

Local, among-site, and regional diversity patterns of benthic macroinvertebrates in high altitude waterbodies: do ponds differ from lakes?

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Abstract In this study we aimed at comparing invertebrate diversity of high altitude lakes and ponds along hierarchical spatial scales. We compared local, among-site, and regional diversity of benthic macroinvertebrates in 25 ponds and 34 lakes in the Tatra Mountains, central Europe. The ponds showed significantly lower local diversity, higher among-site diversity and similar regional diversity than the lakes. The species–area relationships (SAR), habitat heterogeneity, and environmental harshness are assumed as drivers for the local diversity patterns. An ecological threshold separating pond and lake systems emerged at an area of 2 ha, where the SAR pattern changed significantly. Differences in species turnover between these systems were likely driven by

greater environmental variability and isolation of the ponds. High altitude ponds neither significantly support greater regional diversity nor higher number of unique taxa than lakes. The higher among-site diversity of ponds relative to lakes highlights the relevance of ponds for regional diversity in mountain areas.

Keywords Zoobenthos · Small waterbodies · Alpha diversity · Beta diversity · Gamma diversity · Tatra Mountains

Introduction

A fundamental challenge in conservation ecology is to identify biodiversity and how it is arranged at different spatial scales (Richardson & Whittaker, 2010). Information on how the biodiversity is structured is essential not only for conservation issues, but also related to the mechanisms that cause observed patterns in diversity (Suurkuukka et al., 2012). In general, lentic ecosystems encompass a large variety of waterbodies, differing in size and ecological processes. Their distinct characteristics and fragility have recently been highlighted (e.g. Catalan et al., 2009a). Although ponds have been far less studied than lakes, especially in alpine regions, it is now clear that ponds support both high species richness and rare species (e.g. Oertli et al., 2002; Nicolet et al., 2004; Søndergaard et al., 2005; Oertli et al., 2008). This makes ponds important freshwater biodiversity

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components on a regional scale. In this study, we hypothesize that the different ecological characteristics in lakes and ponds may generate distinct diversity patterns, specific for each type.

Following MacArthur & Wilson's (1967) species–area relationship, waterbodies with larger areas support more species, mainly because small waterbodies are more isolated, more difficult to colonize, and have higher extinction rates that in turn cause lower local diversity. Catalan et al. (2009b) found that ecological thresholds in community assemblages of mountain lakes across Europe were related to critical changes in their size of around approximately 3 ha, but not other size values. If small and large lakes are simply too different ecosystems so as to be compared simply in terms of size, the same will probably apply for the comparison of ponds and lakes. Therefore this study measured the biodiversity patterns between ponds and lakes. If there is a significant difference, this would indicate the existence of specific ecological features in each of the two systems, which should be taken into account when studying and managing lentic water systems in mountain areas.

Habitat diversity also affects species diversity (Williams, 1964), especially at small spatial scales. At smaller spatial scales, habitat diversity appears to explain species richness more efficiently than area alone (Triantis & Sfenthourakis, 2005 and references therein). When it comes to regional richness, ponds support the largest plant and macroinvertebrate diversity relative to other waterbody types throughout Europe (Williams et al., 2003; Davies et al., 2008b). This may simply be the result of higher β diversity, perhaps as the result of higher isolation, regardless of environmental conditions. However, according to Kiflawi et al. (2003) the key to high regional richness is having a greater variety of pond types over a small spatial scale. Indeed, ponds often have small catchment areas (Davies et al., 2008a) resulting in a greater degree of physicochemical conditions across the region (Svitok et al., 2011) that may promote greater biodiversity at regional scale (Williams et al., 2003).

In the Tatra Mountains, lakes have been studied intensively over the last decades both in terms of their biota and physico-chemical patterns (see Bitušik et al., 2006a for more details), but little is known about the ponds of the region (Kownacki et al., 2006; Dumnicka & Galas, 2012) and the existing data are usually pooled together with lakes (e.g. Čiamporová-

Zaťovičová & Čiampor, 2011). We took semi-quantitative samples of macroinvertebrates from 34 high altitude lakes and 25 ponds located at the same lake district, and tested whether or not ponds and lakes have equal (i) α -diversity, (ii) β -diversity, and (iii) γ -diversity. This kind of study could be useful to shed light into the differences of potential indicator capacities of mountain ponds and lakes. It is also the first step to disentangle the potential of pond and lake communities to respond to disturbance and global changes as emphasized by Céréghino et al. (2008).

The present study is the first step to provide information on the biota and diversity of Tatra ponds and compare it with that of lakes situated at the same region and altitudinal range. To our knowledge, this is the first time when standardized comparison of invertebrate communities between the system of ponds and lakes has been reported.

Materials and methods

Study area and sampling sites

The Tatra Mountains are situated at the border between Slovakia and Poland (the West Carpathians; 20°10'E and 49°10'N). They experience rapid changes in temperature and precipitation along an altitudinal gradient. The average annual air temperature decreases with elevation by 0.6°C per 100 m (Konček & Orlicz, 1974). The amount of precipitation varies from ~1,000 to ~1,600 mm year⁻¹ but can reach >2,000 mm year⁻¹ in some valleys (Chomitz & Šamaj, 1974). Snow cover usually lasts from October to June at elevations above 2,000 m a.s.l. All of the surveyed waterbodies are of glacial origin. The study area is situated on granitic bedrock, mainly covered by undeveloped podsol, leptosols, and regosols (Gorek & Kahan, 1973; Nemčok et al., 1993). Comprehensive general description of the relevant hydrology, soil, and vegetation attributes of the Tatra Mts. was given elsewhere (see Kopáček et al., 2004, 2006).

The studied waterbodies comprise 25 ponds and 34 lakes located both at Slovak and Polish part of the Tatra Mts., encompassing a broad range of altitude (from 1,089 to 2,157 m), and catchment characteristics. To distinguish lakes from ponds, we used a frequently used definition taking waterbody area into account (Biggs et al., 2005). We defined the pond

versus lake threshold area as 1 ha that acceptably separated shallow and small ponds from larger and deeper lakes (Fig. 1). The environmental characteristics of studied lakes and ponds are summarized in Table 1. All the lakes are soft-water and oligotrophic, though some lower located ponds are dystrophic. All sampled lakes and ponds are free from direct anthropogenic influence except for the few waterbodies ($n = 5$) where fish have been introduced.

Field sampling and laboratory works

Data on the benthic communities come from an extensive survey conducted in September 2004. Kick samples of littoral benthic communities were taken using a D-shaped hand net (Frost et al., 1971). Dominant substrate types of individual waterbodies were sampled, considering the relative dominance of the different substrate types, and the total amount of sampling effort was equal in all the sites (3 min). Collected material was preserved with 4% formaldehyde and stored in plastic bottles. In the laboratory, organisms were hand sorted and identified to the lowest possible taxonomic level. Due to incomplete identification, Oligochaeta were excluded from any further analysis.

Data analysis

The data obtained were summarized in a taxa incidence matrix. We used qualitative information only, since it is robust to inter-annual fluctuations in population size, easy to understand, and allows direct

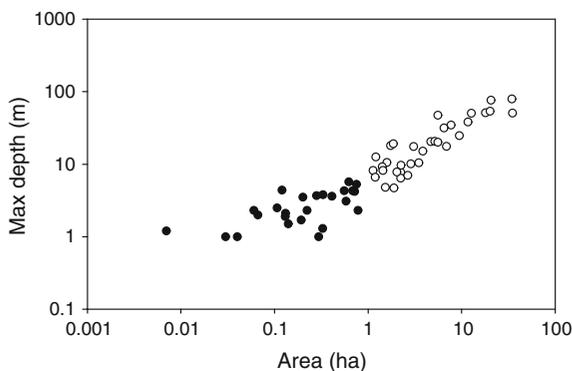


Fig. 1 The distribution of the study ponds (filled circle) and lakes (open circle) in a space defined by their area and depth. Note the log scaling of axes

comparison with other studies. Following Whittaker (1960), we separately compared local (α) diversity, among-site (β) diversity, and regional (γ) diversity between lakes and ponds of the same lake district.

For the purpose of this study, α diversity was defined as the taxa richness of individual waterbodies. The difference in α diversity between lakes and ponds was assessed using a randomization test. The procedure involved the comparison of an observed statistic with a distribution of randomly reshuffled data (Manly, 1997). The difference between the mean species richness observed in lakes, and the mean species richness observed in ponds ($\Delta\bar{x}$) was used as the test statistic and ran 10,000 randomizations to generate null distribution to which the observed statistic was compared. From this comparison, the probability of detecting a difference greater than or equal to the observed value was computed. Unlike standard parametric tests, randomization tests make no distributional assumptions and do not require the distribution of the test statistics to be known. We displayed mean values and confidence intervals for both waterbody types in order to provide information on the magnitude of the differences and precision of the estimates. Ninety-five percent confidence intervals were estimated using 10,000 non-parametric bootstrap replications and applying the bias-corrected and accelerated percentile method (Efron, 1987). Again, the procedure avoids parametric assumptions when computing confidence intervals.

To gain more insight into the species–area relationship, we directly regressed the α diversity on waterbody area (log transformed to improve linearity). Catalan et al. (2009b) identified threshold in lake size where changes in the ecosystem organization are particularly likely. Thus, we conducted piecewise linear regression (Muggeo, 2003) in search for such an ecological threshold (breakpoint) in our data set. As first, we tested for an existence of a breakpoint (ψ) using Davies' test (Davies, 1987). Then a piecewise regression model was fitted to the data using the estimated breakpoint from Davies' test as the initial value. Since the residuals showed some evidence of heteroskedasticity, we took this data structure into account using heteroskedasticity consistent covariance matrix estimator (Cribari-Neto, 2004) and applied the partial quasi-t tests for model parameters.

We expressed β diversity of ponds and lakes as a variation in the identities of taxa among particular

Table 1 Summary environmental characteristics of studied lakes and ponds

	Lakes	Ponds	Δ	<i>P</i>
Location				
Altitude (m) ^{a,b}	1,804 (1,395; 2,157)	1,733 (1,089; 2,141)	71	0.2487
Distance to the nearest waterbody (m) ^c	561 (25; 1,987)	1,886 (105; 5,391)	−1325	0.0001
Morphometric parameters ^{a,b}				
Surface area (ha)	7.16 (1.13; 34.93)	0.31 (0.01; 0.78)	6.85	0.0001
Maximum depth (m)	23.85 (4.70; 79.30)	2.80 (1.00; 5.70)	21.0	0.0001
Habitat heterogeneity ^d				
Number of substrates presented	4.91 (3; 7)	3.76 (3; 6)	1.15	0.0001
Physico-chemical parameters ^b				
pH	6.81 (6.08; 7.35)	5.72 (4.87; 7.24)	1.1	0.0001
ANC ($\mu\text{mol l}^{-1}$)	108.3 (14.4; 335.2)	41.1 (−11.7; 228.9)	67.3	0.0018
Cl [−] ($\mu\text{mol l}^{-1}$)	4.4 (2.7; 8.6)	5.9 (0; 13.3)	−1.5	0.0130
SO ₄ ^{2−} ($\mu\text{mol l}^{-1}$)	22.8 (15.3; 49.8)	21.9 (6.2; 42.0)	0.8	0.7257
NO ₃ [−] ($\mu\text{mol l}^{-1}$)	21.9 (9.9; 30.6)	12.1 (0; 49.1)	9.8	0.0007
NH ₄ ⁺ ($\mu\text{mol l}^{-1}$)	0.84 (0.21; 1.64)	1.57 (0.28; 6.50)	−0.73	0.0093
Na ⁺ ($\mu\text{mol l}^{-1}$)	15.10 (7.50; 24.55)	14.88 (4.26; 26.40)	0.19	0.8865
K ⁺ ($\mu\text{mol l}^{-1}$)	2.68 (1.74; 4.41)	4.10 (0.21; 13.92)	−1.41	0.0098
Ca ²⁺ ($\mu\text{mol l}^{-1}$)	71.8 (32.2; 171.7)	32.9 (4.7; 103.3)	38.8	0.0004
Mg ²⁺ ($\mu\text{mol l}^{-1}$)	7.9 (1.1; 62.0)	10.6 (1.0; 73.1)	−2.7	0.5081
Al ($\mu\text{mol l}^{-1}$)	0.30 (0.01; 1.76)	3.24 (0.16; 12.09)	−2.94	0.0001
Si ($\mu\text{mol l}^{-1}$)	28.1 (11.0; 38.8)	25.6 (2.5; 52.3)	2.5	0.3951
DOC ($\mu\text{mol l}^{-1}$)	35.0 (11.7; 97.5)	209.8 (4.2; 814.2)	−174.7	0.0001
TON ($\mu\text{mol l}^{-1}$)	6.6 (3.6; 11.8)	18.1 (3.4; 70.5)	−11.5	0.0001
TP ($\mu\text{mol l}^{-1}$)	0.09 (0.04; 0.16)	0.40 (0.06; 2.01)	−0.31	0.0001
Ch- <i>a</i> ($\mu\text{g l}^{-1}$)	1.80 (0.32; 8.43)	8.22 (0.09; 57.42)	−6.43	0.0045

Mean values (minimum; maximum), mean differences (Δ), and corresponding probabilities (*P*) based on 10,000 randomizations are displayed

ANC acid neutralizing capacity (Gran titration), TP total phosphorus, DOC dissolved organic carbon, TON total organic nitrogen, Ch-*a* chlorophyll-*a*

Based on data from ^a Gregor & Pacl (2005) and ^b Kopáček et al. (2006)

^c Measured as a ground distance to the nearest waterbody of the same type within the group of studied waterbodies (Google Earth version 5.1)

^d Substrate classification was derived from AQEM system (AQEM Consortium, 2002) with a total of 8 types presented in the studied waterbodies (megalithal, macrolithal, mesolithal, microlithal, akal, mud, CPOM, macrophytes)

waterbodies. This was defined by Whittaker's original measure of β diversity [$\beta_W = \gamma/\bar{\alpha} - 1$, where $\bar{\alpha}$ is average local diversity (see above) and γ represents total number of taxa (see below)], and also by Jaccard's coefficient, which is closely related to β_W (Tuomisto, 2010; Anderson et al., 2011). We used both of the measures since the first, classical approach calculates one of the most frequently employed measures of β diversity (Koleff et al., 2003) and thus allows comparison with other studies and the second

approach facilitates presentation of variation in community structure in multivariate space. We used randomization test (see above) to test the differences in β_W between ponds and lakes. In the first step, the difference in Whittaker's β diversities between ponds and lakes was computed ($\Delta\beta_W$) and subsequently compared to a null distribution of this statistic based on 10,000 unrestricted randomizations of waterbody categories among individual sites. Anderson et al. (2006) proposed that β diversity can be measured as

the average dissimilarity from individual sites to their group centroid in multivariate space.

We calculated Jaccard's coefficients among individual waterbodies, converted the coefficients to distances and submitted this resemblance matrix to non-metric multi-dimensional scaling (NMDS) (Kruskal, 1964). NMDS allowed visual comparison of variation in community structure between ponds and lakes. A random starting configuration with a maximum number of 1,000 starts was employed in searching for stable two-dimensional solution. Statistical significance of observed differences in community variation (spread) between lakes and ponds was assessed using the test for homogeneity of multivariate dispersion (Anderson, 2006). The test is a multivariate analog to Levene's test and compares average distance to centroids among groups using analysis of variance. The null hypothesis of no difference in β diversity between ponds and lakes was assessed using 10,000 permutations of residuals.

We expressed γ diversity using three approaches: (1) total number of taxa, (2) interpolated (rarefied) estimation of taxa numbers, and (3) extrapolated estimations of true taxa numbers. Randomization test was employed to test the null hypotheses that there are no differences in raw total numbers of taxa between ponds and lakes. We used difference in raw taxa counts ($\Delta\gamma$) as the test statistic and ran randomization with the same setting as before. Indeed, such defined γ diversity inevitably increases with increasing number of sampling sites. Consequently, the observed $\Delta\gamma$ could be an artifact of different numbers of lakes ($n = 34$) and ponds ($n = 25$) sampled. Moreover, raw taxa counts can be validly compared only when species accumulation curves have reached an asymptote (Gotelli & Colwell, 2001). Thus, sample-based rarefaction curves were plotted to compare γ diversity on the same basis. Rarefaction curves with 95% confidence intervals were computed using the analytical formulas of Colwell et al. (2004). In order to compare rarefaction curves in terms of the number of taxa (not taxa densities), rarefied values on the y-axis should be plotted against the number of individuals (Gotelli & Colwell, 2001). However, the information on abundance is missing in our data. Thus, we rescaled the x-axis of rarefaction curves to the incidence units (number of taxa occurrences) (Longino et al., 2002; Colwell et al., 2012). Finally, beside the raw taxa counts and their interpolated

estimates, we also estimated gamma diversity of compared waterbodies through extrapolation. Simple non-parametric estimator called Chao2 (Chao, 1987) was employed to estimate true number of taxa in lakes and ponds, respectively. The estimator requires only the presence-absence data and provides reasonably accurate estimates of true species richness even for small sample sizes (Colwell & Coddington, 1994). We used a classical form of Chao2 which is recommended for sampling heterogeneous communities with unequal species detection probabilities (Chao & Shen, 2012), such as the sampling conducted here (coefficient of variation for infrequent taxa >0.7 for both waterbody types).

Analyses were performed in EstimateS (Colwell, 2009), SPADE (Chao & Shen, 2010), and R (R Development Core Team, 2011), in this latter using the libraries *boot* (Canty & Ripley, 2011), *permute* (Simpson, 2011), *rich* (Rossi, 2011), *sandwich* (Zeileis, 2004), *segmented* (Muggeo, 2008) and *vegan* (Oksanen et al., 2011).

Results

Our sampling of Tatra Mts. ponds and lakes yielded a total of 69 taxa (details are given in Online Resource 1), from which 44 taxa were recorded in ponds and 48 in lakes. The number of taxa shared by both systems was 23, while 21 taxa were uniquely recorded in ponds and 25 taxa in lakes. The richest pond site supported 11 taxa compared to the 18 taxa found in the most diverse lake. The richest group both for ponds and lakes was Chironomidae (Diptera) constituting about half of the total diversity (23 and 20 taxa recorded in ponds and lakes, respectively) followed by Trichoptera with 9 taxa collected in ponds and lakes, respectively. Except for Plecoptera (7 taxa) and Odonata (3 taxa), the rest of higher taxonomic groups recorded were represented by 1–2 species/taxa. Odonata and Chaoboridae (Diptera) only occurred in ponds, while Amphipoda, and the dipterans Pediciidae and Limoniidae were recorded in lakes only.

There was a significant difference between the α diversities of ponds and lakes ($\Delta\bar{\alpha} = 2.3$, $P = 0.023$). Ponds with an average of 6.6 taxa supported lower richness than lakes with 8.9 taxa in average (Fig. 2A). The scatter plot of α diversity against the size of waterbodies shows a sudden change in species–area

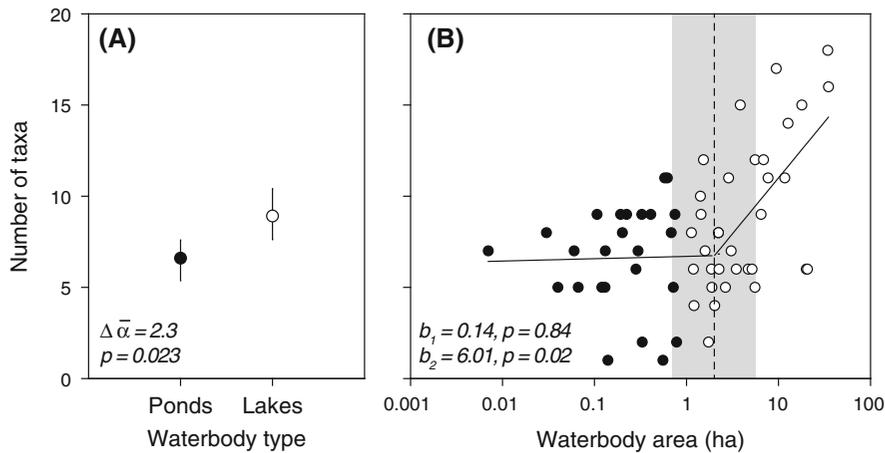


Fig. 2 Comparison of α diversity of ponds (filled circle) and lakes (open circle). Average values (circles), bootstrapped 95% confidence intervals (error bars) and test results are displayed (A). Species–area relationship with fitted piecewise regression

relationship (Fig. 2B). The breakpoint was estimated to ψ (95% confidence limits) = 2.0 (0.7–6.2) ha and was statistically significant ($P = 0.014$, Davies' test), i.e., the slopes of regression lines below and above this threshold were significantly different. The α diversity was not significantly related to area for small waterbodies (<2 ha) (regression slope b (95% CL) = 0.14 (–1.20 to 1.48), $P = 0.837$) while showed a relatively strong positive linear relationship (on a log scale) for larger waterbodies ($b = 6.01$ [1.01–11.01], $P = 0.016$).

Whittaker's β diversity was significantly different between ponds and lakes ($\Delta\beta_W = 1.28$, $P = 0.017$) but showed opposite pattern to that of α diversity. Taxa turnover of ponds was higher (5.7) compared to that of lakes (4.4). This is evident from the higher dispersal of pond scores in multivariate space (Fig. 3). Pond invertebrate communities were significantly more heterogeneous than those of lakes (pseudo- $F = 26.73$, $P < 0.001$) (Fig. 3).

We found no significant difference between ponds and lakes in their total taxa numbers ($\Delta\gamma = 4$, $P = 0.768$). At regional scale, both systems supported similar richness: ponds accumulated 44 and lakes 48 taxa across the surveyed region as a whole. When rarefaction equalized the amount of information in each dataset, ponds showed higher total number of taxa than lakes (Fig. 4). However, the difference was not significant as judged from the overlap of confidence intervals of rarefaction curves. Rarefaction

model (B). Regression lines (solid lines), threshold (dashed line) and its 95% confidence interval (gray) are shown along with the estimates of slopes (b) and corresponding probabilities (P). Note the log scaling of abscissa

curves did not reach an asymptote, indicating that further sampling will probably recover more species. The extrapolated total richness derived from Chao2 estimator was higher in lakes (110 taxa) than ponds (83 taxa) (Fig. 4C). Again, the 95% confidence intervals of those estimates widely overlapped, indicating no significant difference in the true taxa richness between ponds and lakes.

Discussion

Local (α) diversity

Catalan et al. (2009b) identified ecological thresholds in European alpine lakes and found pronounced changes in the whole community at an area of about 3 ha. Here, we used an a priori threshold of 1 ha for classification of ponds and lakes. Both of those thresholds are statistically indistinguishable from the breakpoint of 2 ha (95% CL 0.7–6.2 ha) that was derived from species–area relationship in our data set. Irrespective of the threshold used (1, 2 or 3 ha), local diversity of ponds was significantly lower than the local diversity of lakes ($P < 0.05$, details omitted).

Large mountain lakes have generally more species than smaller lakes in the region (e.g., Bitušík et al., 2006b). This is consistent with the theory of island biogeography (MacArthur & Wilson, 1967), where larger areas have higher probabilities of colonization

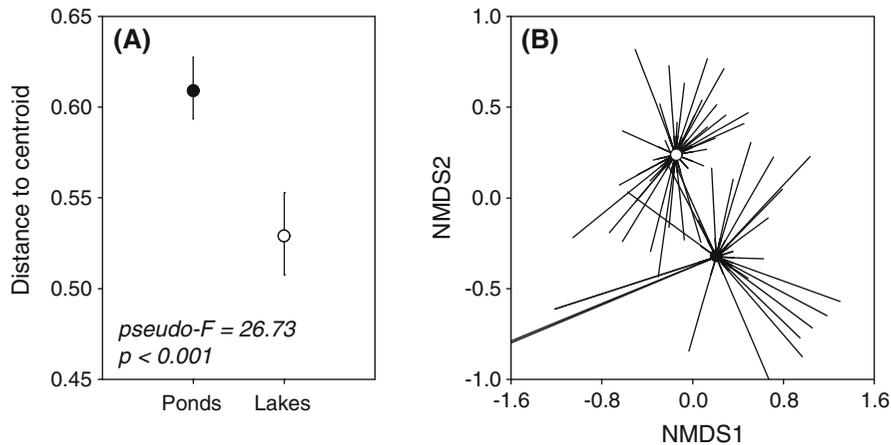


Fig. 3 Comparison of β diversity of invertebrate communities of ponds (filled circle) and lakes (open circle). Average distance to common centroids (circles), bootstrapped 95% confidence intervals (error bars), and test results are displayed (A).

Heterogeneity of communities visualized in an ordination space of NMDS based on Jaccard dissimilarity (stress = 16%) (B). Vectors connect particular sites with their centroids

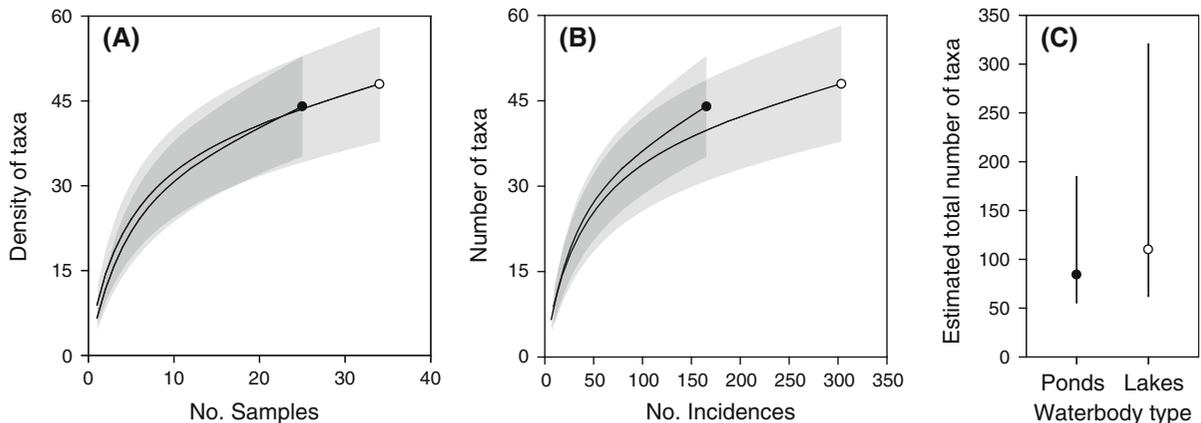


Fig. 4 Comparison of interpolated and extrapolated taxa richness of ponds (filled circle) and lakes (open circle). Sample-based rarefaction curves with 95% confidence intervals (gray area) are plotted with the abscissa scaled by samples

(waterbodies) (A) and taxon occurrences (B), respectively. Estimates of true species richness derived by Chao2 estimator and their 95% confidence intervals are displayed (C)

and lower probabilities of extinction than smaller, more isolated areas (details on geographical isolation are given in Table 1). However, it appears that this theory does not apply to ponds. In this case study of Tatra Mts. waterbodies, species–area relationship was fitted by a broken-stick model where α diversity of ponds was unrelated to its area while lakes showed a stronger positive relationship between diversity and size. There are several other studies on ponds, where the species–area relationship was not found (Hinden et al., 2005; Hamerlík & Brodersen, 2010; Martínez-Sanz et al., 2012b) or was shown for specific taxa only

(Gee et al., 1997; Oertli et al., 2002). Meta-analysis by Drakare et al. (2006) revealed extensive variation of species–area relationships, and that spatial complexity and isolation affect the degree at which species richness increases with area. In this study, we conclude that alpine lakes and ponds are not only nested subsets of different size, but are systems with distinct organization and functioning.

Beside the colonization-extinction dynamics proposed by MacArthur & Wilson (1967), higher local richness of lakes can be explained by greater habitat diversity (Williams, 1964). The habitat diversity

hypothesis suggests that larger waterbodies have a higher probability of containing more habitat types which, in turn, support higher local diversity through niche partitioning among species (e.g., Triantis & Sfenthourakis, 2005; Drakare et al., 2006). In our case, lakes contained significantly more habitat types than ponds (Table 1).

More specific features linked to local diversity pattern of high altitude waterbodies may involve temperature regime and pH. High altitude ponds communities are exposed to more extreme and unstable temperature regimes than lakes (Novikmec et al., 2013). Freezing period is particularly harmful for invertebrate communities of shallow alpine ponds compared to lakes. The shallowest ponds are likely to freeze solid. The duration and extent of ice- and snow-cover control the limnological conditions of high altitude lakes (Smol, 1988) and thus the harsh, unstable environment could reduce local diversity in ponds. Similarly, pH in the studied waterbodies represent a broad range of pH (4.9–7.4) with the ponds having considerably lower pH than lakes (see Table 1). Not surprisingly, some of the studied ponds are dystrophic having naturally lower pH. Moreover, smaller waterbodies are generally more sensitive to acidification due to the limited buffering capacity of their smaller catchments (Kopáček et al., 2002). Thus, local diversity of ponds could be affected more intensively by acidification, which is known to decrease species richness in mountain lakes (Bitušik et al. 2006a) and which was indeed strong in the Tatra Mts. lake district (Kopáček et al., 2006).

Overall, studied lakes and ponds are qualitatively different systems where differences in local diversity are primarily driven by habitat heterogeneity, and environmental harshness.

Among-site (β) diversity

We have shown that the Tatra Mts. ponds have higher β diversity than the lakes of the same lake district. Studies comparing community heterogeneity of different waterbody types throughout Europe (Williams et al., 2003; Davies et al., 2008b) found that ponds and lakes have higher β diversity than streams, rivers, and ditches. Unfortunately, closer comparison of our results with other studies is difficult because they usually merge ponds and lakes together for the analyses.

There is a general trend for smaller lentic waterbodies such as ponds and ditches to have more variable physico-chemical characteristics than larger ones (Davies et al., 2008b). Habitat heterogeneity is often suggested to be the key mechanism for promoting β diversity (Suurkuukka et al., 2012). In our study, environmental characteristics of ponds showed significantly higher heterogeneity than those of lakes (pseudo- $F = 31.94$, $P < 0.001$) (Fig. 5) and ponds were also more variable in terms of substrate heterogeneity (pseudo- $F = 105.99$, $P < 0.001$). The ponds represent wider range of environmental conditions and hence they can support a wider range of communities, a feature reflected in higher β of this system relative to lakes.

Another interpretation is the effect of spatial isolation. In general, ponds as small, relatively isolated waterbodies show high community heterogeneity relative to other aquatic habitats due to low connectivity (Jeffries, 2005; Scheffer et al., 2006). This trend was found in the Tatra Mts. ponds, which were significantly more isolated than lakes (see Table 1). Though, little knowledge on dispersal scales in freshwater invertebrates may evoke speculations about the role of dispersal in promoting β diversity (Suurkuukka et al., 2012). In high altitude ecosystems, lakes and ponds are often separated by distinctive topographic barriers. Therefore, isolation and low connectivity can be important drivers of among-site diversity in both systems. Ponds, however, can be assumed as more isolated than lakes, not only due to their smaller size, but also because they frequently lack water course connections. In addition, in ponds, the within-year environmental variability is likely to be more extreme than in lakes, perhaps imposing a stronger filter for the resident fauna. This implies that in ponds, macroinvertebrate communities possibly rely more on periodic re-colonization, compared to lakes. In the end, this increases the “isolation” of ponds, relative to lakes. We propose that higher environmental heterogeneity combined with higher isolation is likely to be responsible for higher dissimilarity of invertebrate communities of ponds, and in turn, higher β diversity compared to lakes.

Regional (γ) diversity

Based on results of previous comparative studies on biodiversity of waterbodies (e.g., Williams et al.,

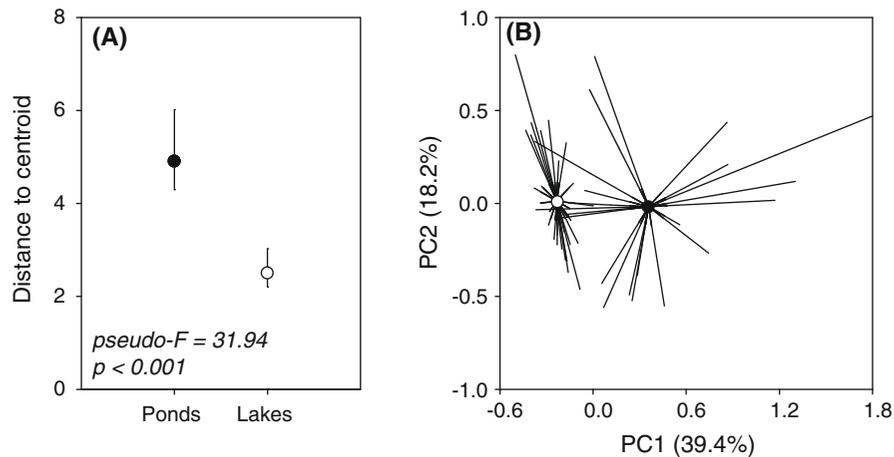


Fig. 5 Comparison of heterogeneity of ponds (*filled circle*) and lakes (*open circle*) based on measured environmental parameters (cf. Table 1). Average distance to common centroids (*circles*), bootstrapped 95% confidence intervals (*error bars*), and test results are displayed (A). Environmental heterogeneity

is visualized in ordination space of principal component analysis conducted on correlation matrix (B). Vectors connect particular sites with their centroids. Proportion of variance explained by particular principal component is given in *parentheses*

2003; Davies et al., 2008a, b; Martínez-Sanz et al., 2012a), we expected that (1) the regional pond diversity would be higher than that of the lakes and (2) ponds would contain greater number of unique taxa (i.e., taxa not observed in lakes). We used different measures of γ diversity (raw data, interpolated and extrapolated estimations), but none of them showed significant differences between ponds and lakes. Moreover, lakes and ponds shared only one-third of the entire species pool while the amount of unique taxa was similar in both systems (25 and 21, respectively). Consequently, on regional level, mountain lakes and ponds seem to accumulate approximately the same amount of taxa but in compositionally different communities.

The contradiction between the published data and our observed results probably stems from differences in sampling schemes. To the best of our knowledge, this is the first time when the systematic sampling protocol and standardized comparison of invertebrate communities between ponds and lakes has been carried out. Thus, comparing our results with published studies is rather problematic. Due to the harsh conditions, benthic fauna of high elevation waters consist of few but well-adapted species (Lencioni, 2004; Füreder et al., 2006), which may differ in their ability to colonize the lakes and ponds. This is reflected in opposite patterns of α and β diversities. Lakes, harboring locally higher number of taxa but

with lower among-site variability of communities regionally support similar taxa number as ponds, which have lower α and higher β diversity.

Finally, it should be emphasized that studies considering only the spatial component of γ diversity may result in inaccurate diversity estimation of the studied systems as a whole and the importance of temporal component to the regional diversity of rare species (a great proportion of γ diversity) should not be overlooked (Suurkuukka et al., 2012). In this context, the true regional diversity of the two systems could be underestimated. Nevertheless, the relative differences between ponds and lakes are still valid.

Perspectives

In our study, we have shown that high altitude ponds have lower local diversity and higher species turnover than the lakes in the same lake district. Local diversity pattern changed significantly at an area of 2 ha, which could be considered an ecological threshold for future classification of high altitude ponds and lakes. Heterogeneous community composition mirrored in higher β diversity of ponds implies a wider array of possible responses to environmental forcing. We can reasonably assume that response of high altitude ponds to environmental changes will differ from that of lakes system of the same region. Shallow water bodies with smaller catchments are generally more

sensitive to environmental changes, such as acidification (see above) or ambient air temperature changes (Novikmec et al., 2013) than lakes.

This leads us to conclude that (i) pond ecosystems could serve as sensitive indicators of environmental changes in mountain areas, and (ii) regarding their high taxa turnover, their contribution to high altitude biodiversity and importance for any conservation purposes should be emphasized.

Further research should focus on disentangling the spatial and temporal components of diversity patterns, in order to precisely assess the indicator potential of mountain ponds, as well as their role in maintaining high regional biodiversity.

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