all ponds are the same age, approximately the same size (1 m^2 × 30 cm deep) and set out in an array across an area of approximately 30 × 30 m. Their close proximity renders them exposed to the same regional environmental conditions; they are as close to replicate ponds as is possible under natural conditions. The ponds' 20 years history of hydrological and ecological monitoring provided data on potentially important drivers of variation in gas exchange, e.g. wet and dry phases or vegetation (Bouchard et al., 2007; Fromin et al, 2010; Turetsky et al., 2014; Catalán et al., 2014; Mo et al., 2015. For detailed site description see Jeffries, 2008, 2010). The region in which they are located forms part of the Northumberland Northeast coastal plain in northeast England, a lowland landscape dominated by intensive arable and livestock agriculture. The climate is relatively cool but also dry due to the rain shadow from hills to the west (Lunn, 2004). Despite the relatively low rainfall the area is rich in ponds, especially shallow, temporary habitats associated with sand dunes or land subsidence over old coal mines (Jeffries, 2012).

The ponds are situated within a meadow field (55°19′04.1″N 1°33′22.1″W), owned by Northumberland Wildlife Trust, at the northern end of Druridge Bay, Northumberland, UK. Originally an opencast coal mine which was restored when mining ceased around 50 years ago, the site is now topped with a rough clay lining and approximately 50 cm topsoil. The clay lining is impermeable and, as such, the ponds are dependent on precipitation, subsequent surface run-off and horizontal throughflow in the topsoil layer for recharge. A slight gradient across the site runs northeast to southwest causing subtle hydrological variations amongst the ponds. The southwest portion of the site is typically marshier and dominated by spike rush, *Eleocharis palustris* (L.) Roem. & Schult., with ponds here being the first to fill during rainfall events, yet also the first to dry during rainfall absence. Contrastingly, the northeast portion of the site is less marshy, dominated by grasses such as marsh foxtail, *Alopecurus geniculatus* L., and glaucous sedge, *Carex glauca* Schreb., yet the ponds hold water for longer. Despite their close proximity and superficial similarity, the ponds have developed a diverse set of plant and animal communities and their hydrological patterns are typical of the ponds and wetlands through the region (Jeffries, 2008, 2010).

Methods

Site description

To quantify CO_2 flux rates and how these change (a) on a fine-grained spatial and temporal scale between adjacent ponds over a few days and (b) in response to drying out of ponds, flux rates of CO_2 (F CO_2) were monitored for all 26 ponds over a 2-week period from 24th August to 4th September 2014, monitoring on days 1, 4, 9 and 12.

Fluxes of CO_2 were measured using a floating chamber method. Our chamber consisted of an upturned 7252 cm^3 container (length = 37 cm; width = 24.5 cm; height = 8 cm) with attached floatation device around the base of the chamber which assured that the volume of the chamber was above the water's surface. The chamber was placed gently on the surface of the water in each pond to avoid disturbance and the inflow and outflow tubes which connected the chamber to the flux metre tethered the chamber in position. The small area of the ponds combined with water levels considerably below the top of the ponds' edges created a sheltered environment. Headspace volume did not change because of varying water level or being lifted by vegetation. For systems that had dried out the chamber was placed directly on vegetation within the centre of the pond and sealed by placing plastic sheeting around the base of the chamber to assure minimal interaction with the atmosphere. It should be noted that the chamber was transparent and allowed for photosynthesis, and as such, fluxes represent the respiration rate of the system as a whole.

Inflow and outflow tubes connected the chamber to an in situ FT-IR (Fourier Transform-Infra Red) analyser pumping at a rate of 2 l per min to allow continual circulation from and back to the chamber. Gas concentrations within the chamber were recorded repeatedly at 20 s intervals over a 5 min period, which was found to be the optimum time to achieve a reliable r^2 (>0.8) yet not too long so that pressure changes would affect flux rates. In between each flux measurement, the chamber was flushed until readings returned to atmospheric concentrations. Note that the volume of the air space within the FT-IR analyser and

tubing was also accounted for in calculations of head space volume and changes in CO_2 concentrations. Every 6th pond was measured in triplicate to assess the precision of the analysis. Monitoring of flux rates for all ponds took approximately 6 h, from 10 am to 4 pm, with each pond sampled in the same order and at roughly the same time on each of the survey days to focus on how the fluxes changed from individual ponds across the sample period. Whilst fluxes from systems are known to vary throughout the day it is this central period at which flux rates are most stable (Chanda et al., 2013).

Flux rates were calculated from the linear regression of the change in concentration over the 5 min period, aiming for $r^2 = >0.8$, and all flux rates were corrected for temperature and atmospheric pressure. Negative values reported herein represent an intake of CO_2 from the atmosphere by the system whilst positive values represent an emission. It should be noted that in several instances changes in concentration within the chamber were lower than the accuracy of the FT-IR analyser (1 ppm), resulting in a poor r^2 (<0.8). However, in this situation values reported are negligible in comparison to high flux rates from active ponds. When referring to the averages across all ponds the term ecosystem flux rate ($E–F\,CO_2$) is used to refer to the ponds as a collective.

Hydrological classification

The hydrological condition of each pond was characterized by personal observation during each site visit, grouping each pond into one of three categories:

1. Aquatic Phase—Ponds contained standing water that covered the base, though with occasional emergent vegetation.
2. Transitional Phase—Ponds contained no standing water with base layer exposed. However, the sediment and vegetative layer were still saturated and moist to touch.
3. Dry Phase—Ponds contained no standing water with sediment and vegetation now dry to touch.

Vegetation classification

Macrophyte vegetation of each pond was surveyed during spring/summer 2014 using a 1 m² quadrat grid with cross wires every 10 cm. The plant species under

each intersection of the cross wires was recorded, to give a % cover for each species (for details on plant survey methods see Jeffries, 2008). TWINSPAN analysis was used to classify the ponds by the plant data, resulting in 4 distinct plant communities. TWINSPAN was run on CAP 3.1.

Data analysis

To assess the changes in CO_2 flux rates over the sampling period a mixed model Repeated Measures Analysis of Variance (ANOVA) was performed. Flux rates from the four sampling days were considered as within-subject variables, factoring in each pond as the subjects of the repeated measurements across the four sampling days. The four types of ponds differing in vegetation classification as defined by the TWINSPAN analysis were used as between-subject factors, to assess any variations in flux rates between broad vegetation types. All statistical analysis was performed using IBM SPSS Statistics 22.

Results

Flux rates of CO_2 amongst ponds varied markedly over the four sampling days (Fig. 1), with mean (± standard deviation, SD) $E–F\,CO_2$ switching from a net intake on Day 1 of -641 ± 1490 mg m^{-2} day^{-1}, to a net emission of 190 ± 1286 mg m^{-2} day^{-1} by Day 4, 1354 ± 1805 mg m^{-2} day^{-1} by Day 9, and 3792 ± 2755 mg m^{-2} day^{-1} by Day 12. The precision of triplicate measurements were mostly <20 % relative standard deviation (RSD) with the exception of three triplicate sets (35, 38 and 49 % RSD) suggesting occasional quick variations in flux rates.

Mean daily flux rates between the four sampling days varied significantly ($F = 41.94$, df 3, 69, $P = <0.00$. NB all tests included interactions terms and ponds as random subjects which reduces the error dfs slightly whilst we only report the results for the main factors) with flux rates being statistically different between days 1–9 ($P = <0.00$) and 1–12 ($P = <0.00$), days 4–9 ($P = 0.04$) and 4–12 ($P < 0.00$), and days 9–12 ($P < 0.00$). Only flux rates on days 1 and 4 were not significantly different ($P > 0.05$).

Note that in the Repeated Measures ANOVA used to compare mean daily flux rates over the sampling

Fig. 1 Box plot of CO_2 flux rates from the 26 ponds surveyed on the four sampling days. The boxplot represents the minimum, lower quartile, median, upper quartile and maximum values. Positive values represent an emission of CO_2 from the ponds to the atmosphere whilst negative values represent an intake
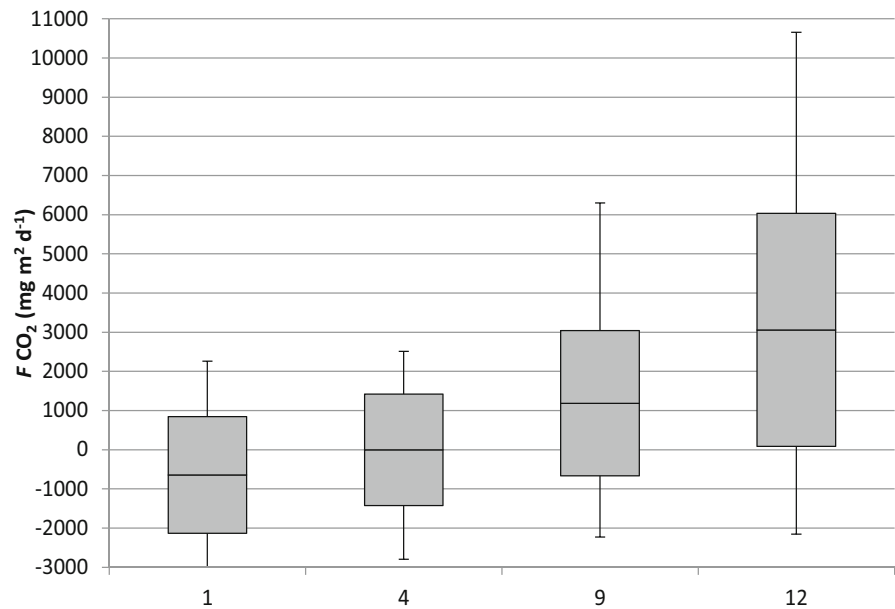
period, Mauchly's test indicated that the assumption of sphericity had been violated ($x^2 = 12.85$, df 5, $P = {<}0.05$), i.e. there was a degree of non-independence of data from individual ponds. Therefore, degrees of freedom were corrected using Huynh–Feldt estimates of sphericity. This is not merely a necessary statistical adjustment but also reveals an important outcome, indicating a significant degree of variability within the data associated with the individual pond being monitored.

There were no major weather variations over the sampling period, with wind speed and atmospheric temperature remaining relatively constant (Fig. 2). The only notable aspect of the weather over the period was the absence of precipitation. The total rainfall in the 3 weeks preceding sampling was 39.37 mm with the last substantial rainfall (6.10 mm) being 11 days prior to sampling on Day 1. With <5 mm rainfall during the middle of the sampling period the ponds quickly dried up, with the softer vegetation in many of the ponds wilting by the end of the sampling period.

Figures 3 and 4 show the F CO_2 on the four sampling days for each of the ponds characterized by their hydrology at the time of sampling. Flux rates were markedly higher in ponds that were dry, and as ponds dried out over the survey period, their flux rates shifted from intake to emission. Not only did the fluxes shift from an intake to emission but the flux also

continued to increase with increasing absence of rainfall.

Subtle variations in the hydrology of the site have led to marked differences in the vegetation between the ponds. Figure 5 shows the location of each pond grouped by the four divisions of the TWINSPAN analysis and their mean daily E–F CO_2 is shown in Fig. 6. Thirty-six species of macrophytes were recorded. Differences between the four groups are subtle with many species found in most ponds, in particular amphibious grasses e.g. *Agrostis stolonifera* L., the rush *Juncus articulatus* L. and the moss *Leptodictyum riparium* (Hedw.) Warnst. Differences between groups resulted from the dominance of particular species. Group 1 was dominated by *Glyceria fluitans* (L.) R. Br. and *Carex otrubae* Podp. and Group 2 characterized by dense *Eleocharis palustris* (L.) Roem. & Schult. Group 3 was a slightly wetter set of pools with *E. palustris* and the filamentous algae *Spirogyra* sp., whilst Group 4 lacked the *E. palustris*. No significant differences were found between the F CO_2 for the four groups of ponds characterized by their plant community communities ($F = 2.24$, df 3, 66, $P = {>}0.05$). However, the overall design is very unbalanced with the majority of ponds in just one plant community group which may explain the lack of differences between the four communities.

Fig. 2 Climatic conditions over the sampling period. Weather data are from the UK Met Office Boulmer Weather Station located approximately 12 km north from Hauxley Nature Reserve. Rainfall is the *solid line*. The *dashed line* is mean temperature, the shading either side maximum and minimum. The columns are mean wind speed with maximum *bars* above
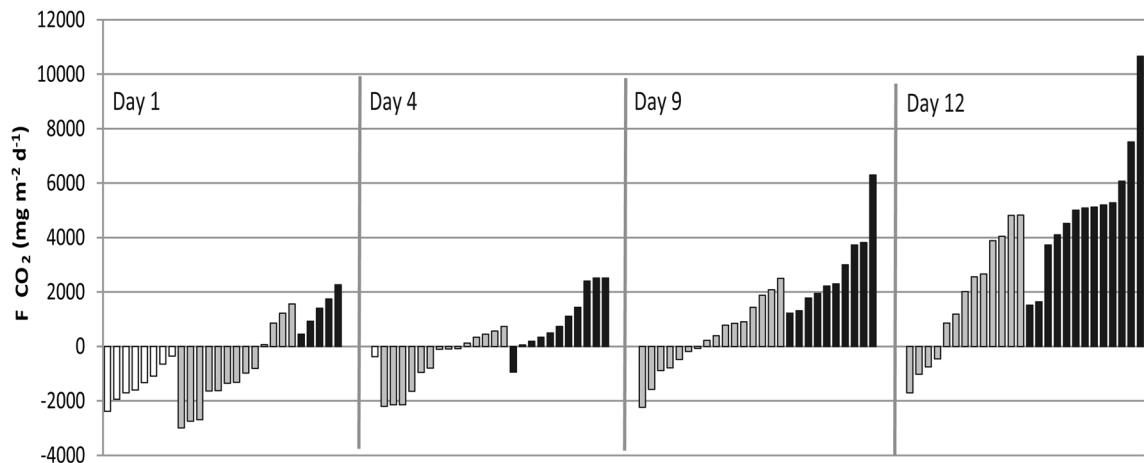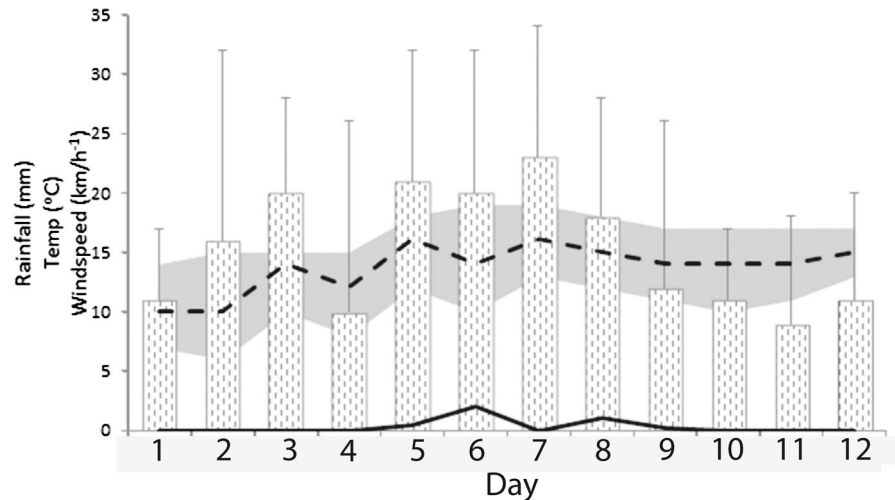
Fig. 3 CO_2 flux for each pond on the four sampling days. Ponds are grouped by hydrology and ordered by flux rates. Over the course of the 4 days more ponds dry out and become net sources of net CO_2. Positive values = net CO_2 emission, negative values = net CO_2 capture. ☐ = wet ponds, ▨ = transitional, ■ = dry ponds

Discussion

The objective of this study was to quantify the changes in the F CO_2 for small temporary ponds: the data provide evidence of very fine-grained spatial and temporal heterogeneity of CO_2 fluxes from these habitats.

Temporal heterogeneity

The E–F CO_2 for all the ponds during the survey period indicates that these small ponds act as a net

source of C to the atmosphere during prolonged absence of rainfall during summer months. This behaviour has been frequently reported for similar temporary aquatic systems during drying periods i.e. ponds, river courses, wetland and tidal regions (Fromin et al., 2010; von Schiller et al., 2014; Catalán et al., 2014).

However, daily means varied significantly. Whilst the cluster of ponds acted as a net sink on Day 1, this had shifted to a net source of CO_2 only 3 days later, and reached a 9-fold increase in CO_2 efflux within 2 weeks. Consequently F CO_2 at the beginning and
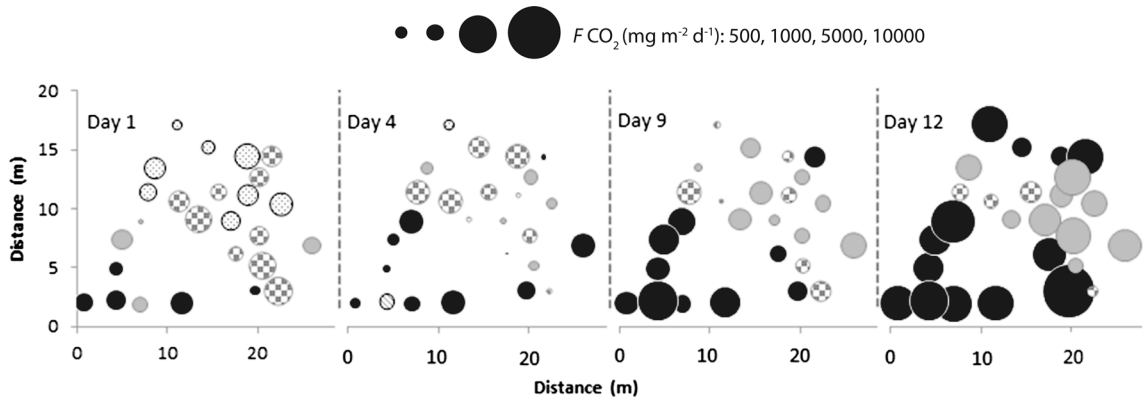
Fig. 4 CO_2 flux for each pond on the four sampling days and their spatial distribution across the site. The position of each pond on the site is shown by a *circle* and the *circle shading* indicates hydrological state and whether the pond is a net CO_2 source or sink. *Circles with fine dots* wet ponds with negative CO_2 flux, *checker board circles* transitional ponds with negative CO_2 flux, *grey circles* transitional ponds with positive CO_2 flux, *circles with diagonal lines* dry ponds with negative CO_2 flux and *black circles* dry ponds with positive CO_2 flux
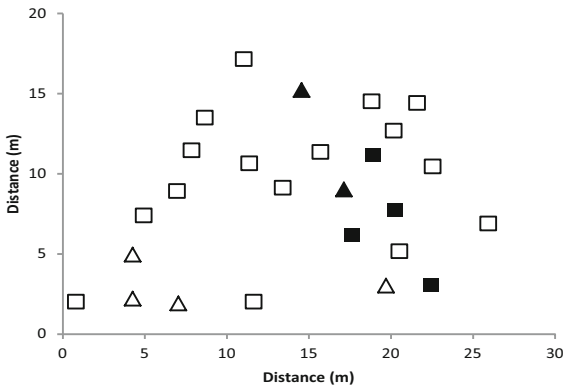
Fig. 5 The distribution of the ponds and plant community types as classified by TWINSPAN. Each marker represents the location of an individual pond spatially across the site, the *y*-axis representing the north–south orientation. The four pond plant communities are represented by *filled square* group 1 (dominated by *Glyceria fluitans* and *Carex otrubae*), *open square* group 2 (dense *Eleocharis palustris*), *open triangle* group 3 (sparser *E. palustris* with *Spirogyra* sp.) and *filled triangle* group 4 (No *E. palustris*). See text for detailed description of plant survey and analysis)
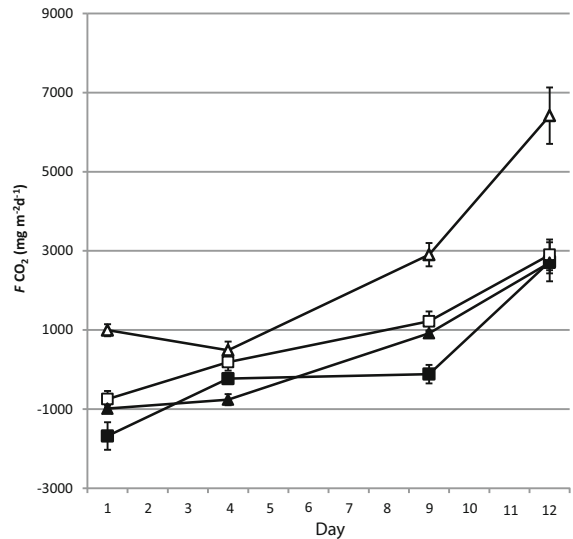
Fig. 6 CO_2 flux rates (mean $\pm$ standard deviation) grouped by vegetation types over the four sampling days. The four pond types are *filled square* group 1 (dominated by *Glyceria fluitans* and *Carex otrubae*), *open square* group 2 (dense *Eleocharis palustris*), *open triangle* group 3 (sparser *E. palustris* with *Spirogyra* sp.) and *filled triangle* group 4 (No *E. palustris*)

end of the sampling period were comparable to both the lower and upper end of effluxes previously reported for freshwater ecosystems, respectively (Raymond et al., 2013).

Similarly, during the drying phase of a temporary pond in southeastern France, Fromin et al. (2010) observed a peak in F CO_2 at the beginning of the drying processes with substrate-induced respiration from microbial activity peaking after 3 weeks. Beyond 3 weeks the CO_2 emissions continued to decrease throughout the drought period. Whilst it is likely that F CO_2 beyond our survey period may decrease when all ponds enter a stable drought phase, our study highlights the severity of F CO_2 emissions during the initial drying phase. For temperate ponds

that undergo several wetting and drying cycles during summer months this poses complications for management practices intended to enhance C capture and storage.

Another factor which might have exacerbated CO_2 emissions between Day 4 and Days 9 and 12 was the slight precipitation on Days 6 and 8. Whilst only small and not enough to fully rehydrate the ponds, rewetting of sediments or soils after dry periods is known to increase C lability and microbial activity resulting in rapid release of CO_2 (Fromin et al., 2010; von Schiller et al., 2014). Equally the resulting water stress on the macrophytes is likely to have reduced photosynthetic activity limiting the intake of atmospheric CO_2, which would counter balance the release of CO_2 during hydrated periods. This may be one factor contributing to the continued increase in CO_2 flux rates over the sampling period as the swards of grasses and moss overlying the bottom of the ponds continued to dry out during the switch from transitional phase to dry phase. Interestingly, the thick vegetation held in moisture, slowing the processes of sediment desiccation compared to ponds with a looser vegetation profile. Whilst no statistical relationship was found between vegetation type and CO_2 flux rates over this two-week study, during periods when rehydration occurs before complete desiccation, these mats might act as a 'buffer' preventing complete sediment desiccation and extensive CO_2 release. The sediments underneath the vegetation were conspicuously darker, damper and apparently anoxic compared to the few ponds lacking extensive vegetation cover.

The organic C content of sediments from other ponds in the area is high compared to adjacent non-wetland habitat indicating a net accumulation of C within temporal aquatic systems (Gilbert et al., 2014). Yet the data presented here highlight the interaction of C fluxes with the atmosphere. Taken together, the sediment storage and flux rates suggest that these ecosystems have the potential to be highly active sequesters of atmospheric C when hydrated during summer months as illustrated by the net intake of CO_2 on Day 1. However, this high degree of temporal variability in the F CO_2 over such a short period of time poses serious complications for extrapolations of measurements to seasonal averages from singular measurements alone and highlights the need for more comprehensive surveys when trying to extrapolate results.

Spatial heterogeneity

Whilst the temporal variability of the F CO_2 over several days poses complications for the infrequent measurement of temporal systems, the variability in F CO_2 amongst superficially similar ponds on the same day is equally variable (Figs. 2, 3). Flux rates amongst all ponds resulted in % RSDs of 232, 1320, 144 and 81 on Days 1, 4, 6 and 9, respectively, indicating high variability in the F CO_2 amongst individual ponds. This was supported by the outcome of the repeated measure ANOVA too, showing that the individual ponds behaved differently, and it matters which pond was being measured. On Day 1 there was a rough divide across the middle of the site between those ponds emitting and those taking in CO_2 (Fig. 3), which typically marks the marsh line as described in "Site description" section. However as the survey period progressed and more ponds began to enter the transitional or dry phase of their hydrological cycle, fluxes of CO_2 amongst ponds became more uniform.

No statistical variation was found in flux rates between vegetation types as characterized by the TWINSPAN analysis indicating that hydrology rather than vegetation is the dominant driver in CO_2 release. However several limitations exist. Firstly this study only represents a 2-week snap shot of the flux rates from these ponds in their life cycle. Vegetation communities in temporary systems change regularly depending on annual climate variations (Jeffries, 2008) and as such plant species that have greater impact on F CO_2 may have been missed in this study. Equally it may be that the previous macrophyte communities, which now form the sediment layer result in differences in the lability of organic matter, and subsequently may be more important than the growth of current plant communities.

This large degree of spatial variability poses complications for accurately quantifying the F CO_2 on a landscape scale if too few ponds or an unrepresentative group is chosen. The use of eddy covariance for monitoring terrestrial net ecosystem exchange over comparably large areas (100 m^2) provides a useful comparison to the flux from individual ponds (Abnizova et al., 2012) or for monitoring F CO_2 from ponds with a larger surface area (Fromin et al., 2010). However the use of eddy covariance on a landscape scale can easily overlook the influence of individual ponds, especially during wet and dry cycles. More

effort is needed to underpin the constraints of hydrology on the frequency of drying and rewetting cycles and their impact on $F\,CO_2$ amongst ponds across the landscape if accurate regional extrapolations of these small systems are to be acquired.

These results also suggest important practical outcomes, notably the potential of small ponds as CO_2 sinks, if the frequency of inundation periods is managed. Ponds and small wetlands are relatively easy to create and constructed wetlands have been widely used for the containment and treatment of a diversity of contaminated effluent (Vymazal, 2014). Typical uses include amelioration of acid mine water discharge (e.g. Shoeran & Sheoran, 2006), excess agricultural nutrients (Fink & Mitsch, 2004), road run-off (Gill et al., 2014) and nutrient-enriched river water (Tang et al., 2013). Small ponds are natural features of intensively used lowland landscapes throughout the world and can bring additional benefits to wildlife, although some studies of constructed wetlands built for controlling contamination show that the optimum designs for effluent reduction may be less suitable for maximizing benefits to wildlife (Hansson et al., 2005) or that the contamination is associated with degraded biodiversity compared to pristine wetlands (Batty et al., 2005). The potential of ponds as C sinks is clear, especially in the longer term when sequestration of CO_2 outweighs methane emissions (Mitsch et al., 2013). Creating ponds as part of our attempts to mitigate against C emissions looks to be both a practical and beneficial strategy. However, the few studies of C fluxes from exiting constructed wetlands, constructed for other purposes, shows they can also be net sources (e.g. Liikanen et al., 2006) and that the plants present can be important drivers of CO_2 emissions but precise outcomes can vary with plant species, e.g. Ström et al. (2005). More encouragingly Teiter & Mander (2005) explored using the example of domestic water treatment wetlands and estimated their C emissions would not be significant globally; a key management outcome from our study is the need to get the design of wetlands right to maximize their effectiveness in the face of natural climate variations and the threat of greater climate variation.

Without complete annual and diurnal flux measurements and C burial rates it would be inappropriate to extrapolate this study to state whether small ponds act as a net sources or net sinks to the atmosphere.

Nonetheless, their flux rates are comparable with those of ecosystems with some of the highest rates of CO_2 sequestration/emissions on the planet highlighting the possibility that small seasonal aquatic systems are important cyclers of atmospheric C.

This study set out to monitor spatial and temporal changes to CO_2 flux rates in small, temporary ponds in a typical lowland European landscape during a summer drying phase. The results show striking temporal change in $E–F\,CO_2$ linked to hydrological changes, with ponds at the start of the 2-week study period being net CO_2 sinks, and as the site dried out the ponds increasingly became net sources of CO_2 to the atmosphere. A 9-fold difference in flux rates from the beginning to end of the study period resulted in $F\,CO_2$ comparable to both the lower and upper flux rates reported for aquatic ecosystems (Raymond et al., 2013). There was a broad spatial gradient in the behaviour of ponds across the site as the site dried out. In addition, the repeated measures analysis of the gas fluxes suggested that the behaviour of individual ponds varied but that the precise plant communities did not affect the CO_2 flux. Small ponds and wetlands like those in this study are found throughout the Earth's terrestrial biomes, from tropics to polar regions. Our results show that small-scale spatial and temporal changes can result in large variations in wetland CO_2 fluxes to the atmosphere suggesting that these ubiquitous habitats may be an important but overlooked component of global C dynamics.

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