Consequences of fish for cladoceran, water beetle and macrophyte communities in a farmland pond landscape: implications for conservation

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Abstract

Traditionally, fish have been neglected in pond ecology and conservation studies although it has been often been assumed that they have a detrimental impact on pond biodiversity and ecosystem function. In order to assess the consequences of fish for pond biodiversity and ecosystem structure we sampled a set of 40 small farmland ponds (20 with and 20 without fish) in eastern England and compared their water chemistry as well as the assemblage characteristics (abundance, diversity, species composition) of three biological groups: cladocerans (zooplankton), water beetles and macrophytes. Water depth was significantly greater in fish ponds, while pond bottom oxygen levels and pH were significantly higher in the ponds without fish. The presence of fish significantly reduced the abundance of macrophytes and altered the community composition of cladocerans and macrophytes, but had no detectable influence on water beetles. Variation partitioning using environmental and spatial variables, indicated all three biological groups were spatially structured. The inclusion of fish however, reduced the importance attributed to space in the case of both cladocerans and macrophytes, suggesting that space effects for these two groups were at least partly the result of a spatially structured predator (i.e. fish) and not because of dispersal limitation or mass effects. In most cases fish did not have an effect on cladoceran and water beetle alpha diversity (number of species, Shannon's and Simpson's index), although the opposite was true for macrophytes. Nevertheless, at the landscape level, gamma diversity (i.e. total number of species) was enhanced for all three biological groups. Our results suggest that fish, at least small pond-associated species, are an important component of heterogeneity in farmland pond networks, thereby increasing landscape-scale diversity of several faunal and floral elements. Consequently, we propose that fish should be more fully included in future pond biodiversity surveys and conservation strategies.

Keywords: cladocerans, farmland ponds, fish, gamma diversity, macrophytes, water beetles.

Introduction

Freshwater research has, to a large extent, focused on rivers and lakes while smaller water bodies, such as ponds, despite often being present at high densities in the landscape, have generally been undervalued by scientists and conservationists alike (Collinson et al. 1995; Angelibert et al. 2004; Biggs et al. 2005; Oertli et al. 2009). This trend is starting to change, however, and an increasing number of recent conservation biology and landscape and dispersal ecology studies are now focusing on ponds (De Meester et al. 2005; Ruggiero et al. 2008; Raebel et al. 2011; Sayer et al. 2012). In particular, a number of studies have highlighted the value of ponds for supporting species of conservation concern in Europe such as great crested newt *Triturus cristatus* (Griffiths & Williams 2000; Edgar & Bird 2006; Gustafson et al. 2009), common spadefoot toad *Pelobates fuscus* (Nystrom et al. 2002; Rannap et al. 2009), crucian carp *Carassius carassius* (Copp et al. 2008; Sayer et al. 2011) and European otter *Lutra lutra* (Ruiz-Olmo et al. 2007; Almeida et al. 2012).

The contribution of ponds to regional or landscape-scale (gamma) species diversity has been an area of emerging research. For example, comparisons between different aquatic habitats (ponds, ditches, streams and rivers) in NW European agricultural landscapes suggest that ponds have the highest regional (gamma) diversity for invertebrates and aquatic plants (Williams et al. 2003; Davies et al. 2008a; Davies et al. 2008b). Likewise, in NW Spain, several mountain ponds combined supported a greater number of invertebrates than a single lake of the same surface area (Martinez-Sanz et al. 2012). The substantial contribution of ponds to regional diversity is often linked to high beta diversity (i.e. low faunal and floral similarity between neighboring sites), in turn attributed to two factors: a) strong differences in biotic and abiotic conditions among systems facilitating high species turn-over between ponds at the landscape scale, and b) stochastic events that tend to have greater influence over biotic assemblages in small waters, resulting in high beta diversity (Scheffer et al. 2006). Clearly, despite their small size and frequent hydrological isolation (Oertli et al. 2002), ponds are important for the maintenance of aquatic diversity. Indeed, networks of ponds are potentially crucial for regional populations of several aquatic groups thought to exist in metapopulations including amphibians, dragonflies, reptiles and zooplankton (Michels et al. 2001; Cottenie et al. 2003; De Meester et al. 2005; Ruggiero et al. 2008; Curado et al. 2011). As a result, ponds have increasingly become the subject of landscape-scale conservation initiatives such as the UK Million Ponds Project (Williams et al. 2010) and the European Pond Conservation Network (Oertli et al. 2005) that seek to increase pond density and connectivity.

The majority of pond ecology and diversity studies have focused on invertebrates (Cereghino et al. 2008; Fuentes-Rodriguez et al. 2013), macrophytes (Della Bella et al. 2008; Williams et al. 2008) and amphibians (Beja & Alcazar 2003; Hartel et al. 2010; Curado et al. 2011), while other biological groups, especially fishes, have been comparatively understudied. Furthermore, where fish have been included in pond studies, fish data has typically been derived from interviews, observations or inadvertent catches made during invertebrate surveys (e.g. Hassal *et al.*, 2011; Jeliazkov *et al.*, 2014) and not from actual fish sampling (e.g. fyke netting, electric-fishing) that more accurately estimates fish presence/absence and community assembly. As well as contributing to pond diversity in their own right, fish have an important influence on community structure and diversity in ponds.

Given a lack of studies of fish effects on pond biological structure that include active fish sampling, we studied cladoceran (zooplankton), water beetle and macrophyte community assembly and diversity in a set of 40 small English ponds with and without fish, with fish presence established by fyke net sampling. Ponds containing common carp (*Cyprinus carpio*) and northern pike (*Esox lucius*) were excluded from the study, as we wanted to focus predominantly on small typical European pond-associated fish, especially crucian carp (*Carassius carassius*), roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*), three-spined stickleback (*Gasterosteus aculeatus*) and tench (*Tinca tinca*). For each biological group we hypothesized that: i) local (i.e. per site) diversity will be similar irrespective of fish presence/absence; ii) community structure will be markedly different due to fish influence via predation and habitat modification; iii) landscape-scale (gamma) diversity will be enhanced by the presence of fish in ponds, thus highlighting their potential beneficial role within pond networks.

Methods

Study area

Our study focused on 20 ponds containing fish and 20 ponds without fish (n = 40) in Norfolk, eastern England. The ponds were selected based on previous fyke net based investigations of fish populations (Sayer et al. 2011). Norfolk is a low-lying (altitude <100 m above the sea level) predominately agricultural region. The geology of the study area is composed of Cretaceous chalk bedrock overlain by Quaternary glacial drift deposits and sandy loam soils. In winter, the ponds are usually iced over for 2–3 weeks, often in short separated intervals. The study ponds are all small (<50 m in maximum diameter, mean surface area = 920 m^2), shallow (0.3–2.4 m, mean = 1 m), man-made and have their origins dominantly as marl pits (n = 30) (Prince, 1964). Other sites originated as livestock watering ponds (n = 3), recently created conservation ponds (n = 4), medieval fish ponds (n = 2), and a small gravel pit (n = 1). Groundwater is the main source of water to the ponds. The majority of the ponds are situated in arable or pasture land and all of the arable ponds are buffered by grass margins (minimum c. 5–10 m diameter). Degree of terrestrialisation and overhead shading by trees and bushes is known to be a key influence on macrophyte and invertebrate diversity in ponds (Sayer et al. 2012). Consequently, to minimise this effect, only relatively open canopy ponds with low-moderate shading (mean = 13% ± 17% standard deviation) were selected for study.

Environmental data collection

Dissolved oxygen profiles (10 cm intervals) were generated for each pond over May-June 2012: only surface (0 cm) and bottom (just above sediment surface) oxygen values were used as explanatory variables in this study. Data for pH, conductivity and alkalinity (measured in the field), total phosphorus (TP), soluble reactive phosphorus (SRP) and nitrate nitrogen (NO_3^--N) were derived from previous surveys undertaken over May-June 2010 and 2011. Conductivity, pH and dissolved oxygen were determined with a HACH HQ30d meter and alkalinity was measured by sulphuric-acid titration undertaken in the field using a HACH AL-DT kit. Water samples for SRP and NO_3^--N were filtered on-site using Whatman GF/C (1.2 μm) filter papers. SRP was determined using the molybdenum blue procedure (Murphy & Riley 1962) and NO_3^--N was measured using the procedures described by Wetzel & Likens (2000). Total phosphorus (TP) was determined for unfiltered water samples by the same method as SRP after microwave digestion (Johnes & Heathwaite 1992). Shading of the pond was estimated visually as the percentage of the pond overhung by trees and bushes (%shading).

Fish surveys

Fish were surveyed (March 2010-2012) by deploying double-ended fyke nets exposed overnight (approx. 16 hours), with the number of nets used proportional to pond size. Fyke nets were set such that they bisected the largest dimension of each pond. Further details on the methods used for fish sampling are given in Sayer et al. (2011). Due to the high number of fish species captured and variable capture efficiency for each species, fish data was used as presence/absence in this study.

Zooplankton sampling

Zooplankton samples were taken from the 40 ponds between May-June 2012. To account for the often observed patchiness of zooplankton in shallow waterbodies (Cryer & Townsend 1988), five whole water column samples were collected from different locations in each pond using a 2.5 m plastic tube (diameter 74 mm) deployed from a small inflatable boat. All samples were filtered through a 53-μm mesh plankton net and subsequently pooled and preserved in ethanol (≥40% industrial methylated spirit IMS).

Cladocerans were enumerated using a Sedgewick-Rafter cell on a compound microscope at 10–40 × magnification. Counting in each sample was stopped when at least 100 individuals of the dominant taxon were encountered in a sub-sample of known volume, although in some instances ($n = 12$) this was not possible due to low abundances (≤ 50 indiv.). Cladocerans were identified to species-level wherever possible, according to the taxonomic schemes of Scourfield & Harding (1966), Amoros (1984), Flössner (2000) and Szeroczyńska & Sarmaja-Korjonen (2007). Identification proved difficult for some groups. Therefore, species in the genus *Ceriodaphnia* were amalgamed as *Ceriodaphnia* spp., and specimens of *Alona costata* and *Alona guttata*, *Alona affinis* and *Alona quandragularis*, *Pleuroxus aduncus* and *Pleuroxus trigonellus* were also combined. Furthermore, the closely related daphnids, *Daphnia longispina, Daphnia rosea* and *Daphnia hyalina* were aggregated under *D. longispina* agg. as recommended by Petrusek et al. (2008).

Water beetle sampling

Using a standard pond net (mesh size 1 mm, frame size 0.2 × 0.25 m) water beetle samples were collected in June 2014 by vigorous sampling of the pond margins for a period of 2 minutes. Collected material was sorted in the field for a maximum of 30 minutes or until the worker was confident that all the water beetles had been picked out. The sorted specimens were then preserved in the field using 70% IMS. Species identifications was conducted using a Zeiss Stemi 2000 stereomicroscope (6.5–45 × magnification) and identifications and nomenclature followed Friday (1988), Foster & Friday (2011) and Foster et al. (2014).

Macrophyte sampling

The macrophyte flora of each pond was surveyed once during May-August 2010–2013. Submerged, floating-leaved and free-floating aquatic macrophytes were recorded on the DAFOR scale (see also Palmer et al., 1992; Sayer et al., 2012) as dominant (5), abundant (4), frequent (3), occasional (2), and rare (1) by visual observation (approx. 30 minutes of searching per pond) assisted by collections made using a double-headed rake.

Statistical analysis

Trends in the diversity and structure of cladoceran, water beetle and macrophyte communities were explored using analysis of similarity (ANOSIM) and 2D non-metric multidimensional scaling (nMDS) using PRIMER 6 (Clarke & Gorley 2006), based on Bray-Curtis similarity matrices generated from log (x+1) abundance (cladocerans, water beetles) and relative abundance (macrophyte DAFOR) data. For improved visualisation of the results, sites with no recorded individuals for a biological group were omitted from the respective nMDS plots. Multivariate dispersion (MVDISP), a measure of community heterogeneity (Anderson et al. 2006), was estimated using the vegan package (Oksanen et al. 2013) in RStudio version 0.99.489 (R Core Team, 2016). Variation in MVDISP in relation to fish presence/absence was assessed by analysis of variance (ANOVA). Controls on community structure for the three organism groups were examined using variance partitioning analysis (Peres-Neto et al. 2006). Three explanatory models were generated using redundancy analysis (RDA): i) an environmental model with forward selected environmental variables following Blanchet et al. (2008); ii) a spatial model with forward selected “spatial variables” (based on the geographical distance between sites) obtained from distance-based Moran’s eigenvector maps (MEM) (Dray et al. 2006). In brief, MEM used geographic coordinate data (latitude, longitude) for each of our study sites to determine spatial relationships between them. These were translated into explanatory (spatial) variables that we could be used in the multivariate analysis; and iii) a fish model based on presence/absence data for each site. Variation in biological assemblages was separated into purely environmental, spatial, and fish components respectively. We ran the analysis twice in each case using different environmental models: one containing information from abiotic variables only; and the other containing information from abiotic as well as biotic variables (cladoceran, water beetle and macrophyte abundance) to identify any significant interactions between the three studied biological groups (i.e. in the case of cladocerans we used water beetle and macrophyte abundance as biotic variables etc). Monte Carlo random permutations were used to test the significance of the three components (environmental, spatial, fish model) and R^2 adjusted values were used for estimates of explained variation (Peres-Neto et al. 2006). Fish are seldom sampled in pond metacommunity studies, but fish presence/absence may often be spatially structured, thus overemphasising the importance of spatial processes. To investigate this, we re-ran the analysis as described above, however, this time we omitted the fish model. Prior to analysis all biotic data were Hellinger-transformed (Legendre & Gallagher 2001). Where appropriate, environmental data were log-transformed (water depth, TP, SRP and NO_3^--N), standardised (i.e. each variable has zero mean and unit variance) (alkalinity, conductivity, bottom and surface oxygen) or arcsine transformed (%shade).

Alpha (per pond) diversity for each biological group (cladocerans, water beetles, macrophytes) was assessed with three different indexes (species richness, Shannon's index, Simpson's index) in Estimates S9 (Colwell 2013) based on raw counts (cladocerans and water beetles) or relative abundance (macrophyte DAFOR) data. The Shannon's Index ($\exp(-\Sigma p_i \log p_i)$) weights species in proportion to their frequency of occurrence, and can be roughly interpreted as the number of 'typical species' in an assemblage. Simpson's index ($1 / \Sigma pi^2$) is heavily weighted towards the most common species and can be interpreted to represent the number of very abundant species in an assemblage. Significant differences in alpha diversity between ponds with and without fish were tested for using Mann-Whitney tests. To compensate for unequal sampling effort in the case of cladocerans (i.e. more water was filtered in deeper ponds), data was rarefied to 55 individuals. Subsequently, we created sample-based rarefaction curves rescaled by individuals (Chazdon et al. 1998; Gotelli & Colwell 2001) comparing species richness in ponds with fish and without fish and all ponds combined. This effectively estimated the effect of fish on gamma (total) diversity for each of the three studied biological groups.

Results

Water chemistry

With the exception of one site, all ponds were base-rich (Table 1) with pH, conductivity and alkalinity ranging from 6.6–9.7 (mean = 8, σ = 0.6), 79–762 μs cm^{-1} (mean = 490.9, σ = 162.7) and 2.46–306 mg $CaCO_3$ L^{-1} (mean = 160.8, σ = 68.1) respectively. Most ponds were eutrophic with total phosphorus (TP), soluble reactive phosphorus (SRP) and nitrate nitrogen (NO_{3^-}-N) ranges of 28.5–1108.5 μg L^{-1} (mean = 234.9, σ = 237.5), 0–709.89 μg L^{-1} (mean = 70.6, σ = 128.9) and 0–1.59 mg L^{-1} (mean = 0.2, σ = 0.39) respectively.

A number of significant differences in environmental descriptors were found between ponds with and without fish (Table 1). In particular, water depth was significantly greater in ponds containing fish ($P = 0.001$), while bottom oxygen concentration and pH were significantly higher in the non-fish ponds ($P = 0.024$ and $P = 0.05$ respectively).

Fish

In total, nine fish species and three fish-hybrids were recorded in the 20 fish-containing ponds. In order of decreasing abundance these included crucian carp (present in 10 ponds), three-spine stickleback (5 ponds), rudd (6 ponds), Eurasian perch *Perca fluviatilis* (3 ponds), roach (7 ponds), tench (4 ponds), nine-spine stickleback *Pungitius pungitius* (2 ponds), European eel *Anguilla anguilla* (2 ponds), goldfish *Carassius auratus* (including natural brown and shubunkin varieties) (2 ponds), hybrids of crucian carp and goldfish (1 pond), hybrids of common carp *Cyprinus carpio* and goldfish (1 pond), and hybrids of roach and rudd (2 ponds).

Cladocera

A total of 21 cladoceran species were recorded from 38 ponds, 16 species from ponds with fish and 16 species from fishless ponds, with each pond type harbouring five unique species not found in the other category (Table 2). Four species were present in more than ten sites (*Chydorus sphaericus* – 33 ponds, *Simocephalus expinosus* – 22 ponds, *Simocephalus vetulus* – 18 ponds, *D. longispina* agg. – 14 ponds). *Daphnia longispina* agg., *D. pulex*, *Ceriodaphnia* spp., *S. expinosus* and *S. vetulus* were significantly more abundant in fishless ponds, while *B. longirostris* was more common in ponds with fish (Table 2).

Cladoceran community composition was significantly related to fish presence/absence (ANOSIM, P = 0.001), as visually confirmed in the nMDS plot (Fig. 1a), with fish-containing ponds clearly separated from non-fish ponds, despite a relatively high stress value (0.15). Although ponds with fish were more widely scattered throughout the plot (MVDISP = 0.43) compared to ponds with no fish (MVDISP = 0.35), additional permutation tests did not find this to be significant (ANOVA, P>0.05).

Variance partitioning using three models (environmental, spatial and fish) demonstrated that compositional patterns in cladoceran assembly were primarily driven by fish presence/absence (Table 3). When fish was removed, however, spatial patterns became important, suggesting a strong spatial structure of fish distribution in the pond dataset.

Despite differences in community composition, statistical comparisons of cladoceran abundance and rarefied alpha diversity (species richness, Shannon’s index) showed little variation across the two pond categories (Fig. 1b). The only exception was Simpson’s index that was significantly higher in ponds without fish (P = 0.05). Rarefaction curves demonstrated that cladoceran species richness was comparable in fish and fishless ponds (Fig. 1c). However, when data from the two pond types were combined, species richness at the landscape-scale (i.e. gamma diversity) was marginally enhanced.

Water beetles

Thirty-five species of water beetle were identified from 34 ponds (27 from fish ponds and 26 from fishless ponds; Table 2). The majority of species had sporadic to rare occurrences with only four being ‘common’ (i.e. present in >8 sites), *Haliphus ruficollis* (12 ponds), *Hyphydrus ovatus* and *Noterus clavicornis* (9 ponds) and *Haliphus* sp. (8 ponds). Some nine and eight species were recorded only in fish and non-fish ponds respectively. *Agabus bipustulatus* and *Ilybius fenestratus* were significantly more common in fishless ponds (Table 2).

Composition of water beetle communities was not affected by fish presence/absence (ANOSIM, $P > 0.05$), as evident by the scatter in the nMDS plot (Fig. 2a) and similar levels of community heterogeneity within each pond category (MVDISP = 0.65 and 0.61 for fish and non-fish ponds, respectively). In fact, variation in water beetle communities was largely driven by spatial variables (Table 3).

Although alpha diversity and abundance were comparable between the two pond groups (Fig. 2b), rarefaction curves highlighted that fish-containing ponds supported more speciose communities compared to fishless ponds. Notably, when data from all sites were combined, estimated species richness (i.e. gamma diversity) lied between that of the two pond categories (Fig. 2c).

Macrophytes

Thirty-five aquatic macrophyte species were found in 38 ponds (Table 2), from which nine were present in >10 sites (*Lemna minor* – 30 ponds, *Potamogeton natans* – 19 ponds, *Lemna triscula* – 18 ponds, *Cladophora* sp. – 17 ponds, *Ranunculus aquatilis* – 15 ponds, *Ranunculus sceleratus* – 14 ponds, *Persicaria amphibia* – 13 ponds, Bryophyte sp. – 11 ponds, *Alisma plantago-aquatica* – 10 ponds). Fish and fishless ponds supported 31 (9 unique) and 26 species (4 unique), respectively. *Ceratophyllum demersum* and *Nymphaea alba* were more common in fish ponds, whereas *Fontinalis antipyretica*, *L. trisulca*, *R. aquatilis*, *R. sceleratus*, and *Veronica anagalis-aquatica* were more common in fishless ponds (Table 2).

Fish presence/absence had a significant effect on macrophyte community composition (ANOSIM, $P = 0.001$; Fig. 3a). Macrophyte assemblages in ponds with fish had significantly ($P = 0.001$) greater compositional heterogeneity (MVDISP = 0.55) compared to ponds with no fish (MVDISP = 0.4).

Variance partitioning showed that environmental conditions (forward selected variables: water depth and NO_3^--N), space and fish presence/absence alike was significant for macrophytes (Table 3). When the fish factor was removed both the environmental and spatial factors remained important, although for space the significance level was greatly reduced. On average, individual fishless ponds had higher macrophyte abundance and diversity (species richness, Shannon's index, Simpson's index, $P = 0.001$ in all cases) compared to fish ponds. However, rarefaction analysis indicated that collectively fish ponds were relatively more species rich compared to fishless ponds (Fig. 3c), while species richness for all ponds combined (i.e. gamma diversity) lied between that of the two pond groups (Fig. 3c).

Discussion

Fish are thought to be important determinants of community assembly and diversity for several biological groups in both ponds and shallow lakes including amphibians (Jeliazkov et al. 2014), water beetles (Fairchild et al. 2000; Bloechl et al. 2010), nematodes (Weber & Traunspurger 2015), cladocerans (Davidson et al. 2010) and macrophytes (van Donk & Otte 1996). While fish occurrence in shallow lake studies has almost always been determined via active sampling, for ponds fishes have generally been recorded by casual field observations, landowner interview and inadvertently via invertebrate surveys (e.g. Ruggiero et al., 2008; Le Viol et al., 2009; Raebel et al., 2011; Jeliazkov et al., 2014). Such an approach is likely prone to underestimating the occurrence of pond fish, especially less visually evident benthic species such as crucian carp and tench. The present study, is one of the few pond ecology studies to employs active fish sampling, in this case fyke netting, a highly effective method for detecting fish presence in ponds, even at low densities (Sayer et al., 2011). The results of our study demonstrated that fish exert a significant influence on some biological components of ponds (cladocerans and macrophytes) but are less important to others (water beetles).

Studies conducted in shallow lakes have found a predominantly negative relationship between fish and cladoceran abundance and diversity (Vanni et al. 1997; Cottenie et al. 2001), although insignificant effects (e.g. Chumchal et al., 2005) and opposing trends have also been reported (e.g. Hessen et al., 2006). In our study fish did not show a significant influence on cladoceran alpha diversity or abundance, but nevertheless clearly affected composition (Fig. 1a), with larger members of the Daphniidae significantly less common in fish-containing ponds (e.g. *Daphnia pulex*; Table 2) undoubtedly due to size-selective fish predation (Brooks & Dodson 1965). Similar effects have been widely documented for shallow lakes (e.g. Lauridsen & Lodge 1996; Jeppesen et al., 2000; Davidson et al., 2010; Liu et al., 2013), and clearly the same applies for ponds. Indeed, the dominance of larger-bodied Daphniidae in non-fish ponds was likely responsible for the suppressed evenness of cladoceran communities compared to ponds containing fish (Fig. 1b; Simpson’s index).

For water beetles, neither abundance, diversity or community composition were affected by fish (Fig. 2a, b). However, other studies from shallow lakes and ponds have highlighted a negative effect of fish on water beetles in terms of both species diversity and abundance (Weir 1972; Fairchild et al. 2000). For example, Schilling et al. (2009) showed water beetles to be significantly less abundant and speciose in fish-containing USA lakes, compared to those lacking fish. Similarly, in a survey of 425 English farmland ponds, similar to those studied here, Hassall et al. (2011) found a negative correlation between water beetle species richness and fish. Such negative correlations suggest a reduced ability of water beetles to avoid fish predation, but our study does not confirm this observation. Clearly further work, based on actual fish sampling, is required to gain a clearer understanding of fish influence over water beetles in small farmland ponds.

Macrophyte abundance and alpha diversity were significantly lower and species composition significantly different in ponds with fish compared to fishless ponds in our study (Fig. 3a, b). Foraging activities of benthic fish such as tench and crucian carp may influence macrophytes through direct sediment and macrophyte disturbance, although both of these fish are widely associated with macrophyte-dominated conditions in shallow lakes (Perrow et al. 1996; Holopainen et al. 1997). It is also possible that fish-induced reductions in *Daphnia*-grazing could decrease aquatic vegetation by increasing phytoplankton densities (Van De Bund & Van Donk 2004). In addition, fish may directly impact on macrophyte abundance through herbivory (Nurminen et al. 2003; Matsuzaki et al. 2009), and, although these reductions are not usually severe (Marklund et al. 2002), it has been suggested that shifts in macrophyte species composition could be a result of preferential grazing by fish (Roberts et al. 1995; Lake et al. 2002). For example it has been demonstrated that rudd and roach preferentially feed on macrophyte species such as *C. demersum*, *Elodea canadensis*, and *Potamogeton pectinatus* in shallow lakes (Prejs 1984; van Donk & Otte 1996). This finding was not supported by our data, however, with all three of these plants more common in fish-containing ponds, even where rudd and roach were present (Table 2).

Several pond landscape studies have found space to be an important factor determining assemblage structure for aquatic taxa (e.g. Cottenie et al., 2003; Shurin et al., 2009; De Bie et al., 2012). When fish were not incorporated in the analysis, spatial variables had a significant effect in structuring all three biological groups; suggesting dispersal limitations or mass effects in a metacommunity context. However, when fish were included, space stopped being a significant structuring variable for cladocerans, while significance was greatly reduced in the case of macrophytes, suggesting the presence of a spatially structured predator. Fish are known to have strong dispersal potential within well-connected river and wetland systems, but dispersal of this group among isolated farmland ponds, as in this study, mainly depends on human translocation (Sayer et al., 2011). Clearly, more work is required to understand how fish distribution patterns affect landscape-scale pond biological structure and diversity.

From a pond-conservation perspective a key finding our study was the impact of fish on landscape-scale species diversity. For the cladocerans, water beetles and aquatic macrophytes, a comparable number of species were found in the fish and non-fish ponds. Importantly, by considering all study sites (fish and fishless ponds) species richness at the landscape-scale (gamma diversity) tended to be similar or somewhat higher compared to fishless ponds for all three biological groups (Figs. 2c, 3c, 4c). These results suggest that landscape diversity of all trophic levels is not harmed by the presence of fish in some ponds but in contrast it can be occasionally slightly increased. Thus, similar to other key structuring variables such as tree-shading and terrestrialisation level (Hassall et al. 2011), fish may be an important hitherto largely neglected driver of biological heterogeneity and species diversity in pond landscapes.

Conclusions

While there are exceptions (e.g. Copp et al., 2005, 2008; Casas et al., 2011; Sayer et al., 2011), fish have mostly been neglected in pond conservation projects. In addition, within the pond conservation literature, fish have frequently been viewed in a predominantly negative way due to presumed detrimental impacts on pond diversity, especially for invertebrates (e.g. Zambrano, Scheffer & Martinez-Ramos, 2001; Broyer & Curtet, 2011) and amphibians (e.g. Hamer & McDonell, 2008; Wright, 2010). Although we did not include amphibians in this study, we show that fish did not pose a threat to pond communities, but instead tend to increase landscape-scale diversity of several faunal and floral elements, in particular cladocerans and macrophytes. Fish are also likely to attract other components of the local fauna such as birds (e.g. kingfisher *Alcedo atthis*, grey heron *Ardea cinerea*) and mammals (e.g. Eurasian otter *Lutra lutra*) that feed on them (Ruiz-Olmo et al. 2007; Almeida et al. 2012), thereby further increasing pond food web complexity. Finally, some pond fish species are highly worthy of conservation in their own right, due to documented European-scale declines, with this especially true of crucian carp (Sayer et al. 2011; Tarkan et al. 2016) and European eel (Dekker 2003). Nonetheless, linked to land reclamation (and consequent pond loss), drought and in particular widespread pond terrestrialisation, due to the cessation of traditional pond management practices, fish are undergoing major declines in farmland ponds (Sayer et al. 2011; Sayer et al. 2013; Tarkan et al. 2016). Our paper suggests that fish, at least typical “pond-associated species”, are important biological components in farmland pond networks that should be more fully included in future biodiversity surveys and pond conservation strategies.

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Author contributions

CDS conceived the study. Data collection for cladocerans, water depth and oxygen levels was conducted by PVS and DA; water beetles by HR and ES; nutrients by HG; aquatic macrophytes, fish, %shade, pH, conductivity, alkalinity by CDS. PVS identified the cladocerans; HR and ES the water beetles; CDS the macrophytes and fish. PVS compiled and analysed the data. TAD provided advice on data analysis and interpretation. PVS prepared the figures and tables. PVS and CDS wrote the main manuscript text with assistance from TAD and DA and all authors provided comments and reviewed the manuscript.

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Table Legends

Table 1 Summary of mean values with standard deviations for environmental and community descriptors for ponds with and without fish. Comparisons between the two pond groups were explored using Mann-Whitney tests. Significance levels: * = 0.1, ** = 0.05, *** = 0.01. Alkalinity (Alk – mg $CaCO_3$ L^{-1}), pH, conductivity (Cond – μs cm^{-1}), % shade, surface dissolved oxygen (O_2 surf – mg L^{-1}), bottom dissolved oxygen (O_2 bot – mg L^{-1}), water depth (m), total phosphorus (TP – μg L^{-1}), soluble reactive phosphorus (SRP – μg L^{-1}), and nitrate nitrogen (NO_3^--N – mg L^{-1}), cladoceran abundance (Clad abund – individuals L^{-1}), water beetle abundance (Beet abund – individuals per unit of sampling effort), macrophyte abundance (Macr abund – DAFOR scale).

Table 2 Cladoceran, water beetle and macrophyte species recorded in the study ponds with and without fish. N_{tot}, N_{FP} and N_{NFP} = number of occurrences in all ponds, fish-containing and non-fish ponds respectively. Species with an asterisk have significantly different abundances between the two pond categories ($P \leq 0.05$; Mann-Whitney test).

Table 3 Results of variation partitioning using three models (environmental, spatial and fish presence/absence) and two models (environmental, spatial) for cladoceran, water beetle and macrophyte communities respectively. Only the unique effect of each model is shown. E1: environmental model without biotic component, E2: environmental model including biotic component, S: spatial model, F: fish model, Total: total explained variation of E1+S+F. Significance levels: * = 0.1, ** = 0.05, *** = 0.01.

Table 1

	Fish-containing ponds	Non-fish ponds
Abiotic variables		
Alk	156 ± 74.1	165.6 ± 63
pH *	7.8 ± 0.4	8.1 ± 0.6
Cond	479.3 ± 158.7	502.4 ± 170
% shading	10.8 ± 7.1	15.25 ± 22.7
O_2 surf	9.5 ± 5.7	8.7 ± 4.1
O_2 bot **	1.8 ± 2.8	4.6 ± 5
Water depth ***	1.3 ± 0.5	0.8 ± 0.4
TP	240.1 ± 217.6	229.7 ± 261.5
SRP	56.8 ± 85.4	84.4 ± 162.6
NO_3^--N $^-$	0.3 ± 0.5	0.1 ± 0.1
Biotic variables		
Clad abund	104 ± 128.5	144.2 ± 147
Beet abund	4 ± 3.6	7.2 ± 5.7
Macr abund ***	10.6 ± 5.6	18 ± 7

Table 2

Group	Family	Species	N_{tot}	N_{FP}	N_{NFP}
Cladocera					
	Daphniidae	*Ceriodaphnia* spp.*	8	Absent	8
		Daphnia longispina agg. *	14	2	12
		Daphnia magna	2	Absent	2
		*Daphnia pulex**	4	Absent	4
		Scapholeberis mucronata	4	3	1
		*Simocephalus expinosus**	21	5	16
		*Simocephalus vetulus**	18	1	17
	Bosminidae	*Bosmina longirostris**	7	7	Absent
	Eurycercidae	*Eurycercus lamellatus*	1	Absent	1
	Chydoridae	*Acroperus harpae*	1	Absent	1
		Alona affinis	5	2	3,
		Alona affinis/ quandrangularis	2	2	Absent
		Alona costata/guttata	8	4	4
		Alona intermedia	1	1	Absent
		Chydorus ovalis	5	2	3
		Chydorus sphaericus	33	17	16
		Graptoleberis testudinaria	1	1	Absent
		Pleuroxus aduncus	4	3	1
		Pleuroxus aduncus/trigonellus	3	2	1
		Pleuroxus denticulatus	1	1	Absent
		Pleuroxus truncatus	3	2	1
Water beetles					
	Dytiscidae	*Agabus bipustulatus**	3	Absent	3
		Agabus paludosus	1	1	Absent
		Agabus sturmii	2	2	Absent
		Colymbetes fuscus	2	1	1
		Hygrotus impressopunctatus	1	Absent	1
		Hygrotus inaequalis	6	3	3
		Hyphydrus ovatus	9	2	7
		Ilybius ater	1	1	Absent
		*Ilybius fenestratus**	4	Absent	4
		Ilybius fuliginosus	5	2	3
		Laccophilus minutus	6	2	4
		Liopterus haemorrhoidalis	1	Absent	1
		Rhantus suturalis	1	1	Absent
		Suphrodytes dorsalis	1	Absent	1

	Gyrinidae	*Gyrinus substriatus*	2	1	1
	Haliplidae	*Haliplus lineatocollis*	2	1	1
		Haliplus ruficollis	12	4	8
		Haliplus sp.	8	5	3
	Helophoridae	*Helophorus aequalis*	1	1	Absent
		Helophorus brevipalpis	2	1	1
		Helophorus grandis	2	Absent	2
	Hydrophilidae	*Anacaena bipustulata*	2	1	1
		Anacaena globulus	3	1	2
		Anacaena limbata	4	1	3
		Enochrus coarctatus	1	1	Absent
		Enochrus testaceus	2	1	1
		Hydrobius fuscipes	3	Absent	3
		Hydroporus angustatus	1	1	Absent
		Hydroporus memnonius castaneus	1	1	Absent
		Hydroporus palustris	7	3	4
		Hydroporus planus	1	1	Absent
		Laccobius colon	1	Absent	1
	Hygrobiidae	*Hygrobia hermanni*	5	2	3
	Noteridae	*Noterus clavicornis*	9	3	6
	Scirtidae	Scirtidae sp.	3	1	2
Macrophytes					
	Alismataceae	*Alisma plantago-aquatica*	10	3	7
	Apiaceae	*Apium inundatum*	5	1	4
		Oenanthe aquatica	1	Absent	1
	Callitrichaceae	*Callitriche* spp.	9	3	6
	Ceratophyllaceae	*Ceratophyllum demersum**	8	7	1
		Ceratophyllum submersum	4	1	3
	Characeae	*Chara globularis*	3	1	2
		Chara hispida	1	1	Absent
		Chara vulgaris	1	Absent	1
	Crassulaceae	*Crassula helmsii*	2	1	1
	Fontinalaceae	Bryophyte sp.	11	1	10
		*Fontinalis antipyretica**	4	Absent	4
	Haloragaceae	*Myriophyllum spicatum*	2	1	1
		Myriophyllum verticillatum	2	1	1
	Hydrocharitaceae	*Elodea canadensis*	1	1	Absent
	Lemnaceae	*Lemna minor*	30	14	16
		Lemna minuta	6	5	1
		*Lemna triscula**	18	4	14
	Nymphaeaceae	*Nuphar lutea*	2	2	Absent
		*Nymphaea alba**	6	6	Absent
	Menyanthaceae	*Nymphoides peltata*	1	1	Absent
	Plantaginaceae	*Hippurus vulgaris*	3	1	2

Polygonaceae	*Persicaria amphibia*	13	4	9
Potamogetonaceae	*Potamogeton berchtoldii*	5	1	4
	Potomogeton crispus	6	5	1
	Potamogeton natans	19	6	13
	Potomogeton pectinatus	2	2	Absent
	Potamogeton polygonifolius	1	1	Absent
	Potamogeton trichoides	3	Absent	3
Ranunculaceae	*Ranunculus aquatilis**	15	1	14
	Ranunculus lingua	1	1	Absent
	*Ranunculus sceleratus**	14	1	13
Ricciaceae	*Riccia fluitans*	1	1	Absent
	Cladophora sp.*	17	5	12
Scrophulariaceae	*Veronica anagallis-aquatica**	7	1	6

Table 3

Three models		E1	E2	S	F	Total
Cladocera	Adj.R^2	-	-	-0.002	0.048*	0.128
Coleoptera	Adj.R^2	-	-	0.015*	-0.006	0.011
Macrophytes	Adj.R^2	0.016*	0.016	0.053**	0.048***	0.157

Two models		E1	E2	S		Total
Cladocera	Adj.R^2	-	-	0.081**		0.081
Coleoptera	Adj.R^2	-	-	0.017*		0.017
Macrophytes	Adj.R^2	0.018*	0.018*	0.058***		0.109

Figure Legends

Fig 1. **a)** nMDS on 21 cladoceran species from 38 ponds. Presence and absence of fish in ponds is indicated by black and grey circles respectively. **b)** Cladoceran abundance, species richness, Shannon's index and Simpson's index in relation to fish presence/absence. Significance level: *= 0.05. **c)** Cladoceran rarefaction curves for ponds with fish (black circles) and without fish (grey circles) and all ponds combined (white triangles).

Fig 2. a) nMDS on 35 water beetle species from 32 ponds. Presence and absence of fish in ponds is indicated by black and grey circles respectively. **b)** Water beetle abundance, species richness, Shannon's index and Simpson's index in relation to fish presence/absence. **c)** Water beetle rarefaction curves for ponds with fish (black circles) and without fish (grey circles) and all ponds combined (white triangles).

Fig 3. a) nMDS on 35 macrophyte species from 38 ponds. Presence and absence of fish in ponds is indicated by black and grey circles respectively. **b)** Macrophyte abundance, species richness, Shannon's index and Simpson's index in relation to fish presence/absence. Significance level: *= 0.001. **c)** Aquatic macrophyte rarefaction curves for ponds with fish (black circles) and without fish (grey circles) and all ponds combined (white triangles).

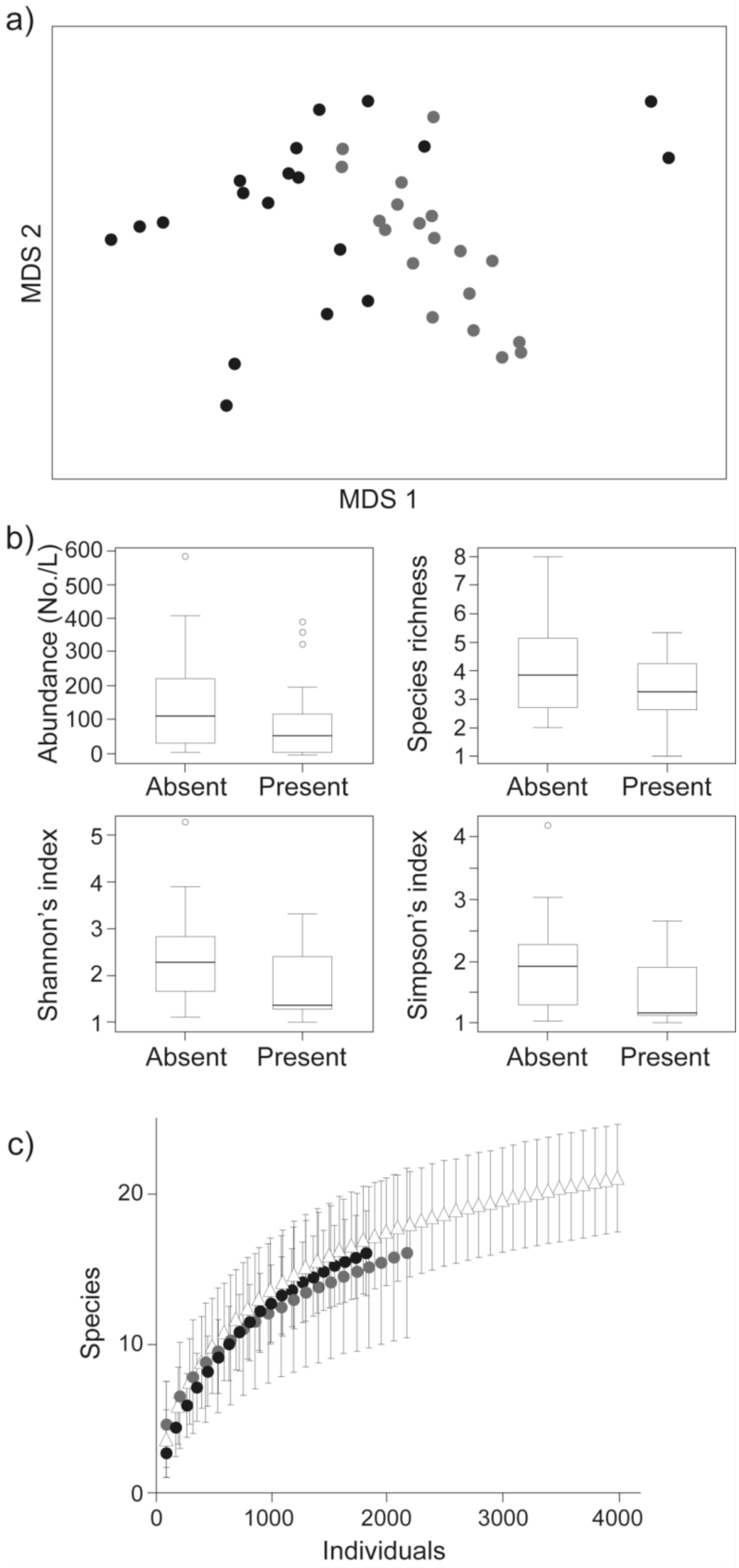
a)
MDS 2
MDS 1
b)
Abundance (No./L)
600
500
400
300
200
100
0
Absent
Present
Species richness
8
7
6
5
4
3
2
1
Absent
Present
Shannon's index
5
4
3
2
1
Absent
Present
Simpson's index
4
3
2
1
Absent
Present
c)
Species
20
10
0
0
1000
2000
3000
4000
Individuals

Fig. 1

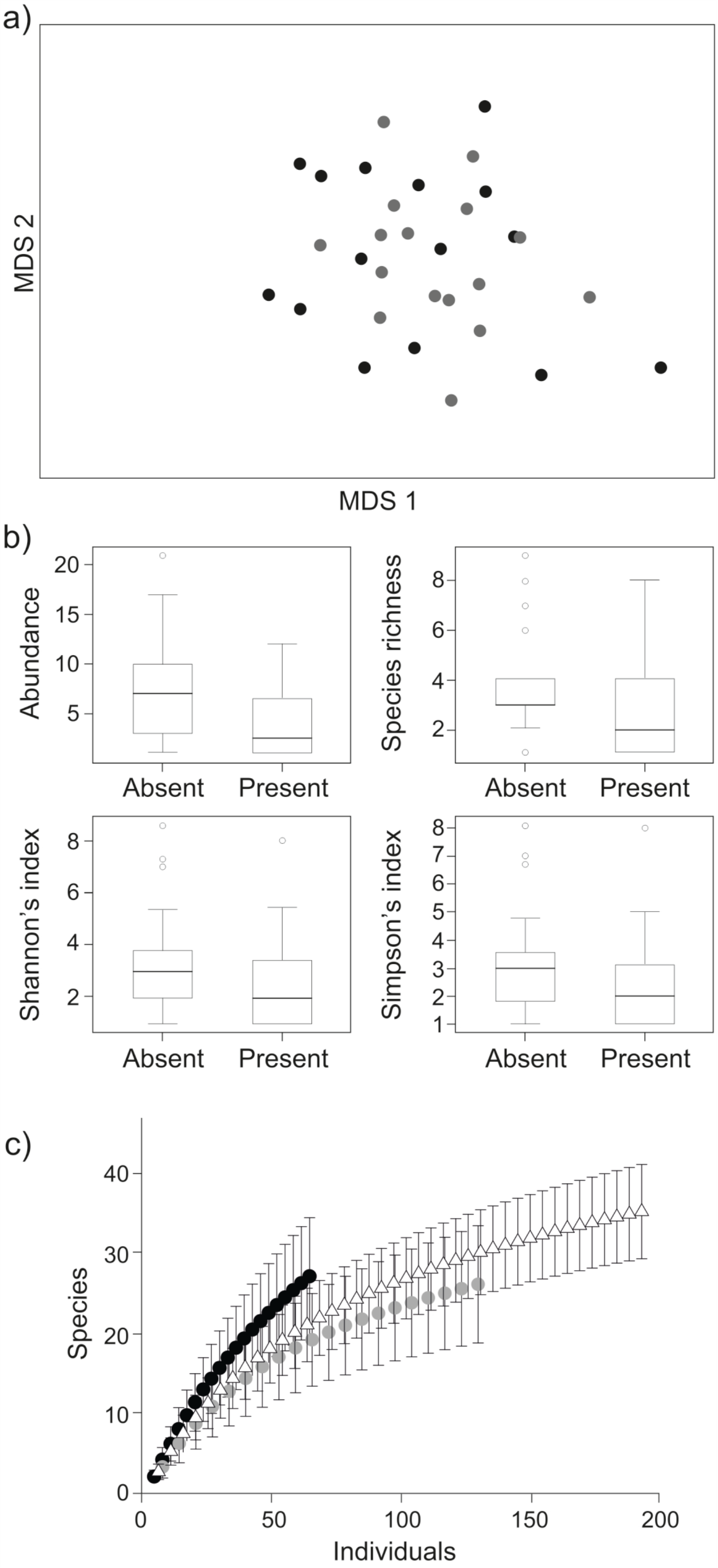
a)
MDS 2
MDS 1
b)
Abundance
20
15
10
5
Absent
Present
Species richness
8
6
4
2
Absent
Present
Shannon's index
8
6
4
2
Absent
Present
Simpson's index
8
7
6
5
4
3
2
1
Absent
Present
c)
Species
40
30
20
10
0
0
50
100
150
200
Individuals

Fig. 2

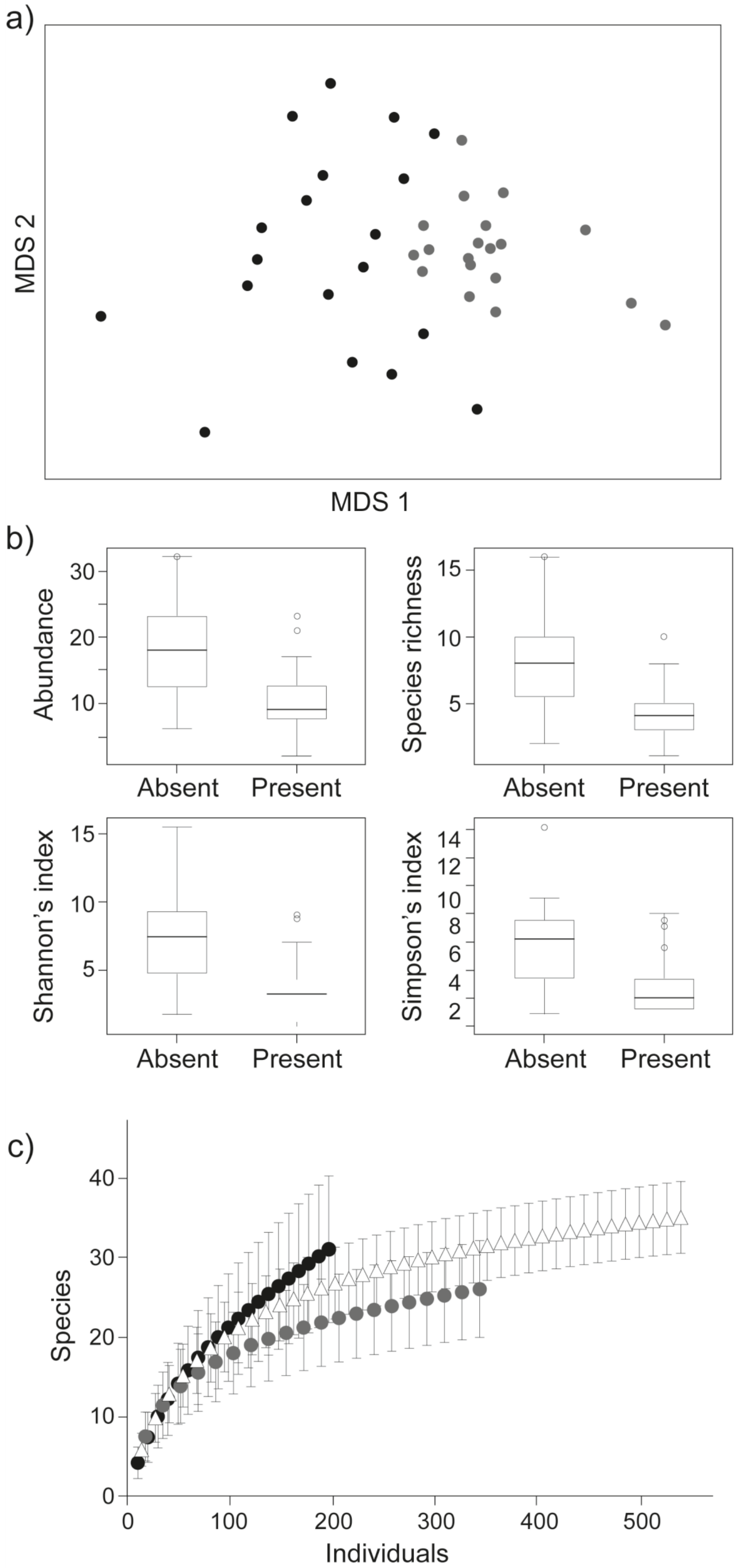
a)
MDS 2
MDS 1
b)
Abundance
30
20
10
Absent
Present
Species richness
15
10
5
Absent
Present
Shannon's index
15
10
5
Absent
Present
Simpson's index
14
12
10
8
6
4
2
Absent
Present
c)
Species
40
30
20
10
0
0
100
200
300
400
500
Individuals

Fig. 3