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**Abstract:**

Wildfires are a global disturbance being enhanced by human-induced pressures. Their frequency and intensity are expected to increase in the near future in regions such as the Mediterranean basin. While responses of terrestrial systems to wildfire have been thoroughly studied, aquatic systems such as temporary ponds have received less attention. Furthermore, previous works have focused on wildfire impacts in aquatic systems from a more functional and trait-based approach, but such disturbances can also impact the diversity of these systems at the local and regional level. In this work, we assess wildfire impacts on alpha and beta diversity of Mediterranean temporary ponds, analysing samples of pond macrofauna after a wildfire that burned part of a cluster of these habitats. The wildfire did not change alpha diversity patterns but differences in beta diversity were observed when considering species abundance. Species with greater contribution to beta diversity were more strongly represented in unburned ponds after the wildfire. These changes occurred mostly during the beginning of the hydroperiod, which increased regional differences in burned ponds. However, these alterations decreased towards the middle and the end of the hydroperiod. Overall, we report a fast recovery of communities after the wildfire, tightly linked to a rapid recolonization that increased similarity. Landscape structure and seasonal succession are key for the recovery of these systems. However, this recovery capacity might be compromised in the future from increasing wildfire and potential for substantial habitat loss.

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**Response to Reviewers:**

Dear Dr. Cunillera-Montcusí,

Reviewers have now commented on your paper, and we are pleased to inform you that your manuscript has been accepted pending minor revisions. If you are prepared to undertake the work required, your paper will be published in Inland Waters.

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If you decide to revise the work, please submit a list of changes or a rebuttal against each point raised when you submit the revised manuscript.

Kind Regards,

David Hamilton, Ph.D.
Editor-in-Chief
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Authors’ answer:

Dear Editor-in-Chief,
We thank your effort in commenting the manuscript and appreciate your effort. We have followed all the suggestions made by you that were just formal corrections and small text amendments. Find therefore the revised version of our manuscript that we just hope that will be finally accepted.

Thanks again for your task.
Best regards,

David Cunillera-Montcusí
Title: Recovery of temporary pond alpha and beta diversity after wildfire disturbance: the role of dispersal and recolonization processes.

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Abstract

Wildfires are a global disturbance being enhanced by human-induced pressures. Their frequency and intensity are expected to increase in the near future in regions such as the Mediterranean basin. While responses of terrestrial systems to wildfire have been thoroughly studied, aquatic systems such as temporary ponds have received less attention. Furthermore, previous works have focused on wildfire impacts in aquatics systems from a more functional and trait-based approach, but such disturbances can also impact the diversity of these systems at the local and regional level. In this work, we assess wildfire impacts alpha and beta diversity of Mediterranean temporary ponds, analysing samples of pond macrofauna after a wildfire that burned part of a cluster of these habitats. The wildfire did not change alpha diversity patterns but differences in beta diversity were observed when considering species abundance. Species with greater contribution to beta diversity were more strongly represented in unburned ponds after the wildfire. These changes occurred mostly during the beginning of the hydroperiod, which increased regional differences in burned ponds. However, these alterations decreased towards the middle and the end of the hydroperiod. Overall, we report a fast recovery of communities after the wildfire, tightly linked to a rapid recolonization that
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Keywords: Disturbance; Fire; Regional diversity; Seasonal changes; Landscape; Recolonization
Introduction

The study of disturbance impacts and their consequences on communities and ecosystems constitutes one of the main topics in ecology (White & Pickett 1985; Vellend 2016; Holyoak et al. 2020). The relevance of disturbances as drivers of change in environmental characteristics such as the landscape structure and species abundance/presence has been central for the advancement and consolidation of an entire theory around disturbances (White & Pickett 1985). These phenomena can have several origins (e.g., natural, anthropogenic), characteristics (e.g., pulses, chronic, extension), and consequences (e.g., blooms of certain groups, changes in nutrient concentrations, changes in species presence) but at the same time, biological consequences of disturbances depend on the features of the impacted communities and systems (Turner 2010). Therefore, in order to understand and cope with disturbances we need to contextualise their consequences within a specific habitat, especially when disturbances regimes are expected to increase and constitute a threat (Moritz et al. 2012; IPCC 2014; Ripple et al. 2019). Wildfires are an example of such a disturbance as they are expected to increase in the future as a consequence of global change; first, because climate change fosters the climatic conditions favouring them (e.g., rise in temperature and decrease in precipitation; Pausas & Fernández-Muñoz 2012; Turco et al. 2018) and second, due to direct human intervention (e.g., intended fires or fuel accumulation; Turner & Gardner 2015; Newman 2019). Although wildfire impacts and consequences have been studied extensively, previous studies have mainly focused on terrestrial ecosystems, ignoring the consequences for aquatic ecosystems (Prepas et al. 2009; Bixby et al. 2015; McCullough et al. 2019). This knowledge gap is even greater for temporary aquatic systems such as streams, ponds, and wetlands (Bixby et al. 2015; but see Verkaik et al. 2015; Cunillera-Montcusí et al. 2019).

The consequences of wildfires in aquatic systems are mostly related to their impacts on the catchment and thus, to the indirect effects (Minshall et al. 1989; Romme et al. 2011). Several
works have analysed their consequences such as causing nutrient enrichment (Spencer & Hauer 1991; Spencer et al. 2003) and increasing primary production due to a greater presence of filamentous algae (Cowell et al. 2006; Verkaik et al. 2013; Rodríguez-Lozano et al. 2015; Venne et al. 2016). Concomitantly, macroinvertebrate functional feeding groups tend to become dominated by shredders, scrapers, and generalist species (Oliver et al. 2012; Lewis et al. 2014; Musetta-Lambert et al. 2020). The denomination of “Fire pulse” has been used to describe such processes, which can increase the export of biomass to the surrounding terrestrial environment (Malison & Baxter 2010a; 2010b). This functional perspective using mostly species traits to understand wildfire impacts has been the major focus of works dealing with such systems and disturbances. Nevertheless, wildfire consequences can go beyond the functional aspect and change the diversity of affected systems. Strong post-fire floods can impact rivers by decreasing species richness (Vieira et al. 2004; Bêche et al. 2005) and modifications of habitat structure can change community composition of burned sites (Robson et al. 2018; Williams Subiza & Brand 2018). Therefore, wildfires can have strong impacts on system biodiversity, especially at the regional scale, by affecting the beta diversity of the impacted systems (Verkaik et al. 2015). Specifically, wildfires can affect large extents of territory, potentially altering landscape structure and inducing changes in dispersal patterns and recolonization for active or passive dispersers (Cunillera-Montcusí et al. 2021).

At the regional scale, wildfires also affect the metacommunity, which is related with the exchange of individuals among communities (Leibold et al. 2004; Leibold & Chase 2018). The impact of a wildfire or any other disturbance on part of this metacommunity may lead to alterations in its characteristics that can induce changes in the regional dynamics, especially in dispersal, thus, changing post-disturbance assembly dynamics (Howeth & Leibold 2010; Altermatt et al. 2011; Vanschoenwinkel et al. 2013). Furthermore, disturbances can favour regional differences between communities and, increase systems beta diversity
counterbalancing dispersal homogenisation (Gascón et al. 2007; Evans et al. 2020). At intermediate levels, disturbances can favour coexistence among certain species (Castorani & Baskett 2020), therefore increasing regional differences. Finally, in more spatially isolated patches, fire-disturbance may foster priority effects and thus increase regional differentiation between burned communities (Han et al. 2018). Therefore, the role of disturbances at regional scale can greatly change assembly processes depending on disturbance intensity. On the other hand, high connectivity and dispersal can foster recovery of affected communities (Whitney et al. 2015; Woods et al. 2016; Rosset et al. 2017), which at high levels of dispersal can override post-disturbance impacts (Altermatt et al. 2011; Cai et al. 2017). Therefore, having connected communities where dispersal is effective can promote higher resilience to disturbances, especially potentially catastrophic ones (Starzomski & Srivastava 2007; Thrush et al. 2013; Rosset et al. 2017; Cunillera-Montcusí et al. 2021).

Within the global change scenarios of increased global wildfires, especially in Mediterranean regions (Turco et al. 2018), and connectivity loss due to fragmentation (e.g., loss of ponds globally and at a regional level; Wood et al. 2003; Pekel et al. 2016; Bastin et al. 2019), it becomes critical to improve our understanding of wildfire impacts, especially for systems such as Mediterranean temporary ponds where wildfire impacts diversity, both local (alpha diversity) and regional (beta diversity). In addition, these systems constitute defined patches in the landscape, connected through the dispersal of their individuals. Therefore, they represent excellent examples for studying metacommunity dynamics (De Meester et al. 2005; Bagella et al. 2016). They stand as highly diverse hotspots that hold uniquely adapted taxa due to their intrinsic functioning and highly heterogeneous characteristics, which favours a high regional specificity (Boix et al. 2016; Boix et al. 2017). Such regional importance is a key asset to maintain their high diversity levels (Horváth et al. 2019). However, due to this importance, an alteration in the landscape structure generated by a disturbance such as a
wildfire may produce a strong change in the diversity of these already endangered systems (EPCN 2008; Bagella et al. 2016; Calhoun et al. 2017). Finally, apart from this strong spatial relevance, these temporary systems are also strongly impacted by seasonal changes related to water level and hydroperiod length and timing (Kneitel 2014; Shin & Kneitel 2019). Hence, the temporal variation also determines diversity patterns at both scales (Lake et al. 1989; Bazzanti et al. 1996; Boix et al. 2004; Culioli et al. 2006), becoming stronger before pond drying (O’Neill 2016).

In this study, our main goal is to assess wildfire effects on alpha and beta diversity of Mediterranean temporary pond faunal communities. Furthermore, we are interested on how these diversity indices will vary temporally along the post-fire hydroperiod (i.e., recovery). The studied cluster of ponds was partially affected by the wildfire during their drought phase, which generated three pond typologies according to wildfire impacts: completely burned ponds (burning the entire pond basin), partially burned ponds (where the wildfire left unaffected parts), and ponds that remained unburned. Previous studies on such ponds have focused on wildfire alteration on community functioning (Cunillera-Montcusí et al. 2019) and trait selection (Cunillera-Montcusí et al. 2020), but wildfire impacts on biodiversity of communities remain unassessed.

**Methods**

**Study site**

The studied Mediterranean temporary ponds are located in the north-eastern Iberian Peninsula. The ten sampled ponds (Figure 1 and Supplemental Material S1) belong to a larger cluster of around 30 shallow temporary water bodies, constituting an outstanding example of a lowland Mediterranean region with endorheic seasonally flooded depressions (Font & Vilar 1998). This area has mostly been agricultural, including for cattle, and is currently under
protection as a Landscape of National Interest. The Mediterranean temporary ponds found there stand as biodiversity hotspots representative of the characteristic Mediterranean temporary pond habitat (Boix et al. 2009; Ruhí et al. 2013), protected under the Habitats Directive (92/43/EEC). The hydroperiod of these systems generally begins in late summer/early autumn with the first rains and lasts until late spring/early summer when ponds dry out due to evapotranspiration. However, inundation length and flooding timing can strongly vary interannually (Boix et al. 2004). In July 2012, the region was affected by a natural wildfire affecting 13,000 hectares. The wildfire spread rapidly due to strong winds which also generated an heterogeneous distribution of their effects throughout the landscape.

**Sampling campaigns**

The wildfire partially affected the cluster of Mediterranean temporary ponds when they were dry. Some ponds were completely burned by it (hereafter Burned ponds B), others were burned in only some parts of their basin as wildfire passed rapidly and patchily across them; hereafter (Partially burned ponds PB), and lastly some other ponds remained completely unaffected, hereafter (Unburned ponds U). Ten ponds in the region (Figure 1) had been sampled in the spring before the wildfire, hereafter referred to as the *May 2012* samples. The ponds were affected by the wildfire during the summer of 2012. Once flooded, we sampled the same ten ponds bimonthly during the entire post-fire hydroperiod from December 2012 until July 2013 (5 sampling campaigns: December 12, February 13, April 13, June 13 and July 13). We sampled all the ponds in all campaigns except two ponds in February 2013 and four in July 2013 that were dry.

**Faunal community sampling**

We sampled pond macrofauna (invertebrates and amphibians) from the 10 ponds, which encompassed the three pond typologies according to wildfire effects (i.e., 3 B, 3 PB and 4 U;
see Supplemental Material S1). In each pond we took twenty sweeps of 0.5 m length each using a dip net with a mesh size of 250 μm and a diameter of 20 cm. The sweeps were proportionally distributed across all pond mesohabitats (e.g., pond shore, macrophytes, water column) in order to capture a higher representation of pond taxa. We identified in situ all amphibian adults and released them back into the pond. We then fixed all the samples in 4% formaldehyde for subsequent identification in the laboratory. We sorted, counted, and identified all sampled organisms to the lowest possible taxonomical level (mostly species or genus). For Oligochaeta and Turbellaria we were unable to identify to the species level, therefore these groups were only classified to family or subfamily level.

Data analysis

To analyse biodiversity changes across pond typologies we calculated several alpha and beta diversity metrics. We analysed alpha diversity for each pond and for each sampling campaign by calculating species richness (S), Shannon-Wiener index (H), and evenness (J). To analyse beta diversity, we used two approaches that provide different information about regional differences among sites. First, we calculated measures based on the overall contribution that each pond and each species has to total beta diversity: local contribution to beta diversity (LCBD) and species contribution to beta diversity (SCBD), respectively (Borcard et al. 2011; Legendre & De Cáceres 2013). These two indices have been widely used in recent years to analyse the relative importance of each site or each species in differentiate communities from a region. These indices highlight the uniqueness of each local community (LCBD) or each species (SCBD). Both are interpreted similarly: higher values imply that the pond community or the species is strongly contributing to the regional differentiation. For SCBD, to compare numbers among ponds, we considered the species with SCBD values higher than the SCBD mean (see Borcard et al. 2011). Secondly, to analyse spatial differences among pond communities we calculated taxonomic beta diversity (pairwise differences between ponds for
each sampling date) with the Podani’s family of indices using the Jaccard index for presence-absence data and its quantitative counterpart, the Ružička index, for abundance data (Borcard et al. 2011). In addition, we partitioned both metrics into replacement and richness/abundance difference (Podani & Schmera 2011). The consideration of both presence-absence and abundance data was done to separately analyse the impact of wildfire on these two biodiversity facets. We used the contribution to beta diversity (LCBD and SCBD) to assess beta diversity patterns comparing all ponds together (total beta diversity).

On the other hand, pairwise taxonomic beta diversity (Jaccard – Ružička indices) was calculated only considering similarities within each pond typology group (burned, partially burned, and unburned) to assess wildfire consequences within each group (e.g., burned ponds become similar due to community homogenization). All biodiversity indices were calculated in R (R-Core Team 2019) using the vegan package (Oksanen et al. 2010).

We considered two main factors in our analysis: pond typology according to wildfire (i.e., B, PB, and U) and temporal succession represented by the post-fire sampling campaigns (i.e., December 12, February 13, April 13, June 13, and July 13). To test for differences related to these two factors we used linear mixed models with Gaussian distribution considering each alpha diversity metric independently (log transformed S, H, and J) as explanatory variables and pond identity as the random factor. For LCBD, Jaccard – Ružička indices and their components (replacement and richness/abundance differences), we conducted beta mixed regressions as LCBD and the Podani’s family of indices vary between 0 and 1. Here, we also considered wildfire (i.e., B, PB, and U) and temporal succession represented by the post-fire sampling campaigns (i.e., December 12, February 13, April 13, and June 13) and pond, or pond pairs as a random factor. For all Podani’s family of indices we accounted for differences within pond typology and did not include July 2013 in the model due to the lack of replicates in this sampling campaign (since four ponds were dry). Moreover, to analyse the
evolution of these indices in a three-dimensional context, we compared them using triangle plots to visualise the trend in each pond typology. Finally, for SCBD, we selected the species having significantly higher SCBDs in each sampling campaign (Borcard et al. 2011) and then compared their abundances according to pond typologies with a linear model with Gaussian distribution (i.e., log transformed abundances). All model analysis considering time (i.e., differences between sampling campaigns) were carried out without considering pre-fire samples (May 2012) to make the comparison balanced (McDonald et al. 2000) and account for strong interannual differences linked to water availability. However, we represented these samples values as a visual reference. To sum up, in all alpha and beta diversity metrics models we accounted for “wildfire”, “time”, and their interaction (i.e., change throughout time among pond types). Non-significant interaction terms were removed. All analyses were conducted using nlme, lsmeans, betareg, and glmmTMB packages (Cribari-Neto & Zeileis 2010; Lenth 2016; Magnusson et al. 2020; Pinheiro et al. 2020). The use of mixed models is recommended in such control-impact analyses because the underlying assumptions of the model are likely to be satisfied, and the interpretation of the estimated parameters is straightforward (McDonald et al. 2000).

Results

Alpha diversity metrics

Pooling together all samples and all pond typologies, we found a total of 214 taxa (Supplemental Material S2). From this general pool, burned ponds had 162 taxa, partially burned ponds 164 taxa, and unburned ponds 170 taxa. When aggregating by sampling campaigns, samples from before the wildfire had 120 taxa and the post-fire ones 117, 81, 124, 126, and 119 taxa from December 2012 until July 2013. These values are similar with the exception of the February 2013 sampling campaign that coincided with a low pond level
period, when two studied ponds were dry. A similar pattern between individual ponds was observed for alpha diversity metrics (Supplemental Material S3) with time (Figure 2; Table 1). Significant differences in richness were only detected between the December 2012 and February 2013 sampling campaigns (Table 2). These sampling events had lower richness values. None of the three studied alpha metrics showed differences related to wildfire impact (Table 2) and the three typologies varied similarly across time, changing concomitantly with temporal succession.

**Ponds and species contribution to beta diversity**

Beta diversity showed different patterns for the whole community (LCBD) and individual species contributions (SCBD). LCBD remained similar in all sampled ponds and sampling campaigns (Figure 3a and Supplemental Material S3). We did not detect significant differences for pond typologies (Supplemental Material S4). However, we detected greater values of LCBD in partially burned ponds at the end of the hydropower (Figure 3a and Supplemental Material S4). From a regional scale (Figure 3b), LCBD did not show any clear pattern, but we observed slightly greater values in sampling campaigns where pond levels were lower and some ponds were completely dry (February 2013 and July 2013). On the other hand, the species that contributed most to beta diversity varied across sampling campaigns (Table 3), with the greatest number in the April 2013 sampling (18 taxa). However, when we analysed the abundances of these taxa among ponds, we observed that species which contributed greatly to regional beta diversity were more abundant in unburned ponds (Figure 4; Supplemental Material S5) during the first two initial post-fire sampling campaigns (i.e., December 2012 and February 2013). We also detected greater abundances in partially burned ponds in the April 2013 sampling campaign. Burned ponds always had lower or slightly lower abundance values than partially burned and unburned ponds (Supplemental Material S5).
Beta diversity pairwise comparisons

We detected different patterns in beta diversity indices and their partitioning when accounting for presence-absence and abundance values. For presence-absence data (Figure 5a), we did not detect significant differences between pond typologies (p-values>0.05, Supplemental Material S4). Clearer differences were related to sampling campaign (Supplemental Material S4), where we observed significant p-values (p-values<0.05 in February 2013 for replacement and April 2013 for richness difference). In both cases, unburned ponds had higher values (Figure 5a, Supplemental Material S4). Although not significant, unburned ponds mainly had lower replacement values and only the February 2013 campaign broke this pattern, coinciding with the drying of some ponds. In contrast, when we considered abundance (Figure 5b), we detected a substantial change in the regional differences between pond typologies. During the post-fire hydroperiod, burned ponds had higher replacement values and correspondingly lower abundance difference values (Figure 5b, Supplemental Material S4). This pattern was mostly present at the beginning of the hydroperiod than the end (Supplemental Material S4). Furthermore, temporal changes were also detected: June 2013 sampling campaign had similar replacement and abundance difference values (Figure 5b). Finally, the representation in triangle plots of beta diversity pairwise values (Figure 6) showed three main patterns: (1) presence-absence and abundance had different outputs, (2) burned ponds experienced a strong seasonal change along the post-fire year compared to partially burned and unburned ponds with species abundance values, and (3) changes were linked mostly to the replacement component. Beta diversity values using presence-absence data varied across the same region in all pond typologies (Figure 6a). By contrast, when using species abundance (Figure 6b), we saw a marked increase in replacement of burned ponds at the beginning of the post-fire sampling campaigns (December 2012, February and April 2013) and the consequent substantial increase of their general mean replacement values.
(Figure 5b). This trajectory depicting a rise and a decrease in replacement’s relevance could be related to wildfire intensity. Partially burned ponds had a similar trajectory to burned ones but milder, whereas for unburned ponds it was negligible (Figure 6b).

Discussion

The interplay between diversity and disturbances constitutes a cornerstone of historical and current ecological theory (White & Pickett 1985; Turner 2010; Turner & Gardner 2015; Pulsford et al. 2016; Newman 2019; Holyoak et al. 2020). How disturbances directly or indirectly impact communities and change their assemblages is key to comprehend the extent in which disturbances affect ecosystems and to develop management strategies to cope with them (Battisti et al. 2016). This is especially true for threatened habitats (e.g., Mediterranean temporary ponds; EPCN 2008; Gómez-Rodríguez et al. 2009; Zacharias & Zamparas 2010; Rhazi et al. 2012; Boix et al. 2020) that will be affected by greater and more intense disturbances such as wildfires (Le Page et al. 2008; Pausas & Fernández-Muñoz 2012; Turco et al. 2018). Throughout this study we explored the effects of wildfire on the alpha and beta diversity from Mediterranean temporary ponds. These systems hold and sustain a unique set of fauna which relies on habitat heterogeneity to maintain high regional diversity (Céréghino et al. 2008; Beklioglu et al. 2014; Boix et al. 2017; Hill et al. 2017; Vad et al. 2017). In fact, we identified 214 taxa, and around half of them were detected in each sampling campaign, implying a great taxonomic variation throughout time and space. This seasonal successional pattern has been long known and widely reported (e.g., Kenk 1949; Lake et al. 1989; Bazzanti et al. 1996; Boix et al. 2004; Culioli et al. 2006) and highlights the relevance that landscape structure has for these habitats by maintaining a diverse community through the exchange of individuals (Horváth et al. 2019). The fact that not all the ponds were affected by wildfire plus this strong regional interaction (i.e., metacommunity rescue effect; Leibold et al. 2004) probably favours a strong resilience of the system (Cunillera-Montcusí et al. 2021) as
ponds were not greatly affected by the disturbance. Nevertheless, we did observe some differences indicating that wildfire affected biodiversity of ponds at some levels.

Wildfire did not affect alpha diversity patterns in pond typologies. In fact, all sampled ponds followed similar trends throughout the hydroperiod, having less richness at the beginning (i.e., late autumn and winter) and increasing towards its end (i.e., spring and end of summer), despite some visual differences between pre- and postfire sampling campaigns. Such successional variation is depicting the seasonal changes in pond communities (Kenk 1949; Lake et al. 1989; Bazzanti et al. 1996). In spring and summer months, better weather conditions favour the arrival of other taxa (e.g., some Odonata and Coleoptera), which overwinter in permanent sites and colonize ponds during warmer months, seeking food and predatory refugia for their offspring (Wiggins et al. 1980; Williams 2006; Boda & Csabai 2009). Pond level fluctuation and rainfall patterns also modulate these changes as temporary systems may have several hydroperiods per year (Boix et al. 2016), which strongly compromises species assembly throughout the wet phase (Kneitel 2014; Florencio et al. 2020). In February 2013, pond levels decreased but not all ponds dried completely, probably contributing to increased regional differences. Indeed, this successional trend related to pond level fluctuation was captured by LCBD values in February 2013 and July 2013. The decrease of pond levels would increase differences among ponds since taxa able to leave them would look for other habitats (e.g., water boatmen such as *Sigara lateralis*, dragonflies such as *Aeshna mixta* or midges such as *Psectrocladius limbatellus*) or the ones that remain by producing resting stages (e.g., fairy shrimps such as *Chirocephalus diaphanus*, snails such as *Gyraulus* sp. or worms such as *Stylaria lacustris*; Williams 2006; O’Neill 2016), something that would raise regional differences between ponds and thus, their contribution to beta diversity.
Beta diversity is a well known concept that is calculated and interpreted in different ways (Baselga 2010; Borcard et al. 2011; Podani & Schmera 2011; Almeida-Neto et al. 2012; Legendre & De Cáceres 2013; Legendre 2014). Interestingly, species with higher contributions to beta diversity (SCBD values) responded to wildfire categories. These species contributed more to the differentiation among local communities. Some of these species were present throughout the whole hydroperiod such as the Chironomidae *Psectrocladius limbatellus* or the Ephemeroptera *Cloeon* spp., but others changed between sampling campaigns. In the first samplings (December 2012 and February 2013) most species were Tubellaria (e.g., *Gieysztoria* sp., *Gieysztoria diadema*, *Dalyellia viridis*), Oligochaeta (e.g., family Tubificidae, Lumbriculidae, *Stylaria lacustris*) or other taxa having passive dispersal (e.g., *Proasellus coxalis*, *Tanymastix stagnalis* or *Hydra* sp.). On the other hand, in spring and summer sampling campaigns (April, June and July 2013), besides these taxa, more Diptera, Gastropoda, and some Heteroptera were detected (e.g., *Gyraulus crista*, *Plea minutissima*, *Chaoborus crystallinus*). These significant taxa are related to the natural successional change along the hydroperiod. However, unburned ponds had greater abundances at the beginning of the hydroperiod. Therefore, in terms of abundance, unburned ponds contributed greatly to beta diversity while they were also present in partially burned and burned ponds but at depleted numbers. This change agreed with pairwise comparison results, showing a similar response when considering both abundance and presence-absence data. Thus, the impacts of wildfire on Mediterranean temporary pond beta diversity were basically detected when considering species identities together with their abundances. In this sense, previous works analysing wildfire impacts with a trait-based approach detected a decrease in abundance of some functional groups at the beginning of the hydroperiod (i.e., passive dispersers aestivating in the pond sediment; Cunillera-Montcusí et al. 2019). This change in abundance was assumed to be similar in all burned ponds (i.e., affecting the same
set of species). Nevertheless, here, the replacement component of beta diversity greatly increased within burned ponds. This increase represented almost the totality of their regional differences, something that would indicate an increase in assembly differences among burned ponds. Thus, wildfire would cause greater within group differences in burned ponds (i.e., greater stochasticity and priority effects) than the observed among partially burned or among unburned ponds (Chase 2007; Ferrenberg et al. 2013; Fukami 2015; Viana et al. 2016; Han et al. 2018).

Wildfire disturbance can generate a wide array of consequences on aquatic systems, affecting communities spatially (Hossack & Corn 2007; Whitney et al. 2015; Banks et al. 2017; Han et al. 2018) and temporally (Gresswell 1999; Minshall et al. 2001; Romme et al. 2011; Verkaik et al. 2015). Here, these two components interacted in pond community assembly, responding to wildfire impacts during the first year after the wildfire. Spatially, after the disturbance there was an increase in the replacement component within each pond typology, coupled with wildfire impact intensity. It is true that a general rise in replacement due to a global wildfire landscape effect, which would compromise colonization across all ponds, could not be ruled out. However, active dispersers were found in the ponds at the beginning of the hydroperiod and most flying species would be able to cover the distances between ponds to colonize them rapidly (Cunillera-Montcusi et al. 2019; 2021). On the other hand, temporally, this change in replacement at the abundance level and within pond groups ceased with hydroperiod advance (i.e., June 2013). Such a temporal pattern was only clear in this facet of diversity while alpha diversity or beta diversity based on presence/absence were much variable, probably related to the strong intraannual variation across ponds. Nevertheless, this temporal rise in replacement could also be expected in unaffected ponds due to initial stochasticity in hatchings and dormant community activation (Florencio et al. 2009; O’Neill 2016; Wisnoski et al. 2019; Bellin et al. 2020; Olmo et al. 2020). Overall, wildfire would make this rise in replacement
more extreme than expected as it would decrease abundances of aestivating organisms (Wells et al. 1997; Chittapun 2011). This would cause a rise in differences between affected ponds. Nevertheless, temporary ponds community adaptations to drought would foster post-disturbance recovery due to a fast recolonization linked to improved weather conditions, pond level stabilization, and unburned ponds proximity, which would counterbalance fire impacts (Boda & Csabai 2009; Bogan & Boersma 2012; Juračka et al. 2019). Therefore, drought adaptation would indirectly raise wildfire resilience in a cross-tolerance response (Thiéry 1979; Anderson & Smith 2004; Strachan et al. 2014; Strachan et al. 2015; Pallarés et al. 2017; Jooste et al. 2020).

Conclusions

Addressing disturbance consequences on specific habitats is nowadays needed to fully comprehend their impacts on ecosystem functioning and diversity. In addition, integrating both spatial (i.e., regional differences) and temporal (i.e., first post-fire hydroperiod) scales within a metacommunity framework allows us to build a better picture to improve our understanding of disturbance consequences on metacommunity assembly. Although wildfire did change the beta diversity of these Mediterranean temporary ponds, rising differences among burned ponds at the beginning of the hydroperiod, dispersal, and landscape structure fostered a rapid recolonization and a return to previous conditions in less than one year. This would indicate a high resilience capacity of the studied metacommunities. Nevertheless, this resilience would rely on ponds’ specific characteristics. These unique features might become compromised by global change through habitat degradation or loss, and rise in disturbance regimes, thus, it is of vital importance to preserve these unique habitats and their diverse nature and regional structure.
Acknowledgements

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Data availability

The dataset and code corresponding to the current manuscript can be found at: 10.6084/m9.figshare.13238720.
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### Table 1: Mean and standard deviation of all alpha diversity metrics across pond typologies for every sampling campaign. S: taxa richness, H: Shannon-Wiener diversity index and J: evenness. B: Burned ponds, PB: Partially burned ponds, U: Unburned ponds.

<table>
<thead>
<tr>
<th></th>
<th>May 2012- Before</th>
<th>December 2012</th>
<th>February 2013</th>
<th>April 2013</th>
<th>June 2013</th>
<th>July 2013</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>sd</td>
<td>mean</td>
<td>sd</td>
<td>mean</td>
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</tr>
<tr>
<td><strong>B</strong></td>
<td>39.70 ±8.50</td>
<td>34.00 ±6.24</td>
<td>24.50 ±7.78</td>
<td>42.30 ±0.58</td>
<td>42.70 ±5.51</td>
<td>49.00 ±4.24</td>
</tr>
<tr>
<td><strong>S</strong></td>
<td>38.30 ±5.03</td>
<td>30.70 ±8.62</td>
<td>25.30 ±3.79</td>
<td>53.30 ±2.52</td>
<td>43.30 ±6.66</td>
<td>55.00 ±11.30</td>
</tr>
<tr>
<td><strong>U</strong></td>
<td>38.80 ±6.90</td>
<td>37.50 ±13.20</td>
<td>32.00 ±5.29</td>
<td>44.20 ±9.07</td>
<td>50.20 ±11.90</td>
<td>49.00 ±2.83</td>
</tr>
<tr>
<td><strong>H</strong></td>
<td>2.28 ±0.35</td>
<td>2.37 ±0.64</td>
<td>2.09 ±0.30</td>
<td>2.06 ±0.72</td>
<td>2.05 ±0.45</td>
<td>2.28 ±0.53</td>
</tr>
<tr>
<td><strong>PB</strong></td>
<td>1.80 ±0.34</td>
<td>2.05 ±0.23</td>
<td>2.07 ±0.34</td>
<td>2.64 ±0.08</td>
<td>2.13 ±0.36</td>
<td>2.46 ±0.40</td>
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<td><strong>U</strong></td>
<td>2.16 ±0.33</td>
<td>2.32 ±0.51</td>
<td>1.83 ±0.43</td>
<td>2.41 ±0.49</td>
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<td>1.50 ±0.17</td>
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<tr>
<td><strong>J</strong></td>
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<td>0.67 ±0.16</td>
<td>0.55 ±0.20</td>
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<td>0.58 ±0.12</td>
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<td><strong>PB</strong></td>
<td>0.49 ±0.09</td>
<td>0.61 ±0.06</td>
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<td>0.57 ±0.08</td>
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<td>0.64 ±0.12</td>
<td>0.66 ±0.05</td>
<td>0.39 ±0.04</td>
</tr>
</tbody>
</table>

### Table 2: Linear mixed models results for alpha diversity metrics considering only post-fire samples. S: taxa richness, H: Shannon-Wiener diversity index and J: evenness. DF indicates number of degrees of freedom. Note that no interaction was significant and for that reason not included in the final model to decrease its complexity.

<table>
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<tr>
<th>Species richness (S)</th>
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<td>-2.88</td>
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<tr>
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<td>0.07</td>
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<td>4.39</td>
<td>&lt;0.001</td>
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<td>0.07</td>
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<td>&lt;0.001</td>
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<td>30</td>
<td>4.06</td>
<td>&lt;0.001</td>
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<td>NB</td>
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<td>0.12</td>
<td>7</td>
<td>0.74</td>
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<table>
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<tr>
<th>Evenness (J)</th>
<th>Factor</th>
<th>Value</th>
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<td>0.03</td>
<td>7</td>
<td>0.50</td>
<td>0.63</td>
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Table 3: Taxa presenting higher SCBD values than the mean in each of the six sampling campaigns. One sampling campaign from before the wildfire and 5 post-fire campaigns. Each taxon has its 6 letters acronym used in Figure 4 to reference.

<table>
<thead>
<tr>
<th>May 2012 - before</th>
<th>December 2012</th>
<th>February 2013</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tetraclis marmorosa</em> - TET_MAR</td>
<td>Tanymastix stagnalis - TAN_STA</td>
<td>Styliaria lacustris - STY_LAC</td>
</tr>
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<td><em>Psectrocladius (P.) limbatellus</em> - PSC_LIM</td>
<td><em>Psectrocladius (P.) limbatellus</em> - PSC_LIM</td>
<td><em>Psectrocladius (P.) limbatellus</em> - PSC_LIM</td>
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<tr>
<td><em>Physa acuta</em> - PHY_ACU</td>
<td>Paratanytarsus grimmii - PTA_GRI</td>
<td>Paratanytarsus grimmii - PTA_GRI</td>
</tr>
<tr>
<td><em>Micropsicta lindrothi</em> - MPS_LIN</td>
<td><em>Pseuclisossalis</em> - PRO_COX</td>
<td>Rhabdocoela type 1 - O_RHA11</td>
</tr>
<tr>
<td><em>Hippeutis complanatus</em> - HIP_COM</td>
<td><em>Piona</em> sp. type 1 - PIO_SP1</td>
<td>Rhabdocoela type 1 - O_RHA11</td>
</tr>
<tr>
<td><em>Hydra sp.</em> - HDA_SP</td>
<td>Hydra sp. - HDA_SP</td>
<td>Hydra sp. - HDA_SP</td>
</tr>
<tr>
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<td>Gyraulus <em>sp.</em> - GYR_CRI</td>
</tr>
<tr>
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</tr>
<tr>
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<td><em>Gyraulus cristina</em> - GYR_CRI</td>
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<tr>
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<td><em>Gyraulus</em> coxalis - PRO_COX</td>
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<td><em>Piona</em> sp. type 2 - PIO_SP2</td>
<td><em>Piona</em> sp. type 2 - PIO_SP2</td>
<td><em>Piona</em> sp. type 2 - PIO_SP2</td>
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<td><em>Pygospio</em> sp. - HDA_SP</td>
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<td><em>Gyraulus</em> cristina - GYR_CRI</td>
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</table>
Figure captions

Figure 1: Location map of the cluster of temporary ponds found in the Albera region. Coloured squares correspond to sampled ponds and grey to non-sampled ponds. Their UTM coordinates can be found in Supplemental Material S1. The black circle in the Iberian Peninsula map indicates the sampling region. Images correspond to Estany de la Cardonera dels Torlits, completely burned during the wildfire, and show its evolution along the post-fire hydroperiod.

Figure 2: Alpha diversity values, mean and standard deviation, for each sampling campaign and pond typology. a) Taxa richness (S), b) Shannon-Wiener diversity index (H) and c) Evenness (J). Note that samples from before the wildfire (May 2012-Before) are also included for visual comparison, although they were not analysed in the model. Alpha values and model results can be found in Supplemental Material S2 and table 2, respectively. Burned ponds in red, Partially burned ponds in orange and Unburned ponds in green.

Figure 3: a) Local contribution to beta diversity (LCBD) values (mean and standard deviation) for each sampling campaign and pond typology. b) LCBD values represented using pond UTMs (Supplemental Material S1) to represent geographically these values. Circle size corresponds to LCBD values. Red area corresponds to the area affected by the wildfire. Burned ponds in red, Partially burned ponds in orange and Unburned ponds in green.

Figure 4: Abundance of highly contributing to beta diversity taxa based on their SCBD values. Each circle corresponds to an individual taxa mean abundance for each pond typology. Burned (B) ponds in red, Partially burned (PB) ponds in orange and Unburned (U)
ponds in green. Circle size corresponds to taxa abundance values. Black squares indicate pond significant differences. Taxa acronyms full names are written in Table 4.

**Figure 5:** Beta diversity pairwise tests for each pond typology (comparisons within each pond category). a) Beta diversity partitions and index calculated using presence-absence data (Jaccard similarity): Replacement, Richness difference and Jaccard index. b) Beta diversity partitions and index calculated using abundance values (Ružička similarity): Replacement, Abundance difference and Ružička index. Burned (B) ponds in red, partially burned (PB) ponds in orange and unburned (U) ponds in green. Coloured asterisks indicate significant differences between each category (asterisk colour corresponds to the significant category). Stronger colours indicate significantly different entire categories (burned category in bottom left and central plots). Black letters indicate temporal differences (the whole sampling campaign is different). Model results can be found in Supplemental Material S4. Note that the May 2012 and July sampling campaigns have not been considered in the analyses, but they are represented for visual reference (white and transparent background).

**Figure 6:** Beta diversity triangle plots for comparisons using a) presence-absence values and b) abundance values for each pond typology. Burned (B) ponds in red colours, partially burned (PB) ponds in orange colours and unburned (U) ponds in green colours. Colour gradient corresponds to each different sampling campaigns ranging from dark (May 2012 - Before) to lighter colours at the beginning of the hydroperiod (December 2012) and stronger colours towards the end (July 2013). Circles numbering also indicates sampling campaigns being 1 May 2012 - Before, 2 December 2012, 3 February 2013, 4 April 2013, 5 June 2013 and 6 July 2013. To represent the triangle plots the inverse value of both Jaccard and Ružička similarity indices is represented (1-Jaccard or 1- Ružička correspondingly).
### Supplemental Material S1: Sampled ponds local names, burned status and location in UTM.

<table>
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<th>Wildfire</th>
<th>UTMx</th>
<th>UTMy</th>
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<td>Estany de Baix de Canadal</td>
<td>B</td>
<td>492588.25</td>
<td>4693730.33</td>
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**Supplemental Material S2:** Taxonomic list of the biocenosis found across all the ponds and sampling campaigns. A detailed list of taxa per site can be found in the electronic document corresponding to the free available PhD thesis: Resilience of aquatic metacommunities: implications for disturbance recovery by Cunillera-Montcusí 2020 ([https://www.tdx.cat/handle/10803/669784](https://www.tdx.cat/handle/10803/669784)).

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**Supplemental Material S3: Sampled ponds alpha diversity metrics:** Local richness (S), Shannon-Wiener diversity index (H) and evenness (J) and the local contribution to beta diversity of each pond (LCBD). B: Burned ponds, PB: Partially burned ponds, U: Unburned ponds. Pond local names are also indicated to match with supplementary S1 information.

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Supplemental Material S4: Beta regression mixed model results for LCBD values, Presence absence beta diversity (Replacement, Richness diversity and Jaccard index) and Abundance beta diversity (Replacement, Richness diversity and Ružička index) considering only post-fire samples. For beta diversity partitions (presence absence and abundance) we also excluded the last sampling campaign due to the lack replicates (July 2013). B burned ponds U unburned ponds and PB partially burned ponds. Grey lines with bold numbers indicate significant results.

| Factors                  | Estimate | Std. Error | z value | Pr(>|z|) |
|--------------------------|----------|------------|---------|---------|
| Intercept (B/December 2012) | -2.34    | 0.13       | -17.60  | <0.001  |
| NB                       | 0.12     | 0.17       | 0.71    | 0.48    |
| PB                       | 0.23     | 0.18       | 1.26    | 0.21    |
| February 2013            | 0.22     | 0.13       | 1.62    | 0.11    |
| April 2013               | 0.13     | 0.12       | 1.10    | 0.27    |
| June 2013                | 0.21     | 0.12       | 1.78    | 0.07    |
| **July 2013**            | **0.52** | **0.13**   | **4.12**| **<0.001**|
| NB : February 2013       | 0.15     | 0.17       | 0.86    | 0.39    |
| PB : February 2013       | -0.06    | 0.17       | -0.36   | 0.72    |
| NB : April 2013          | -0.21    | 0.16       | -1.32   | 0.19    |
| PB : April 2013          | -0.13    | 0.17       | -0.77   | 0.44    |
| **NB : June 2013**       | **-0.36**| **0.16**   | **-2.22**| **0.03**|
| PB : June 2013           | -0.22    | 0.17       | -1.32   | 0.19    |
| NB : July 2013           | -0.03    | 0.17       | -0.20   | 0.84    |
| PB : July 2013           | 0.19     | 0.17       | 1.15    | 0.25    |

| Factors                  | Estimate | Std. Error | z value | Pr(>|z|) |
|--------------------------|----------|------------|---------|---------|
| Intercept (B/December 2012) | 0.24     | 0.22       | 1.09    | 0.28    |
| NB                       | -0.61    | 0.27       | -2.24   | 0.03    |
| PB                       | -0.12    | 0.32       | -0.37   | 0.71    |
| February 2013            | -0.31    | 0.39       | -0.79   | 0.43    |
| April 2013               | 0.03     | 0.26       | 0.13    | 0.90    |
| June 2013                | -0.12    | 0.26       | -0.48   | 0.63    |
| **NB : February 2013**   | **1.11** | **0.45**   | **2.46**| **0.01**|
| PB : February 2013       | 0.32     | 0.46       | 0.70    | 0.49    |
| NB : April 2013          | 0.25     | 0.32       | 0.78    | 0.44    |
| PB : April 2013          | 0.10     | 0.37       | 0.28    | 0.78    |
| NB : June 2013           | 0.10     | 0.32       | 0.33    | 0.74    |
| PB : June 2013           | -0.02    | 0.37       | -0.06   | 0.95    |

| Factors                  | Estimate | Std. Error | z value | Pr(>|z|) |
|--------------------------|----------|------------|---------|---------|
| Intercept (B/December 2012) | -1.67    | 0.50       | -3.32   | <0.001  |
| NB                       | 0.72     | 0.60       | 1.20    | 0.23    |
| PB                       | 0.48     | 0.68       | 0.70    | 0.49    |
| February 2013            | 0.74     | 0.80       | 0.92    | 0.36    |
| **April 2013**           | **-2.71**| **0.79**   | **-3.44**| **0.00**|
| June 2013                | -0.21    | 0.59       | -0.36   | 0.72    |
| NB : February 2013       | -1.52    | 0.96       | -1.58   | 0.11    |
| PB : February 2013       | -1.48    | 0.98       | -1.51   | 0.13    |
| **NB : April 2013**      | **2.05** | **0.86**   | **2.38**| **0.02**|
| PB : April 2013          | 1.31     | 0.98       | 1.34    | 0.18    |
| NB : June 2013           | -1.17    | 0.78       | -1.51   | 0.13    |
| PB : June 2013           | -0.39    | 0.81       | -0.49   | 0.63    |

| Factors                  | Estimate | Std. Error | z value | Pr(>|z|) |
|--------------------------|----------|------------|---------|---------|
| Intercept (B/December 2012) | 0.92     | 0.16       | 5.84    | <0.001  |
| NB                       | 0.04     | 0.17       | 0.26    | 0.80    |
| PB                       | 0.01     | 0.20       | 0.03    | 0.98    |
| February 2013            | -0.01    | 0.15       | -0.06   | 0.95    |
| **April 2013**           | **-0.44**| **0.12**   | **-3.70**| **0.00**|
| June 2013                | **-0.46**| **0.12**   | **-3.95**| **0.00**|
| Factors                        | Estimate | Std. Error | z value | Pr(>|z|) |
|-------------------------------|----------|------------|---------|----------|
| Intercept (B/December 2012)   | 1.09     | 0.35       | 3.14    | <0.001   |
| NB                            | -0.93    | 0.34       | -2.74   | 0.01     |
| PB                            | -0.88    | 0.38       | -2.33   | 0.02     |
| February 2013                 | 0.75     | 0.42       | 1.77    | 0.08     |
| April 2013                    | 0.00     | 0.34       | -0.01   | 0.99     |
| **June 2013**                 | **-1.11**| **0.35**   | **-3.13**| **0.00** |

| Factors                        | Estimate | Std. Error | z value | Pr(>|z|) |
|-------------------------------|----------|------------|---------|----------|
| Intercept (B/December 2012)   | -1.73    | 0.40       | -4.33   | <0.001   |
| NB                            | **1.03** | **0.41**   | **2.51**| **0.01** |
| PB                            | **1.09** | **0.46**   | **2.39**| **0.02** |
| February 2013                 | -0.86    | 0.51       | -1.68   | 0.09     |
| April 2013                    | 0.01     | 0.41       | 0.02    | 0.98     |
| **June 2013**                 | **1.00** | **0.41**   | **2.42**| **0.02** |

| Factors                        | Estimate | Std. Error | z value | Pr(>|z|) |
|-------------------------------|----------|------------|---------|----------|
| Intercept (B/December 2012)   | 1.90     | 0.43       | 4.37    | <0.001   |
| NB                            | 0.71     | 0.55       | 1.30    | 0.19     |
| PB                            | 0.12     | 0.61       | 0.19    | 0.85     |
| February 2013                 | 0.47     | 0.55       | 0.85    | 0.40     |
| April 2013                    | 0.50     | 0.37       | 1.33    | 0.19     |
| June 2013                     | 0.82     | 0.40       | 2.04    | 0.04     |
| NB : February 2013            | -0.06    | 0.72       | -0.08   | 0.94     |
| PB : February 2013            | -0.76    | 0.63       | -1.20   | 0.23     |
| **NB : April 2013**           | **-1.39**| **0.46**   | **-3.00**| **0.00** |
| PB : April 2013               | 0.42     | 0.54       | 0.77    | 0.44     |
| **NB : June 2013**            | **-1.73**| **0.49**   | **-3.56**| **0.00** |
| PB : June 2013                | -0.29    | 0.53       | -0.55   | 0.58     |
**Supplemental Material S5:** Abundance values of the taxa that presented greater SCBD values than average for each sampling campaign. Abundance values were logarithmically transformed to meet normality. P-values from each model are indicated in the plots, red font text indicate significant p-values for burned, unburned and partially burned ponds respectively for each of the models.

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Figure 1

[Map showing burned area with different colors representing unburned, partially burned, and burned ponds, along with non-sampled ponds.]

[Images of the area in May 2012, Summer 2012, December 2013, February 2013, April 2013, and June 2013, showing changes over time.]
Figure 2

(a) Richness (S)

(b) Shannon-Wiener index (H)

(c) Evenness (J)
Figure 4
Figure 5

(a) PA - Replacement

(b) Ab - Replacement

Abundance index

Ruzicka index