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Is eutrophication really a major impairment for small waterbody biodiversity?

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Summary

1. Eutrophication remains a major stress for freshwater biodiversity. Its deleterious consequences on biodiversity are well documented for large waterbodies. However, the impact of eutrophication may differ in smaller waterbodies, such as ponds and small lakes, which generally support naturally high levels of nutrients in lowlands. Furthermore, this response could depend on the scale considered, from local (individual waterbody, alpha diversity) to regional (the network of waterbodies, gamma diversity). It is also unclear whether the richness of threatened species responds in the same way as the richness of the whole assemblage.

2. The present study investigates local- and regional-scale consequences of eutrophication on taxonomic richness (all taxa) and conservation value (threatened taxa) in temperate lowland small waterbodies. Five taxonomic groups were investigated: macrophytes, gastropods, water beetles, adult dragonflies and amphibians, in a set of natural waterbodies and a set of enriched waterbodies covering a large nutrient gradient from mesotrophic to hypertrophic conditions.

3. Globally, our study did not reveal consistent, systematic responses to eutrophication. For macrophytes, the richness and conservation value suffered from eutrophication at both local and regional scales. In contrast, for amphibians and gastropods, eutrophication did not impair biodiversity at the local nor the regional scale. Dragonflies and water beetles showed intermediate situations, with an impairment by eutrophication varying according to the type of waterbodies considered. At the regional scale, each trophic status, even the nutrient richest, brought an original contribution to biodiversity.

4. *Synthesis and applications.* The management of eutrophication for small lowland waterbodies has to be considered differently than for lakes. For an individual waterbody (the local scale), nutrient enrichment is not necessarily a major impairment and its impact depends on the taxonomic group considered. Conversely, at the landscape scale, eutrophication is a major pressure on small waterbody biodiversity, especially because nutrient-rich small waterbodies are dominant in the landscape. Therefore, conservation efforts should integrate the notion of pond regional networks or 'pondscapes', where the regional biodiversity is supported by a mosaic of trophic conditions, and promote the presence of less rich waterbodies.

Key-words: amphibians, dragonflies, freshwaters, macroinvertebrates, macrophytes, nutrient status, ponds and small lakes, species richness, threatened species

Introduction

Eutrophication is still a major stress for freshwater biodiversity in the 21st century (Brönmark & Hansson 2002;

Schindler 2006). Climate warming, land-use changes and other human pressures act in synergy to increase eutrophication, and its impact on ecological communities is expected to increase in the future (e.g. review in Hering *et al.* 2010).

Eutrophication is known to have deleterious effects on large waterbodies such as lakes, including algal blooms

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and disappearance of submerged macrophytes (Brönmark & Hansson 2002). Understanding the effects of eutrophication on lake biodiversity requires a good knowledge of the response of biodiversity to trophic status or primary productivity. Large variations in the pattern and strength of the relationship between primary productivity and taxonomic richness have been reported for a variety of terrestrial and aquatic ecosystems, depending on the spatial scale or taxonomic group (Waide *et al.* 1999; Mittelbach *et al.* 2001). Studies conducted in aquatic systems are underrepresented in comparison with terrestrial systems (Waide *et al.* 1999), but most demonstrate a hump-shaped pattern on both local and regional scales (Waide *et al.* 1999; Mittelbach *et al.* 2001), that is, low diversity at low and high productivities and maximal diversity at intermediate productivity.

Contrary to larger freshwater systems, small waterbodies (defined here as 'shallow waterbodies between 1 m² and several hectares in area, which may be permanent or seasonal, and include both man-made and natural waterbodies', adapted from Biggs *et al.* 2005; De Meester *et al.* 2005) from temperate lowland areas in general support naturally high levels of nutrients and range from eutrophic to hypertrophic conditions (Menetrey *et al.* 2005; Sondergaard *et al.* 2005), excepting occasional cases of phreatic supply or small watersheds. Indeed, eutrophication is part of the natural ageing process of many small waterbodies due to their low volume compared to natural organic matter enrichment through wind or run-off. Despite their high nutrient conditions, lowland small waterbodies collectively (i.e. at the regional scale) support a very diverse, and sometimes unique biodiversity, often richer than those found in other types of freshwaters, such as running waters or larger lakes (Williams *et al.* 2004).

The consequences of eutrophication on small waterbody biodiversity are poorly understood. At the local scale, as in larger systems, a hump-shaped productivity–richness relationship was demonstrated, for several taxonomic groups: fish, phytoplankton, benthic invertebrates, macrophytes and macroalgae from ponds or shallow lakes (Jeppesen *et al.* 2000; Chase & Leibold 2002; Menetrey *et al.* 2005). However, at the regional scale, a positive linear relationship was evident, due to an increase in dissimilarity of the individual pond communities (Chase & Leibold 2002). Some mesocosm experiments conducted in small artificial ponds provided contradictory information. For example, in some experiments, only slight consequences of nutrient additions were observed on taxonomic richness or abundance of freshwater communities, such as macrophytes, macroinvertebrates and zooplankton (McKee *et al.* 2002; Moss *et al.* 2003). Conversely, other experiments showed major effects, such as a decrease in plant species richness or an increase in floating plant biomass (Feuchtmayr *et al.* 2009).

Globally, most investigations of freshwater ecosystems have focused on a restricted set of taxonomic groups, such as planktonic organisms and plants, and did not

consider simultaneously a large range of taxonomic groups. Moreover, there is a lack of evidence concerning effects of eutrophication on threatened species richness compared with effects on total species richness.

The present study aims to investigate the consequences of eutrophication for both regional and local biodiversity of lowland small waterbodies from temperate climates, with five different taxonomic groups: macrophytes, gastropods, water beetles, adult dragonflies and amphibians. This was conducted for a set of natural waterbodies, covering a large nutrient gradient from mesotrophic to hypertrophic conditions. An additional set was investigated to describe more precisely the end of the nutrient gradient: it included therefore only enriched waterbodies, encompassing eutrophic and hypertrophic conditions.

In a first step, we investigated the local scale (individual waterbody), and particularly the relationship between nutrient status and both taxonomic richness and conservation value of assemblages. We hypothesized that eutrophication will decrease alpha diversity in these eutrophic to hypertrophic waterbodies (Hypothesis 1), in accordance with the decreasing part of the largely reported hump-shaped pattern. Nevertheless, as most lowland small waterbodies are naturally nutrient rich and as their biodiversity has always faced high nutrient levels, we expect the relationships to be weak (Hypothesis 1). Our second step addresses the regional scale (network of waterbodies), and particularly the quantification of the contribution of temperate small waterbodies of different nutrient status to the regional taxonomic richness. We hypothesize that waterbodies of high nutrient status may support a particular biodiversity and therefore contribute significantly to the regional diversity (Hypothesis 2).

Materials and methods

STUDY SITES

Two sets of temperate lowland waterbodies encompassing different ranges of nutrient status and with different anthropic uses were investigated (Table 1). The first set, situated in Switzerland, includes rarely managed natural waterbodies, ranging from mesotrophic to hypertrophic conditions according to the OCDE (Organization for Economic Co-Operation and Development, 1982) and the Wetzel (1983) classifications. These 55 lowland waterbodies were studied in the context of other projects (Oertli *et al.* 2002; Indermuehle *et al.* 2010). Fish were present in most of these waterbodies, but in natural densities, and their presence had therefore no significant impact on the species richness and conservation value of the five investigated taxonomic groups (Mann–Whitney tests with $P > 0.42$, unpublished data from the above-mentioned projects). The second set of waterbodies in eastern France (the Dombes, north-east from Lyon) includes waterbodies regularly enriched for extensive fish production, explaining their eutrophic and hypertrophic conditions. These 82 waterbodies located in a very dense network within an area of 1000 km² were studied through a project aiming at assessing the

Table 1. Description of the two data sets of temperate lowland small waterbodies: natural waterbodies in Switzerland and enriched waterbodies in France

| | Natural | Enriched |
|---|--|-------------------------|
| Number of studied small waterbodies | 55 | 82 |
| Median waterbody area (min–max) (m ²) | 1240 (6–5800) | 91 000 (22 900–795 600) |
| Median waterbody depth (m) | 1.3 | 0.65 |
| Range of altitude (m.a.s.l.) | 210–700 | 265–310 |
| Range of nutrient status | Mesotrophic–hypertrophic | Eutrophic–hypertrophic |
| Origin | Mainly natural | Artificial |
| Main uses | Nature conservation Recreation Gravel or clay extraction | Fish farming |

ecological value of fish ponds as well as environmental and management impacts (Arthaud *et al.* 2012). Fish pressure (expressed as the annual weight of fish caught per year and per hectare) had neither a significant impact on species richness, nor on conservation value of the five investigated taxonomic groups (linear regressions with $P > 0.14$, unpublished data). This was likely to be due to the spatial structure and heterogeneity of the shoreline, often soft slopes with dense vegetation, which provided shelter from predation. As the two data sets differed in several key parameters potentially determining biodiversity (range of nutrient concentrations, morphometry, anthropic use), the two data sets were not merged and were analysed separately.

MEASURES OF BIODIVERSITY

Five taxonomic groups were chosen, differing in their ecology and biology (e.g. life cycles, habitats): macrophytes, gastropods, water beetles (larvae and adults), dragonflies (adults) and amphibians (adults, subadults, larvae). In both sets of waterbodies, they were sampled on the basis of the PLOCH-IBEM standardized method (abbreviations from the French 'Plans (PL) d'eau (O) suisses (CH) and Indice de Biodiversité des Etangs et Mares, Oertli *et al.* 2005; Indermuehle *et al.* 2010). Inventories were undertaken in both open water and interface between water and land. The sampling effort was proportional to pond area. Macrophytes were sampled once during summer in square plots equally distributed along transects perpendicular to the longest axis of each waterbody. Gastropods and water beetles were sampled once during the spring or summer months with a small-framed hand net (frame 14 × 10 cm, mesh size 0.5 mm) following a stratified strategy across the dominant mesohabitats. Adult dragonflies were inventoried twice, at the end of spring and in mid-summer, in plots (10 × 30 m) distributed in all the habitats occurring along the shore. Their autochthony was assessed through behavioural and biological criteria, and spatio-temporal abundance and frequency according to Chovanec *et al.* (2005). Amphibian presence was recorded exhaustively two to four times in the year by means of search by flashlight, identification of calls and net dipping following the method of Schmidt & Zumbach (2005).

Taxonomic richness was assessed at species level for macrophytes, dragonflies and amphibians, and at genus level for gastropods and beetles. The conservation value of assemblages was calculated for the three taxonomic groups identified at the species level using the Csp value. The Csp value is a Swiss application (Oertli *et al.* 2002) of the Species Quality Score developed in the United Kingdom (Foster *et al.* 1989). Species are ranked according to their degree of rarity on the national Red List in geometric progression, successively doubling from 1 (commonest species) to 32 (rarest). The Csp value is the average of the scores of all species present at the site. Swiss Red Lists were used in Switzerland. No French Red Lists are currently available, so the Swiss Red Lists were used as a surrogate because of geographical proximity and species pool similarity (90% of the recorded French macrophyte, dragonfly and amphibian species are present in Switzerland). The Csp value was chosen because it provides additional information over species richness as evidenced by Rosset *et al.* (2012).

MEASURES OF NUTRIENT STATUS

To determine nutrient status, an integrative index was calculated by combining total nitrogen (N) and total phosphorus (P) concentrations. These two parameters were combined because either N, P or both nutrients contribute to primary productivity or nutrient status in small waterbodies (Sager 2009). N and P concentrations were measured in samples of water at a standard point in all waterbodies, the maximal depth. Water was sampled in the first metre of the water column with a Van Dorn water sampler from the end of the winter period to the autumn period in the enriched waterbodies, and during the end of the winter period in the natural waterbodies. For the natural waterbodies, sampling was conducted once or only a few times, while the enriched ones (larger size) were sampled weekly.

The determination of the index of nutrient status of each waterbody was based on classes defined by OCDE (1982) and Wetzel (1983): oligotrophic, mesotrophic, eutrophic and hypertrophic (see Table S1, Supporting information). Following the same progression, a fifth class, 'highly hypertrophic', was added for very high nutrient concentrations to fit the highest values occurring in the data sets (Table S1, Supporting information). Each of the five classes was subdivided equally into ten subclasses (Table S1, Supporting information). Each waterbody was thus classified in one of these 50 classes according to its N and P concentrations. The highest subclass of each class was retained as representative of the nutrient status of the waterbody, in accordance with the philosophy of the European Water Framework Directive (WFD), which classifies waterbodies by the worst value of the physico-chemical parameters measured.

STATISTICAL ANALYSIS

Local observed taxonomic richness was calculated, except when the sampling was not exhaustive as indicated by species accumulation curves. In these cases, the observed taxonomic richness was transformed by a statistical estimator (Jackknife-1, Burnham & Overton 1979) to estimate the true richness of the waterbody. The relationship between nutrient status and both taxonomic richness and conservation value was investigated using robust linear regressions [lmrob function in the robustbase package of R (Rousseeuw *et al.* 2011)] with both data sets and with a subset of the natural waterbodies corresponding to the range of the

enriched waterbodies. When no significant robust linear regressions were evidenced, polynomial regressions were conducted to test for a potential hump-shaped pattern.

The contribution of waterbodies with different nutrient status to the regional biodiversity was evaluated for each nutrient status represented by at least five waterbodies and for each taxonomic group through three facets. First, the contribution of the different trophic conditions was quantified through gamma richness and gamma conservation value. Gamma richness was calculated as the observed richness and the estimated richness based on the Jackknife-1 estimator (Burnham & Overton 1979), and the gamma conservation value was calculated as the observed conservation value. The contribution of the different trophic conditions to the overall dissimilarity in species composition was then quantified through beta diversities. Beta diversity was measured as the complement of the Sorensen similarity index, $1 - \text{Sorensen}$ (Chao *et al.* 2005). The mean beta diversity of a trophic status was calculated as the mean of all beta diversities between the waterbodies of the trophic status considered and all other waterbodies. Finally, a qualitative analysis consisted of taxon cumulative curves based on the same principle as the single to large (STL) and large to single (LTS) curves, also named single large or several small (SLOSS) curves (Oertli *et al.* 2002; Fattorini 2010), but using nutrient concentrations instead of ecosystem area. They will therefore be named here the LTH curve 'low to high trophic status' and the HTL curve 'high to low trophic status'. If the LTH curve lies above the HTL curve, it is indicative that a set of low trophic status waterbodies are superior to a set of nutrient-richer ones in generating diversity and vice versa. The statistical significance of the differences was tested using Mann-Whitney nonparametric tests.

Results

RESPONSE OF LOCAL BIODIVERSITY TO NUTRIENT INCREASE

Taxonomic richness

Three different responses of the taxonomic richness of an individual waterbody to eutrophication were observed according to the taxonomic group considered (Fig. 1, Table 2).

First, a significant decrease in richness with nutrient increase was observed for macrophytes in both data sets. Macrophyte species richness decreased linearly in the natural waterbodies ($P = 0.005$, Fig. 1a) and in the enriched ones ($P = 0.002$, Fig. 1b). Secondly, for gastropods and amphibians, no significant relationship (linear or polynomial) between nutrient status and taxonomic richness was seen in either data set (Fig. 1). Thirdly, an intermediate situation occurred for water beetles and dragonflies; a significant decrease in richness was observed in only one of the two data sets (Fig. 1). Dragonfly richness decreased linearly with nutrient status in the enriched waterbodies ($P = 0.03$), but not in the natural ones ($P = 0.42$). Water beetle richness decreased linearly with nutrient status in natural waterbodies ($P = 0.006$), but not in the enriched waterbodies ($P = 0.47$).

For all the taxonomic groups, relationships were also tested on a subset of the natural waterbodies corresponding to the nutrient range of the enriched waterbodies, but none were significant (Fig. 1).

Conservation value (threatened species)

From the three taxonomic groups determined at the species level, only the conservation value of macrophyte assemblages responded negatively to eutrophication: a significant decrease ($P = 0.01$) was revealed for the natural waterbodies but not for the enriched ones (Fig. 2, Table 2). The conservation values of dragonfly and amphibian assemblages were not related to nutrient values.

CONTRIBUTION OF WATERBODIES WITH DIFFERENT NUTRIENT STATUS TO THE REGIONAL BIODIVERSITY

Taxonomic richness

The five taxonomic groups studied showed three different trends (Fig. 3, Table 2) globally consistent with the trends observed at the local scale (Fig. 1). First, for macrophytes and water beetles, the gamma (regional) taxonomic richness for a given trophic status considered alone was lower than the values for all trophic status pooled (Fig. 3). Thus, none of the trophic categories alone can shelter the whole regional biodiversity, even if the difference could be small (24% on average). Each trophic stage hosts a particular biodiversity. Moreover, macrophyte and water beetle gamma richness decreased with increasing nutrient status, but only in natural waterbodies, indicating that high trophic stages contribute less to regional diversity than lower trophic stages.

Secondly, for amphibians and gastropods, hypertrophic or highly hypertrophic waterbodies alone were able to shelter as many species as all waterbodies considered together (Fig. 3). Their gamma richness increased with nutrient conditions, underlining the high contribution of hypertrophic waterbodies to regional diversity.

An intermediate situation occurred for dragonflies (Fig. 3). For natural waterbodies, none of the trophic categories alone can shelter all species, but for enriched waterbodies, a trophic category alone was able to shelter as many species as all waterbodies considered together.

Conservation value

Two different trends consistent with the trends observed at the local scale (Fig. 2) were revealed at the regional scale (Fig. 4, Table 2). First, for macrophytes, the gamma (regional) conservation value for a given trophic status considered alone was lower than the values for all trophic status pooled (Fig. 4). Thus, none of the trophic categories alone can shelter the whole regional biodiversity (45% of difference on average). Secondly, for amphibians and dragonflies, hypertrophic or highly

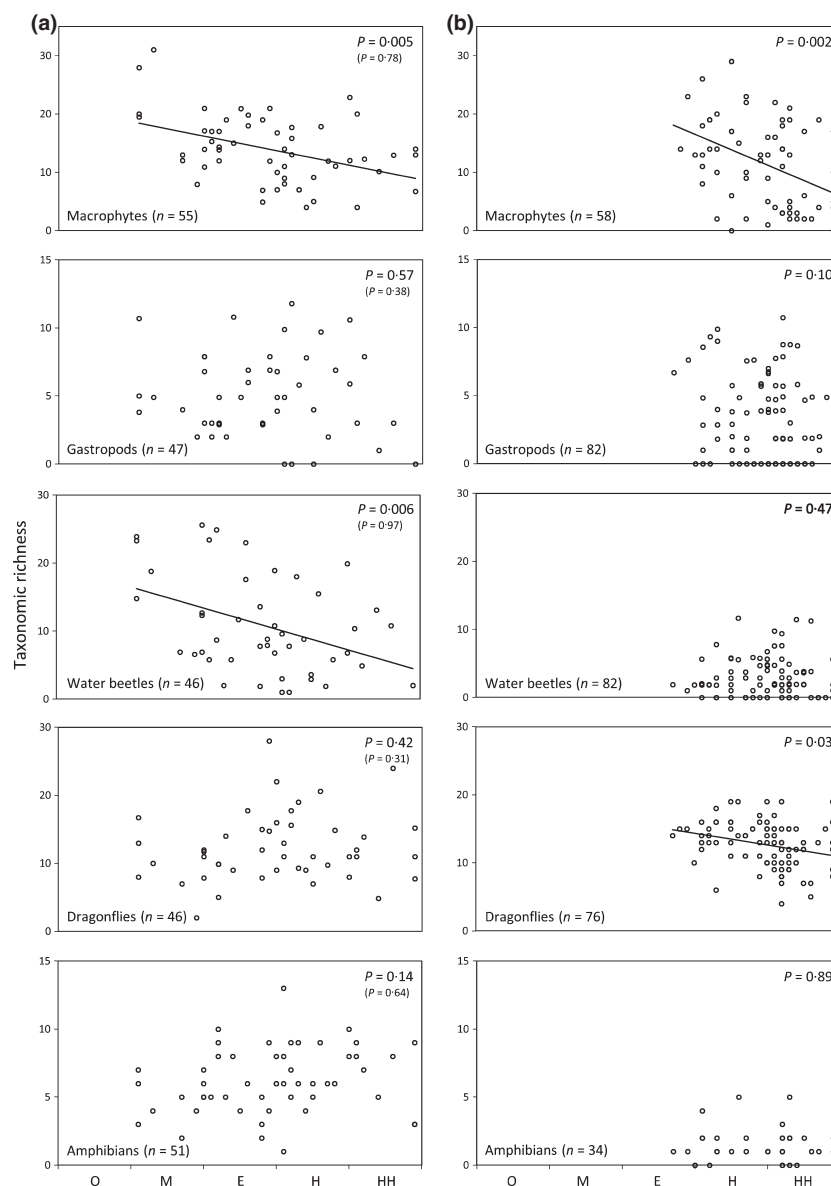


Fig. 1. Scatter plots of macrophyte species richness, gastropod genus richness, water beetle genus richness, dragonfly species richness and amphibian species richness along a trophic gradient (O: oligotrophic, M: mesotrophic, E: eutrophic, H: hypertrophic, HH: highly hypertrophic) for (a) the natural waterbodies and (b) the enriched waterbodies. Robust linear regressions and polynomial regressions are represented when significant ($P < 0.05$). P values in brackets correspond to regressions on a subset of natural waterbodies corresponding to the same trophic range as the enriched waterbodies.

hypertrophic waterbodies alone were able to shelter as many threatened species as all waterbodies considered together.

Taxonomic composition

The dissimilarity (beta diversity) between waterbodies of each trophic status compared with all waterbodies varied slightly (9% on average, see Fig. S1, Supporting information). The dissimilarity of nutrient-rich waterbodies was higher or equal to the dissimilarity in the nutrient-poorer waterbodies (Table 2). The beta diversity in nutrient-rich waterbodies was significantly higher than in less rich waterbodies for macrophytes in both data sets, for gastropods and water beetles in natural waterbodies and for dragonflies in enriched waterbodies. Nevertheless, these differences were well marked only for gastropods (27%). Consequently, each trophic status had a consequent contribution to the regional diversity.

The taxonomic cumulative curves of the five taxonomic groups studied showed three different trends (Fig. 5, Table 2) globally consistent with the trends observed at the local scale (Fig. 1). First, the LTH curve lay below the HTL curve for amphibians in both data sets and for gastropods and dragonflies in the natural waterbodies (Mann–Whitney $P < 0.004$), indicating that a set of nutrient-rich waterbodies could shelter more taxa than a set of nutrient-poorer waterbodies. This trend was particularly well marked for gastropods. Secondly, an opposite pattern was revealed for the water beetles of the natural waterbodies and for the macrophytes, gastropods and dragonflies of the enriched ones (Mann–Whitney $P < 0.0006$, Fig. 5), indicating that a set of nutrient-poor waterbodies could shelter more taxa than a set of nutrient-richer waterbodies. Finally, for macrophytes in natural waterbodies and for water beetles in the enriched waterbodies, the LTH curve lay on the HTL curve (Mann–Whitney $P = 0.31$ and 0.86 , respectively, Fig. 5). Thus, a set of

Table 2. Synthesis of the trends observed for the five studied taxonomic groups. Arrows correspond to an increase, no changes or a decrease. L corresponds to low nutrient waterbodies and H to high nutrient waterbodies. 'H < all' means that a set of high nutrient waterbodies shelters less biodiversity than all waterbodies; L ~ H means that a set of low nutrient status waterbodies shelter as many taxa as a set of high nutrient status waterbodies

| | | Local | | Regional | | | | | |
|---------------|----------|----------|--------------------|----------|--------------------|--------------|---------------|-------|---|
| | | Richness | Conservation value | Richness | Conservation value | Accumulation | Dissimilarity | | |
| Macrophytes | Natural | ↘ | ↘ | H < all | ↘ | H < all | ↘ | L ~ H | ↗ |
| | Enriched | ↘ | → | H < all | → | H < all | → | L > H | ↗ |
| Gastropods | Natural | → | – | H = all | ↗ | – | – | H > L | ↗ |
| | Enriched | → | – | H = all | → | – | – | L > H | → |
| Water beetles | Natural | ↘ | – | H < all | ↘ | – | – | L > H | ↗ |
| | Enriched | → | – | H < all | → | – | – | L ~ H | → |
| Dragonflies | Natural | → | → | H < all | → | H = all | → | H > L | → |
| | Enriched | ↘ | → | H = all | → | H = all | → | L ~ H | ↗ |
| Amphibians | Natural | → | → | H = all | ↗ | H = all | → | H > L | → |
| | Enriched | → | → | H = all | ↗ | H = all | → | H > L | → |

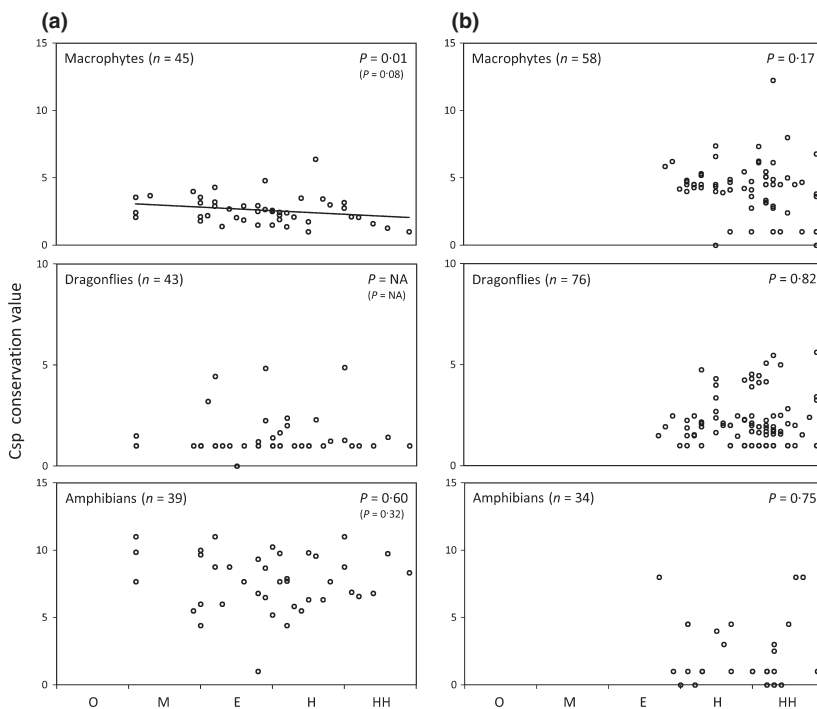


Fig. 2. Scatter plots of macrophyte, dragonfly and amphibian Csp conservation value (mean conservation value per site) along a trophic gradient (O: oligotrophic, M: mesotrophic, E: eutrophic, H: hypertrophic, HH: highly hypertrophic) for (a) the natural waterbodies and (b) the enriched waterbodies. Robust linear regressions and polynomial regressions are represented when significant ($P < 0.05$). NA corresponds to values not available due to statistical limits of the robust linear regression method. P values in brackets correspond to regressions on a subset of natural waterbodies corresponding to the same trophic range as the enriched waterbodies.

eutrophic waterbodies shelters the same number of taxa as a set of hypertrophic waterbodies, although taxa might be completely different at both extremes.

Discussion

GENERAL IMPACT OF EUTROPHICATION ON SMALL WATERBODY BIODIVERSITY

As hypothesized, lowland small waterbody biodiversity was not always strongly impaired by eutrophication. At the local scale, alpha biodiversity did not decrease with eutrophication for all taxonomic groups (Hypothesis 1) and, at the regional scale, small waterbodies of high nutri-

ent status contributed markedly to gamma richness (Hypothesis 2). Some experimental studies have also shown only a slight effect of nutrients on taxonomic richness of freshwater communities (McKee *et al.* 2002; Moss *et al.* 2003).

Globally, our study did not reveal consistent, systematic responses to eutrophication. The impact of eutrophication was heterogeneous according to the taxonomic group considered – from a decrease in biodiversity to no changes. The absence of a surrogate taxonomic group able to describe the whole community was often observed in ecology (review in Saetersdal & Gjerde 2011), despite the tempting concept of surrogacy. As no surrogate taxonomic group alone could describe the impact of

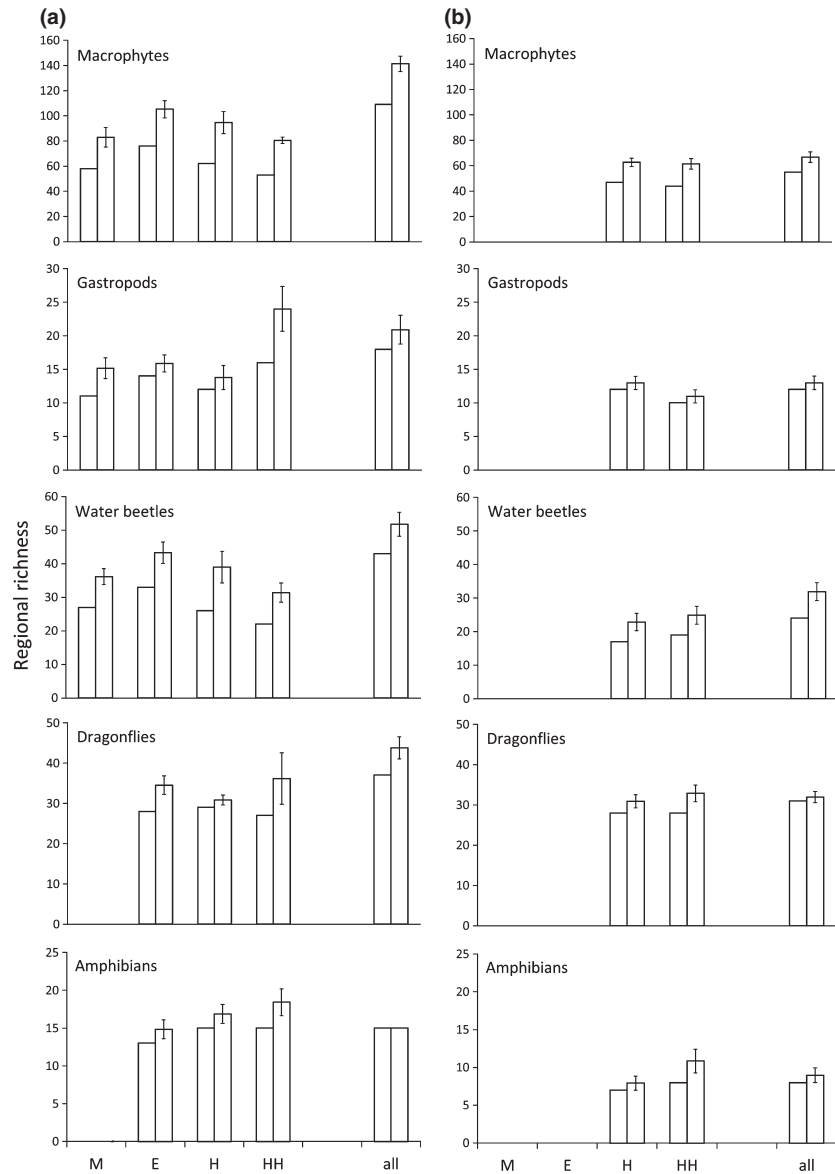


Fig. 3. Observed taxonomic richness (left bar) and estimated taxonomic richness (right bar, Jackknife-1 estimator) for waterbodies of each trophic status (M: mesotrophic, E: eutrophic, H: hypertrophic, HH: highly hypertrophic) and for all waterbodies (all), for (a) the natural waterbodies and (b) the enriched waterbodies.

eutrophication on small waterbody biodiversity, this impairment needs to be tackled by managers differently according to the taxonomic group.

The lack of systematic response to eutrophication suggests other drivers of biodiversity. Numerous studies have underlined that freshwater biodiversity is driven by multiple environmental gradients instead of by a single gradient (Jeppesen *et al.* 2000; Declerck *et al.* 2005). Other disturbances present in the studied areas (e.g. anthropic use of the enriched waterbodies) may have been important drivers of biodiversity, leading to a loss of all sensitive taxa from the regional species pool. However, both temporal and spatial heterogeneity could change the influence of disturbances (Townsend & Hildrew 1994), and the intermediate disturbance hypothesis is not always observed (Bornette *et al.* 2001; Maloney, Munguia & Mitchell 2011). To add to the complexity of responses to disturbance, disturbance and productivity influence the relationship of each other with biodiversity (Kondoh

2001). The coarse taxonomic resolution of macroinvertebrates may explain partly the lack of systematic response to eutrophication. This may change the strength of the relationship between diversity and eutrophication, but would probably not hinder the detection of a response to eutrophication, as suggested by several macroinvertebrate studies (King & Richardson 2002; Chessman, Williams & Besley 2007) and by the relative high number of mono- or bi-specific macroinvertebrate genera in the studied areas (60–77%). A too small number of natural waterbodies at the hypertrophic end of the gradient may also have hindered detection of a response to eutrophication, and highlights the importance of including the enriched waterbody data set in our study to enhance understanding the impact of eutrophication.

Our results highlight, for some taxonomic groups, a relative tolerance of pond and small lake communities to eutrophication. As most lowland small waterbodies are naturally nutrient rich, some of their communities may be

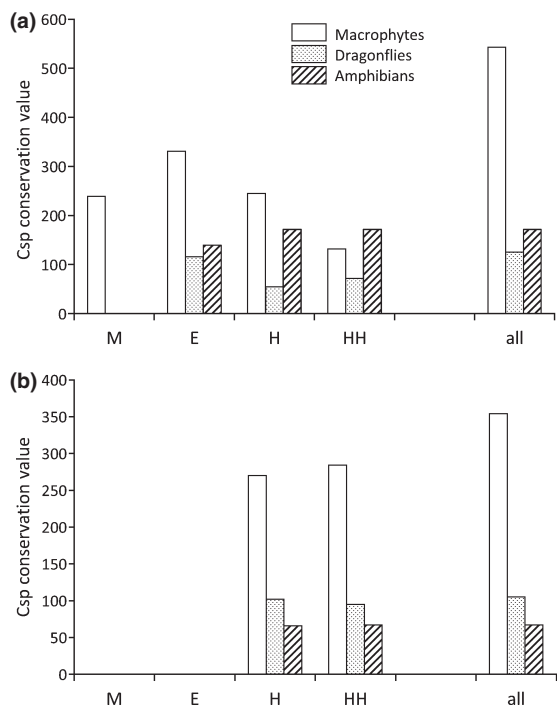


Fig. 4. Conservation value (Csp value) of macrophyte, dragonfly and amphibian assemblages for waterbodies of each trophic status (M: mesotrophic, E: eutrophic, H: hypertrophic, HH: highly hypertrophic) and for all waterbodies (all), for (a) the natural waterbodies and (b) the enriched waterbodies.

more adapted to eutrophication than the communities of larger waterbodies. Indeed, adaptations of species to environmental perturbations such as increased primary production have already been reported for freshwater plants and animals (Paine & Levine 1981; Grimen 2002). In small waterbodies particularly, large-scale studies have evidenced that communities are adapted to a broad range of physical and chemical conditions (Cereghino *et al.* 2012).

DIFFERENCES IN RESPONSE OF BIODIVERSITY TO EUTROPHICATION ACCORDING TO TAXONOMIC GROUPS

The responses of biodiversity to eutrophication evidenced by the present study were globally similar at the local and regional scales, but differed largely depending on the taxonomic group considered.

A negative effect of eutrophication on both local and regional biodiversity was observed for vascular plants. This trend is consistent with the decreasing part of the well-known hump-shaped pattern reported by the reviews of Mittelbach *et al.* (2001) and Waide *et al.* (1999) as well as by more specific studies conducted in freshwaters (Jeppesen *et al.* 2000; Chase & Leibold 2002; Feuchtmayr *et al.* 2009). This response is also in agreement with the high sensitivity of vascular plants to eutrophication widely recognized in freshwaters (Forsberg 1964; Bornette &

Puijalon 2011). Moreover, the indirect negative impact of eutrophication on macrophytes due to phytoplankton-induced turbidity has been widely reported (e. g. Scheffer & van Nes 2007). Only few macrophyte species were unique to one end or the other of the trophic gradient, and no particular trends in their ecological or biological traits were revealed.

For two other taxonomic groups, dragonflies and water beetles, the impact of eutrophication on local and regional taxonomic richness varied according to the data set investigated. Contrasting responses to productivity among types of ecosystems have already been reported by Mittelbach *et al.* (2001). The local and regional water beetle diversity was negatively impacted by eutrophication in natural waterbodies, but not in enriched ones. This absence of relationship in the enriched waterbodies may relate to its smaller range of trophic conditions or to the high connectivity among waterbodies. Some other environmental variables could also be important for water beetles, such as shoreline configuration or periodic drying-out phases. The sensitivity of water beetles to eutrophication revealed in the natural waterbodies is in accordance with previous studies dealing with Irish wetlands (Cooper *et al.* 2005). Local and regional dragonfly species richness diversity was not negatively affected by eutrophication except at the local scale in the enriched waterbodies. This absence of relationship may be explained by some other environmental variables, such as pond area and habitat diversity around waterbodies, explaining a large part of the variability of dragonfly assemblages (Corbet 1999) and could be of greater importance for dragonflies than nutrient conditions.

Finally, the diversity of gastropods and amphibians did not decrease with eutrophication at both local and regional scales. This tolerance to eutrophication is not totally surprising. Indeed, gastropods have a greater affinity for nutrient-rich conditions than other macroinvertebrate orders. As an example, 20% of all Swiss gastropod genera prefer nutrient-rich conditions, contrasting with other freshwater macroinvertebrates such as mayflies and caddisflies whose only 7% and 2% genera prefer nutrient-rich conditions (unpublished data coupling ecological traits from Tachet *et al.* 2010 with Swiss data bases). The tolerance of amphibians to eutrophication may be related to their high plasticity and high dispersal abilities, which enable them to occupy a large range of environmental conditions (Feder & Burggren 1992) and to the minor role played by water chemistry on their diversity (Hecnar & McLoskey 1996). Another explanation may stem from the great importance of land use and waterbody connectivity for established assemblages (Joly *et al.* 2001). Nevertheless, focused laboratory studies evidenced the sensitivity of some amphibian larvae to nutrients (Watt & Oldham 1995). Therefore, the observations in situ could be the consequence of complex interactions such as the cascade effect of nutrient concentrations on oxygen depletion and on amphibian predators' survival (e.g. fish).

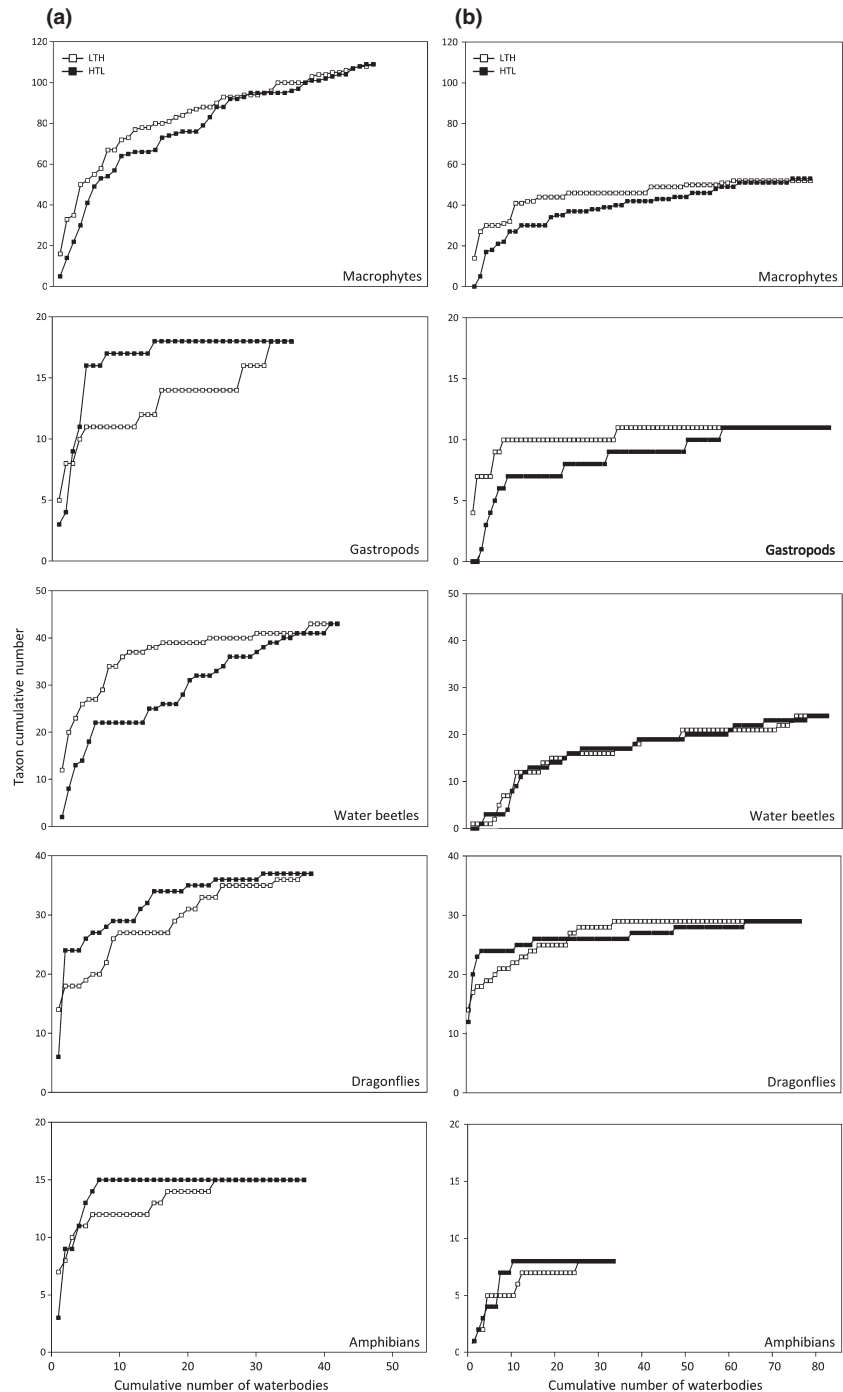


Fig. 5. Low to high (LTH nutrient status) and high to low (HTL nutrient status) accumulation curves: cumulative number of macrophyte species richness, gastropod genus richness, water beetle genus richness, dragonfly species richness and amphibian species richness plotted against the cumulative number of waterbodies ranked in increasing or decreasing order of nutrient status for (a) the natural waterbodies and (b) the enriched waterbodies.

APPLICATION TO LOWLAND SMALL WATERBODY MANAGEMENT

Eutrophication has been frequently described as a major stress for freshwater biodiversity, for large lakes and small waterbodies (Brönmark & Hansson 2002). Our study stresses nevertheless that, in European temperate areas, the management of eutrophication for lowland small waterbodies has to be considered differently than for lakes. Indeed, for an individual waterbody in the landscape (the local scale), we suggest here that nutrient enrichment is not always a major impairment. A hyper-

trophic small waterbody can make a valuable contribution when part of a network. This depends nevertheless on the taxonomic group considered. At the landscape scale, the story is clearly different. If most lowland small waterbodies are naturally eutrophic under temperate climates, anthropic activities and climate warming clearly shift them today towards hypertrophic conditions. Thus, present lowland waterbodies' networks are homogenized and dominated by hypertrophic waterbodies, a pattern which will worsen in our future landscape. In this sense, at the global scale, eutrophication is a major impairment for small waterbody biodiversity.

The present study suggests, however, that each trophic status, even the nutrient richest, brings an original contribution to regional diversity. Nevertheless, at the landscape scale, the proportion of hypertrophic waterbodies exceeds the proportion of less nutrient-rich systems. Conservation efforts should therefore promote the less rich small waterbodies currently lacking in the networks. Our results reinforce the notion of pond regional networks or ‘pondscapes’, where the regional biodiversity is promoted by the coexistence of a mosaic of trophic conditions in networks of waterbodies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Limits of total nitrogen and total phosphorus concentrations used to determine the trophic status.

Fig. S1. Beta richness (with respect to all ponds) for waterbodies of each trophic status.