Taxonomic and functional macroinvertebrate diversity of high-altitude ponds in the Macun Cirque, Switzerland

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Abstract

1. Global environmental change is threatening freshwater biodiversity with ecological impacts predicted to be particularly severe in high-altitude regions. Despite this, an ecological understanding of high-altitude pond networks remains patchy, with only limited knowledge of the environmental and spatial predictors of taxonomic and functional diversity. Moreover, previous studies of pond ecosystems have focused primarily on taxonomic richness and largely overlooked functional diversity.

2. This study examined the influence of local environmental and spatial factors on taxonomic and functional alpha and beta diversity (including the turnover and nestedness-resultant components) of 17 high-altitude (~2,500 m.a.s.l) pond macroinvertebrate communities, in the Macun Cirque, Switzerland.

3. Spatial processes (pond connectivity) were important drivers for taxonomic alpha diversity, while local environmental variables (pond permanence and surface area) were important determinants of functional alpha diversity. Species turnover was the most important component of beta diversity for taxonomic composition, and functional composition demonstrated a nested spatial pattern.

4. Variation in taxonomic and functional composition (and the turnover and nestedness components of beta diversity) were determined by local environmental variables despite the limited environmental gradients within the pond network. No significant effects of spatial variables on community composition were recorded for either facet of diversity, indicating that compositional variation was determined at a local scale. Water temperature, depth and pond permanence were consistently the most important measured drivers of diversity.

5. Given the importance of both spatial and environmental variables in structuring taxonomic and functional diversity, landscape-scale conservation and management activities that aim to improve or protect high-altitude freshwater biodiversity should focus on maintaining connectivity among ponds and environmental heterogeneity, particularly pond surface area, water depth, and hydroperiod. Understanding the mechanisms driving taxonomic and
functional diversity will be critically important for the management and conservation of
macroinvertebrate communities in high-altitude pond networks in the face of climatic
warming.

Key Words: alpine, biodiversity, connectivity, functional traits, environmental filtering, mountain
ponds, spatial structure, species richness
1. Introduction

Global environmental change is threatening freshwater and terrestrial biodiversity (Cardoso et al. 2020). In particular, climate change poses a significant threat with average global temperatures increasing by approximately 0.85°C between 1880 and 2012 (Intergovernmental Panel on Climate Change (IPCC), 2014). However, climatic warming does not occur evenly across the surface of the globe with temperature increases predicted to be particularly high in arctic and high-altitude regions (Nogues-Bravo et al., 2007). Warming temperatures have been shown to have significant effects on mountain ecosystems, driving changes in species compositions and food web interactions, increasing opportunities for the colonization of new species of flora and fauna, and increasing extinctions of species adapted to colder climatic regimes (Halofsky & Peterson, 2018; Rogora et al., 2018). Among freshwater ecosystems, climatic warming has been implicated as a primary cause of the rapid loss of mass from glaciers and snowpacks, altering the temperature and hydrology of mountain streams, thereby threatening the persistence of stream species adapted to cold conditions (Giersch et al., 2017).

However, increasing temperatures have also been reported to result in increased taxonomic richness in streams (Brown, Hannah & Milner 2007) and some mountain pond communities (Rosset, Lehmann & Oertli, 2010). Ponds are defined here as still water bodies between 1m$^2$ and 2ha in size (Hill et al., 2017b).

Although biotic communities and their environmental correlates in mountain streams have been relatively well studied (Hotaling et al., 2017), knowledge remains limited regarding the importance of different spatial and local environmental factors structuring high-altitude (alpine regions >2,500 m.a.s.l) pond communities (Wissinger, Oertli, & Rosset, 2016). Altitude is a primary environmental variable known to influence the structure of pond communities, with taxonomic richness typically being negatively associated with increasing altitude (Jones, Li & Maberly, 2003; Ilg & Oertli, 2014). Owing to the dominance of altitude and closely related environmental variables such as temperature in structuring pond diversity patterns, the influence of other spatial and environmental variables on the richness and composition of pond communities is often masked (Hinden et al., 2005). Identifying
other important environmental variables can be achieved by examining biodiversity–environment relationships specifically among high-altitude ponds in a similar altitude belt, thereby constraining the influence of altitude (Hinden et al., 2005). The limited research undertaken focusing specifically on high-altitude ponds has reported that aquatic macroinvertebrate richness and composition only weakly tracks environmental gradients and is largely influenced by spatial factors, particularly geographical distance and hydrological connectivity among ponds (Oertli et al., 2007).

Recently, research examining functional diversity has increased, with its contribution to enhancing understanding of freshwater community assemblages now being widely recognized (Gianuca et al., 2018, Garcia-Giron et al., 2019). Among pond habitats, however, studies examining spatial patterns have largely focused on taxonomic facets of diversity. Functional diversity reflects the variation of morphological, physiological and ecological traits within a biological community (Petchey & Gaston, 2006) and has typically been shown to provide a better explanation of ecosystem functioning than taxonomic richness (Devictor et al., 2010). Furthermore, functional diversity may provide critical information on the resilience of pond habitats to human and natural stressors (Thornhill et al., 2018). Recent research has found that functional and taxonomic alpha diversity (richness within an individual site) and beta diversity (compositional variation in communities among sites) in lowland lentic habitats can be largely explained by local environmental conditions with limited contributions from spatial factors (Heino et al., 2017a; Hill et al., 2019). Beta diversity can be further partitioned into turnover (species replacement from one site to another) and nestedness components (where taxa in species-poor sites represent a subset of taxa within high richness sites; Legendre, 2014), both of which have previously been demonstrated to be predominantly influenced by local environmental factors among lowland pond networks (Hill et al., 2019). However, all previous pond studies examining the effects of functional diversity were undertaken on low altitude or lowland ponds where significant environmental heterogeneity exists. The relative contribution of spatial and local environmental factors to taxonomic and functional alpha and beta diversity may be different in high-altitude ponds, where local environmental conditions may be more homogeneous.
Mountainous freshwater habitats provide important biodiversity reservoirs for species adapted to colder climates (Fait et al., 2020). There is clearly a need to identify the key environmental variables influencing taxonomic and functional diversity within pond habitats to provide the required information to protect, manage and restore high-altitude pond networks. This information is also vital for enabling the development of effective strategies to mitigate the continuing effects of climate change that threaten to eradicate these unique communities as thermal gradients shift altitudinally (Ilg & Oertli, 2014). Understanding patterns in functional diversity alongside taxonomic richness may provide opportunities to identify key sites that support resilient communities and that are able to withstand disturbance, thereby enabling comprehensive and effective biodiversity conservation of high-altitude pond networks (Strecker et al., 2011). However, to our knowledge no studies have examined the biodiversity and environmental drivers of functional diversity in high-altitude ponds. Given the paucity of information regarding the key environmental and spatial correlates of taxonomic and functional diversity in high-altitude ponds, this study aimed to assess the relative influence of local environmental and spatial factors on taxonomic and functional alpha and beta diversity (and turnover and nestedness components). It is hypothesized that; (i) spatial variables are the primary factors driving taxonomic and functional alpha diversity, and (ii) spatial variables are the most important factors driving taxonomic and functional beta diversity, reflecting reduced local environmental heterogeneity of high-altitude alpine ponds (Oertli et al. 2007).

2. METHODS

2.1 Study sites

The Macun Cirque (~3.6 km²) is situated in the high alpine zone of the Alps (alpine regions >2,500 m.a.s.l) in the Swiss National Park of the Canton Graubünden, Switzerland (Lods-Crozet, Oertli & Robinson, 2012). The Macun Cirque has > 35 small lakes and ponds (ephemeral and perennial) and a 1st and 2nd order headwater stream network (Oertli et al., 2007). Two origins of surface water have
been identified in the area: a north basin fed predominantly by snowmelt and a south basin fed by
glacial meltwater from surrounding rock glaciers (Robinson & Oertli, 2009). Bedrock geology is
crystalline rock and the drainage area of each pond is dominated by two land cover types – rock and
alpine grassland (Lods-Crozet, Oertli & Robinson, 2012) with large areas of bare bedrock
commonplace. Precipitation in the study area is relatively low, typically 850 mm yr\(^{-1}\), and temperature
ranges from -15°C in winter to >20°C in summer with extended ice cover present for approximately 9
months each year (Oertli et al., 2007). Field sampling was undertaken over two days in late July 2019.
Seventeen of the 35 ponds were selected for study in the Macun Cirque, all situated between 2,600
and 2,700 m.a.s.l (Figures 1, 2). Ponds were selected based on accessibility and to ensure that a wide
connectivity gradient was recorded. Three of the ponds were ephemeral (one of which was completely
dry and discarded from the study) while 15 had a perennial hydroperiod. Five of the ponds examined
were interconnected by streams (ponds 10, 11 12, 13 and 17; Figure 1).

2.2 Environmental and spatial data

At each pond, altitude (m.a.s.l), surface area (m\(^{2}\)), mean water depth (cm: recorded at five locations)
and water permanence (ephemeral or perennial, based on researcher expertise by colleagues with >10
years of annual sampling of ponds in the Macun Cirque) were recorded. Conductivity (\(\mu S \text{ cm}^{-1}\)), pH
and water temperature (°C) were measured using a Hanna Hi 9813-6 multiprobe, and dissolved oxygen
content (DO; mg L\(^{-1}\)) was measured using a WTW FDO 925 probe. None of the ponds were overhung
by littoral vegetation, or supported emergent, submerged or floating macrophytes and as such these
variables were not considered further. Historic sampling of the Macun ponds (Oertli et al., 2007)
recorded fish in only two of the ponds sampled (pond 1 and pond 9) which were artificially stocked in
1993. Unfortunately, more recent data are not available on the current status of fish in these ponds and
as a result fish presence and density were not examined in this study.
Three spatial variables were assessed: distance-based Moran’s eigenvector maps (dbMEMs), pond connectivity and hydrological connectivity. Hydrological connectivity refers to the number of water bodies hydrologically connected (e.g. by a small stream) to each pond site, and pond connectivity refers to the total number of waterbodies within 500 m of the pond (Hill et al., 2019). These two measures of connectivity are defined here as ‘hydrological proximity effects’ (Hill et al., 2017b), and were recorded using field observations, maps and aerial imagery (Google Earth, 2020). Distance-based Moran's eigenvector maps (dbMEMs) were calculated to generate a series of spatial variables that quantified the overall spatial structure of the high-altitude pond network. These were calculated using the *dbmem* function in the adespatial package in R (Dray et al., 2020) with the longest distance in the minimum spanning tree calculated as the truncation threshold (Legendre & Legendre, 2012). Only eigenvectors that model positive spatial autocorrelation were used in subsequent analyses (Hill et al., 2017b). A total of three positive dbMEMs with a significant Moran’s I (*p* < 0.05) were used in this study. All Moran’s values were calculated using a random permutation test (999 permutations) using the function *moran.randtest*. The first dbMEMs derived represent broader spatial structures whereas the latter two represent finer spatial scales (Liu et al., 2020).

**2.3 Macroinvertebrate communities**

Aquatic macroinvertebrates from each pond were sampled for a total of 3 min (Biggs et al. 1998) using a sweep technique with a standard pond net (diameter: 250mm, 500 μm mesh size). Sample time was divided equally between the mesohabitats present (e.g. boulder, cobble and gravel substrates). If a single mesohabitat dominated the pond, sampling time was further divided to reflect this. An additional 60 s hand search for macroinvertebrates was undertaken of larger substrates (e.g. boulders) that could not easily be sampled with a pond net. Biotic samples were processed in the field and preserved in 70% ethanol for subsequent identification in the laboratory. Macroinvertebrates were identified to species level, although Gerridae, Tipulidae, Limoniidae, Dolichopodidae, Stratiomyidae, Empididae, Oligochaeta, Collembola were recorded as such.
Functional traits were assigned to macroinvertebrates using the European trait database Tachet et al. (2010). The grouping features (a functional trait category) and traits (modalities within individual grouping features; see Schmera et al., 2015) selected in this study represent the fundamental biological and phenotypic characteristics of freshwater macroinvertebrates rather than their ecological preferences. In total, 63 traits with 11 grouping features were used: life cycle duration, body size, mode of respiration, potential number of cycles per year, aquatic stages, mode of reproduction, resistance forms, locomotion-substrate relation, mode of dispersal, food, and feeding habit (Table 1).

Trait information within the Tachet et al. (2010) database is typically available at species- or genus-level. Where trait information was only available at the genus level, macroinvertebrate species were aggregated to this coarser level (see Table S2 for full list of species that were aggregated to genus level). All taxa recorded at a resolution coarser than the trait database (e.g. family level) were excluded (early Limnephilidae instars, Gerridae, Simuliidae, Empididae and Colemoblla) as highly variable genus- and species-specific trait variations are likely to be overlooked (Jones, 2008). A total of 18 taxa were assigned functional traits.

2.4 Statistical analysis

All statistical analyses were undertaken in the R environment (R Development Core Team, 2019). Prior to alpha and beta diversity analyses the species-abundance macroinvertebrate data were converted to a presence–absence matrix.

2.4.1 Alpha diversity

Taxonomic alpha diversity was calculated as the number of taxa (taxonomic richness) in each pond. Mean pairwise distance (MPD) was selected as the functional alpha diversity index (Heino & Tolonen, 2017a). To calculate functional alpha diversity, Gower dissimilarity was calculated using the function gowdis from the FD package (Laliberte, Legendre & Shipley, 2014) on the original trait data to determine trait distances between taxa. Mean pairwise distance (MPD) indices were then calculated.
using the taxonomic presence–absence dataset and the Gower dissimilarity of the trait dataset using
the function `ses.mpd` in the picante package (Kembel et al., 2020). The `ses.mpd` function can use any
species-by-species distance matrix (e.g. Gower dissimilarity) as input in addition to a site-by-species
matrix (Heino & Tolonen, 2017a; Hill et al., 2019).

The response of taxonomic and functional alpha diversity (dependent variables) in relation to the
individual effect of each local environmental (area, altitude, depth, dissolved oxygen, pH,
conductivity and, temperature) and spatial (pond connectivity, hydrological connectivity, dbMEM1,
dbMEM2 and, dbMEM3) variable (independent variables) were explored via separate sets of
statistical models, each testing a unique dependent–independent pairwise combination (n = 24; 12
independent x 2 dependent variables) to ensure that models were not overfitted (White et al., 2017).
Each of these statistical sets contained four traditional regression models within which the
independent variable was modelled via linear, quadratic, exponential and logarithmic statistical
functions, with the optimal statistical function for each environmental variable in each statistical set
being derived from the model showing the lowest AIC (Fornaroli et al., 2019). Subsequently, pairwise
regression analyses were fitted for all explanatory (dependent) and response (independent) variables
in their optimal (linear, quadratic, exponential or logarithmic) structure (n = 24). The amount of
statistical variation explained ($r^2$) and significance of the optimal model within each statistical set was
determined. The $\alpha$ significance level was adjusted to reduce the likelihood of Type I errors by
multiplying the degrees of freedom of statistical models by 0.05 and then dividing by the total number
of tests (an alternative adjustment to the Bonferroni correction - see Dolédec et al., 2006).
Correlograms were constructed to examine the spatial autocorrelation of community structure in the
ponds. These correlograms were based on Moran I statistics of taxonomic and functional
macrornvertebrate distance matrices (Euclidean) in relation to the geographical distance using the
`correlag` function in the pgirmess package (Giraudoux et al., 2018).
2.4.2 Beta diversity

For functional beta diversity analyses, the dimensionality of the original trait data was reduced first by calculating trait distances between taxa using the Gower distance (Gower, 1971; using the function gowdis), and second by undertaking a Principal Coordinates Analysis (PCoA) on the trait Gower dissimilarity matrix (using the function pcoa in the ape function; Paradis et al., 2020). Only the first two PCoA vectors were used to calculate convex hull volumes shaping any two communities in functional space as further dimensions caused overly long computational times (Heino & Tolonen, 2017b). Total taxonomic and functional beta diversity (based on Sørensen dissimilarity) were partitioned into taxonomic turnover and nestedness components using the function beta.multi for the taxonomic dataset and the function functional.beta.multi for the functional dataset from the package betapart (Baselga et al., 2020). Total functional beta diversity, functional turnover and functional nestedness-resultant pairwise distance matrices were calculated (using a site-by-species matrix and quantitative trait data; the two PCoA trait vectors) using the function functional.beta.pair in the betapart package (based on Sørensen dissimilarity; Baselga et al., 2020). For taxonomic beta diversity analyses, three pairwise distance matrices accounting for total beta diversity, turnover, and nestedness-resultant components, were calculated using the beta.pair function in the betapart package (based on Sørensen dissimilarity). PCoA analyses were undertaken on the derived taxonomic and functional dissimilarity matrices (total beta diversity, turnover and nestedness-resultant) using the pcoa function with a Lingoes correction to account for negative eigenvalues (Legendre, 2014). The derived principal coordinates (eigenvectors) outlined above were used as six response variables (total beta diversity, turnover and nestedness-resultant for both functional and taxonomic communities) in separate RDA and variance partitioning analyses.

RDA analyses using a forward selection process (using the function ordiR2step in the vegan package; Oksanen et al., 2020) were performed on the environmental data in association with one of the six dissimilarity matrices to identify significant spatial and local environmental parameters for each of the dissimilarity matrices. Variables from only one predictor group (local environmental conditions,
dbMEM eigenvectors, or hydrological proximity effects) were significant in individual RDA models, so variance partitioning analysis was not considered further, and results are based on the RDA analyses. For each of the six RDA models constructed the significance of the whole model was examined using the `aov` function.

3. RESULTS

3.1 Description of faunal community

Forty macroinvertebrate taxa were recorded from the 17 high-altitude ponds. Taxonomic richness within the ponds varied between five and 17 taxa (mean ± SE taxon richness: 8 ±0.94). The most commonly occurring taxa were generalists that are often recorded from pond habitats: *Limnephilus coenosus* (Order: Trichoptera, recorded from 13 ponds), *Paratanytarsus austriacus* (Order: Diptera, 11 ponds), Oligochaeta (nine ponds) and *Hydroporus memnonius* (Order: Coleoptera: nine ponds), and one cold stenothermal species *Hydroporus foveolatus* (Order: Coleoptera, 10 ponds; see Table S1 for a full list of macroinvertebrate taxa recorded from the study ponds). Other cold stenothermal species recorded in this study included *Agabus lapponicus* (Order: Coleoptera), *Helophorus glacialis* (Order: Coleoptera), *Arctocorisa carinata* (Order: Hemiptera) (Wissinger, Oertli, & Rosset, 2016).

Several species of Chironomidae recorded in this study were cold adapted including two species from the genus *Pseudodamesa* (Lodz-Crozet, Oertli & Robinson, 2012).

3.2 Alpha diversity

There was limited variation in the altitude of the ponds (range 146m) and relatively similar local environmental conditions were recorded among the ponds, although surface area and temperature demonstrated greater variability (Table 2). Variation in the degree of connectivity among the ponds studied was observed and three Moran eigenvector maps were constructed. Preliminary analysis indicated that: (i) there was no significant correlation between taxonomic and functional alpha diversity (Pearson correlation: $r = 0.02, P=0.9$); (ii) dissimilarity in taxonomic and functional communities (based on Sørensen dissimilarity) was significantly correlated (Mantel test: $r=0.56$, $P<0.05$).
Pond connectivity was significantly positively associated with taxonomic alpha diversity, explaining 19% of the variation (adj. $R^2=0.19$, $F=4.83$, $P<0.05$; Table 3). No local environmental variables were identified as being significantly associated with taxonomic alpha diversity. Pond permanence (adj. $R^2=0.30$, $F=8.01$, $P=0.01$) and surface area (adj. $R^2=0.47$, $F=15.19$, $P<0.01$; Table 3) were significantly associated with functional alpha diversity, explaining 31% and 51% of variation in functional alpha diversity respectively. No spatial variables were significantly associated with functional alpha diversity.

3.3 Beta diversity

Aquatic macroinvertebrate communities demonstrated high levels of taxonomic (Sørenson’s dissimilarity: 0.882) and functional beta diversity (Sørensen’s: 0.779). Compositional variation in taxonomic beta diversity could be explained almost entirely by turnover (94%) rather than the nestedness component of beta diversity (4%). In total, 24 of the 40 macroinvertebrate taxa sampled were recorded from either one or two ponds (Table S1), with only three taxa being recorded from 10 or more ($L. coenosus$, $H. foveolatus$, $P. austriacus$). However, the opposite pattern was observed among functional beta diversity with nestedness (59%) contributing more than turnover (41%) to total functional beta diversity. Here 10 of the 63 biological traits studied were recorded in fewer than 10 ponds with five of these being completely absent from the Macun cirque assemblage (body size: $>8cm$, resistance form: housing against desiccation, respiration method: hydrostatic vesicle, locomotion: permanently attached, feeding group: absorber; Table S5). Five traits were dominant,
occurring in 50% of the entire pond network (life cycle duration: <1 year, voltinism: 1, reproduction: clutches cemented, resistance form: none, respiration method: tegument; Table S5).

When the relationships with spatial and environmental variables were examined, three local environmental variables (temperature, water depth and conductivity) were shown to be significantly associated with patterns in total taxonomic beta diversity (Table 4: Figure 4a). In total, 27% of variation in total taxonomic beta diversity was significantly explained by the final RDA model (adj. $R^2=0.27$, $F=2.99$, $P<0.01$). dbMEMs or hydrological proximity effects did not significantly influence total taxonomic beta diversity. For taxonomic turnover, 30% of the variation was significantly explained by the final RDA model (adj. $R^2=0.30$, $F=3.31$, $P<0.01$) which was associated with three local environmental variables (temperature, water depth and conductivity: Table 4; Figure 4b). None of the local environmental variables, hydrological proximity effects or spatial eigenvectors dbMEM significantly influenced patterns of taxonomic nestedness.

For functional communities, three significant local environmental variables (permanence, water depth and temperature) were shown to influence the variation in total functional beta diversity, which explained 54% of the variation in the RDA model (adj. $R^2=0.54$, $F=7.14$, $P<0.01$; Table 4; Figure 4c). No hydrological proximity effects or spatial eigenvectors significantly influenced patterns of functional total beta diversity. Functional turnover was significantly influenced by two local environmental variables (depth and permanence) with the final RDA model explaining 26% of the variation (adj. $R^2=0.26$, $F=3.77$, $P<0.01$; Figure 4d). One local environmental variable (permanence) significantly influenced patterns in functional nestedness with the final RDA model significantly explaining 24% of the variation (adj. $R^2=0.24$, $F=6.03$, $P<0.05$; Table 4; Figure 4e). No hydrological proximity effects or spatial eigenvectors (dbMEMs) significantly influenced the variation in functional turnover or nestedness.
4. DISCUSSION

Different environmental and spatial variables were found to be important drivers of taxonomic and functional diversity and composition in the Macun Cirque ponds. Given the importance of different environmental and spatial variables for functional and taxonomic alpha diversity it is not surprising that these two components of diversity were not correlated in this study, in contrast to other studies (Hill et al., 2019; Heino & Tolonen, 2017a). Overall, macroinvertebrate richness in the high-altitude ponds was low when compared with richness recorded in lowland pond communities (Davies et al., 2008). The annual winter freezing of high-altitude ponds such as the Macun Cirque and high UV radiation in the summer can create extreme environmental conditions that may limit macroinvertebrate biodiversity within this pond network (Wissinger, Oertli, & Rosset, 2016).

However, Oertli et al. (2007) stated that the richness among ponds in the Macun cirque can be considered regionally high when compared with other alpine freshwater bodies and is known to support 50% of the species of Dytiscidae recorded from the Swiss Alps.

4.1 Predictors of taxonomic richness and functional diversity (alpha diversity)

The taxonomic richness of macroinvertebrates from the Macun ponds was correlated only with pond connectivity, supporting the first hypothesis of this study (see also Oertli et al., 2007; Hampel, Cocha & Vimos, 2010). The dominance of spatial processes in this study contrasts with lowland ponds and other freshwater systems where taxonomic richness has been found to be predominantly driven by local environmental variables (Hill et al., 2019). The importance of the spatial arrangement of the pond network for taxonomic richness suggests that spatially structured dispersal processes largely determine alpha diversity (see Cottenie et al., 2003). Source–sink dynamics, rather than dispersal limitation, may be the predominant dispersal process in this pond network, given the close proximity and high connectivity of the Macun pond network. This high connectivity provides opportunities for both active and passively dispersing taxa to migrate throughout the pond network (Heino et al., 2015; Cottenie et al., 2003). However, explaining dispersal-related processes using spatial predictors is challenging owing to the increasing importance of stochasticity on small habitats and the relatively
small number of species recorded in this study (Heino et al., 2015; Jeffries, 2005). The importance of
pond connectivity in the high-altitude ponds studied here may reflect the broadly similar local
environmental conditions recorded among the ponds. This may limit the environmental gradients that
can be tracked by species and the distinction of sites with more (or less) suitable conditions, thereby
reducing the importance of environmental conditions in determining taxonomic richness and
subsequently increasing the importance of spatial processes.

Functional alpha diversity was positively associated with pond surface area and negatively associated
with hydrological permanence, and in marked contrast to taxonomic alpha diversity was not
significantly affected by spatial factors, leading to a partial rejection of the first study hypothesis.
‘Area effects’ have been well documented to drive taxonomic richness in freshwater habitats
(MacArthur & Wilson 1967; De Marco et al., 2014), but have only recently been acknowledged as an
important determinant of functional alpha diversity (Heino, 2008; Smith et al., 2013). Larger ponds
may have more complex and heterogeneous habitat conditions compared with smaller ponds
(Lomolino, 2001), including greater substratum variability, larger chemical gradients, increased
macrophyte complexity, variable water depths and a range of food resources. The increased variability
in local habitat conditions among larger ponds provides a wider range of functional niches for
macroinvertebrates to exploit, thereby increasing functional alpha diversity (Heino, 2008). Pond
permanence has also been well documented to influence biodiversity, reflecting the extreme
conditions that can arise as a result of pond drying (Della Bella, Bazzanti & Chiarotti, 2005; Hill et
al., 2017a). This suggests that hydrological permanence drives functional alpha diversity by affecting
certain traits that reflect specific adaptations for enabling persistence in intermittent ponds (see Tachet
et al., 2010). However, the functional attributes among permanent and temporary Mediterranean
ponds were found not to be significantly different, although only a limited number of functional traits
(functional feeding groups, and locomotion and substrate relation) were considered (Bazzanti, Della
Bella & Grezzi, 2009).
4.2 Predictors of taxonomic and functional compositional variation (beta diversity)

Clear differences in the organization of taxonomic and functional facets of diversity were recorded from the ponds in the Macun Cirque. Taxonomic composition within the ponds was almost exclusively driven by species turnover (highlighted by 24 of the 40 taxa sampled in this study being recorded from either one or two ponds) suggesting a replacement of taxa from one pond to the next, reflecting findings from most lowland lentic studies (Viana et al., 2016; Hill et al., 2017b; Epele, Brand & Miserendino, 2019). Only three taxa were recorded from 10 or more of the ponds (L. coenosus, H. foveolatus, P. austriacus). However, nestedness was the most important component of functional beta diversity, indicating that sites with low functional diversity formed subsets of sites with high functional diversity (Heino & Tolonen, 2017b). In contrast to the taxonomic facet, only 10 of the 63 biological traits were recorded in fewer than 10 of the 17 ponds (five of the missing 10 traits were completely absent from the Macun cirque). This may reflect functional redundancy within high-altitude ponds with many species sharing similar functional roles, or that the species present are generalists possessing multiple traits for each grouping category. High functional redundancy has been reported to result in stable community structure and is often present in communities subject to extreme environmental conditions or disturbances (Biggs et al., 2020). Given the harsh environmental conditions present in the Macun Cirque associated with the large temperature range from -15°C in winter to >20°C in summer and extended ice cover for about 9 months each year, functional redundancy is probably vital to enable communities to persist.

Total taxonomic and functional beta diversity were primarily determined by local environmental variables leading us to reject the second hypothesis of this study. These results suggest that taxonomic and functional composition in the ponds were determined at a local scale (Cottonie et al., 2003; Hill et al., 2019). The negligible effect of spatial processes probably reflects the small geographical area studied (Heino & Tolonen, 2017b). High species turnover and the dominance of local environmental variables determining taxonomic composition, even in an environmentally similar pond network, may reflect the tracking of weak environmental gradients (niche mechanisms) by macroinvertebrates. This
indicates that more environmentally distinct sites supported different species compositions. However, the highly nested pattern and dominance of local environmental variables in determining functional composition in this study may reflect the high spatial connectivity among ponds, facilitating increased dispersal overriding niche processes, enabling macroinvertebrates to colonize less suitable functional niches and thereby increasing functional nestedness. Depth and water temperature were identified as key environmental variables determining taxonomic and functional composition in the high-altitude ponds. Ponds with variable depths are less likely to dry during summer months and more likely to support heterogeneous habitat conditions (Heino et al., 2017). This in turn enhances habitat suitability for a wider range of species and functional traits. In addition, macroinvertebrate species are reliant on optimum temperatures to survive (Lancaster & Downes, 2013), and in high-altitude pond sites there may be large variability in pond temperatures, as recorded in this study. A number of taxa that are cold stenothermal or cold adapted were recorded including *Hydroporus foveolatus*, *Helophorus glacialis* and two representatives of *Pseudodiamesa*. The differences in water temperature observed in this study may have been driven by differences in the water source, with the north basin fed predominantly by snowmelt and the south basin fed by glacial meltwater from surrounding rock glaciers (Robinson & Oertli, 2009), and associated with their aspect (as illustrated by the separation of northern and southern pond sites along a temperature gradient). In addition, warmer water temperatures are likely to increase macroinvertebrate predator activity (Yee & Kehl, 2015), further influencing taxonomic and functional composition.

Local environmental variables were found to be the primary determinants of patterns of taxonomic and functional turnover and nestedness, similar to patterns reported for lowland lentic systems (Heino & Tolonen, 2017b; Hill et al., 2019). Taxonomic turnover was influenced by temperature, depth and conductivity, whereas patterns in functional turnover and nestedness were influenced by permanence and depth. Conductivity values were very low in some of the ponds (minimum value of 1.7 $\mu$S cm$^{-1}$), and may have contributed to the turnover of species by filtering those taxa that are unable to survive at low conductivities. Taxa from the orders Diptera and Trichoptera were largely absent from ponds.
with the lowest conductivities. As with temperature, there was a north–south divide in conductivity values with higher conductivity typically recorded from ponds located in the southern part of the Macun Cirque, and lower conductivity from ponds in the northern area. These differences most likely reflect the source of water and indicate that the water source may be a large-scale driver of compositional variation in this pond network. Pond permanence may also influence functional turnover and nestedness by selecting traits that reflect adaptations (such as dormancy or diapause, which was the dominant resistance trait recorded from one temporary pond in this study) that enable persistence in intermittent pond habitats. Even a limited variability in water depth may provide more functional niches for taxa to use as illustrated by the separation of the deepest sites in the RDA models (ponds 9 and 10; Heino et al., 2017). However, given the limited explanatory power of the RDA models, the weak environmental and spatial gradients, and that none of the environmental or spatial variables recorded were found to influence patterns of taxonomic nestedness, there are likely to be other unmeasured environmental variables (e.g. presence and density of fish and nutrient concentration; Knapp, Matthews & Sarnelle, 2001) that are important drivers of taxonomic and functional composition.

4.3 Implications for conservation

The results of this study have shown that alpine ponds have high conservation value. They make an important contribution to biodiversity, supporting not only a wide range of aquatic macroinvertebrates but also several cold stenothermal species that are recorded only within cold climatic areas, a finding that has been recorded for ponds in other mountain regions (Martinez-Sanz et al., 2012). Examining both the functional and taxonomic facets of alpha and beta diversity can provide important information to advance fundamental understanding of the spatial patterns and the mechanisms driving macroinvertebrate communities in high-altitude pond networks, thereby enabling the development of more effective conservation and management strategies.
Spatial processes were important for taxonomic richness, while local environmental variables (despite the relatively limited environmental gradients) were important drivers of functional diversity, and functional and taxonomic beta diversity, indicating that community composition is determined at a local scale. These results suggest that taxonomic and functional facets of alpha diversity cannot provide surrogates of one another, but that conservation of pond macroinvertebrates requires a multi-faceted approach (Hill et al., 2019). Given the importance of both spatial and environmental variables in driving of taxonomic and functional diversity, management activities that aim to improve or protect high-altitude freshwater biodiversity at a landscape-scale should focus on maintaining both connectivity among ponds and increased environmental heterogeneity. In this respect, the environmental variables of pond surface area, water depth, temperature and permanence regime, were found to be key drivers of taxonomic and functional diversity and compositional variation in this study and reflects findings reported in other lowland pond studies (Hassall, Hollinshead & Hull, 2011; Florencio et al., 2014). As functional and taxonomic facets of biodiversity were driven by contrasting processes, focusing only on the taxonomic facet of biodiversity and subsequently using measures to conserve this may lead to a loss of functional biodiversity. This in turn could result in a loss of ecological resilience to future disturbances, particularly climatic warming (Elser et al., 2020). Considering both functional and taxonomic facets of biodiversity when monitoring high-altitude sites will enable more effective and targeted management to increase ecological resilience to future pressures and disturbances.

Species turnover was found to be the most important component structuring taxonomic composition, whereas functional composition displayed a highly nested spatial pattern. High species replacement recorded among the taxonomic facet of diversity would suggest that conservation would be most effective at the landscape scale, protecting as many ponds in the landscape as possible (Hill et al., 2017b). In contrast, the high functional nestedness indicates that conservation should focus on protecting those sites with greatest functional diversity to ensure that the maximum possible functional diversity is maintained in the regional pool. This raises challenges for conservation.
practitioners; however, recent advances in beta diversity analyses may provide opportunities to
conserve both taxonomic richness at a landscape scale and individual sites of greatest functional
diversity. Analyses of Local Contribution to Beta Diversity (LCBD: Legendre 2014) identifies
individual ponds with the greatest taxonomic uniqueness and may enable a greater proportion of the
regional species pool to be protected (without having to protect every pond in the network) where
species turnover is the dominant pattern (Hill et al., 2021). Protecting the most taxonomically distinct
ponds (resulting from high taxonomic turnover), and those ponds with the greatest functional diversity
(reflecting high functional nestedness), will ensure that the maximum possible taxonomic and
functional diversity is protected within the Macun Cirque. Given the competing mechanisms driving
the temporal and spatial patterns of both functional and taxonomic facets of biodiversity,
understanding and monitoring both facets is vital to enable high-altitude pond networks to be
effectively managed and conserved. The results suggest that if pond monitoring and conservation
efforts were to focus on one of the biodiversity facets (taxonomic or functional), important
biodiversity losses may be overlooked or lost. As high-altitude aquatic ecosystems often harbour
deremic species, conservation efforts that protect all facets are vital in the face of climate change.

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CONFLICT OF INTEREST

MJH, KLM and PJW declare no conflict of interest.
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are both important. *Hydrobiologia*, 543(1), 207–220. https://doi.org/10.1007/s10750-004-7452-9


### Table 1 - Grouping features and biological traits used as taken from the database in Tachet et al. (2010).

<table>
<thead>
<tr>
<th>Grouping feature</th>
<th>Trait</th>
<th>Grouping feature</th>
<th>Trait</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum potential size</td>
<td>≤0.25cm</td>
<td>Locomotion and substrate relation</td>
<td>Flier</td>
</tr>
<tr>
<td></td>
<td>&gt;0.25- 0.5cm</td>
<td></td>
<td>Surface swimmer</td>
</tr>
<tr>
<td></td>
<td>&gt;0.5- 1cm</td>
<td></td>
<td>Full water swimmer</td>
</tr>
<tr>
<td></td>
<td>&gt;1- 2 cm</td>
<td></td>
<td>Crawler</td>
</tr>
<tr>
<td></td>
<td>&gt;2- 4 cm</td>
<td></td>
<td>Burrower</td>
</tr>
<tr>
<td></td>
<td>&gt;4- 8cm</td>
<td></td>
<td>Interstitial</td>
</tr>
<tr>
<td></td>
<td>&gt;8cm</td>
<td></td>
<td>Temporarily attached</td>
</tr>
<tr>
<td>Life-cycle duration</td>
<td>≤1 year</td>
<td>Food consumed</td>
<td>Microorganisms</td>
</tr>
<tr>
<td></td>
<td>&gt;1 year</td>
<td></td>
<td>Detritus &lt;1mm</td>
</tr>
<tr>
<td>Voltinism</td>
<td>&lt;1</td>
<td></td>
<td>Dead plant ≥1mm</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td></td>
<td>Living microphytes</td>
</tr>
<tr>
<td></td>
<td>&gt;1</td>
<td></td>
<td>Living macrophytes</td>
</tr>
<tr>
<td>Aquatic stages</td>
<td>Egg</td>
<td>Feeding group</td>
<td>Absorber</td>
</tr>
<tr>
<td></td>
<td>Larva</td>
<td></td>
<td>Deposit feeder</td>
</tr>
<tr>
<td></td>
<td>Nymph</td>
<td></td>
<td>Shredder</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td></td>
<td>Scraper</td>
</tr>
<tr>
<td>Reproduction</td>
<td>Ovoviviparity</td>
<td></td>
<td>Filter-feeder</td>
</tr>
<tr>
<td></td>
<td>Isolated, free eggs</td>
<td></td>
<td>Piercer</td>
</tr>
<tr>
<td></td>
<td>Isolated, cemented eggs</td>
<td></td>
<td>Predator</td>
</tr>
<tr>
<td></td>
<td>Clutches, cemented</td>
<td></td>
<td>Predatory</td>
</tr>
<tr>
<td></td>
<td>Clutches, free</td>
<td></td>
<td>Parasite</td>
</tr>
<tr>
<td></td>
<td>Clutches, in vegetation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Clutches, terrestrial</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Asexual</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dispersal</td>
<td>Aquatic passive</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Aquatic active</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Aerial passive</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Aerial active</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resistance form</td>
<td>Eggs/statoblasts</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cocoons</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Housings against desiccation</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Diapauses / dormancy</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>None</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Respiration method</td>
<td>Tegument</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gill</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Plastron</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spiracle</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hydrostatic vesicle</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2 - Summary table of environmental and taxonomic characteristics for the 17 high-altitude pond sites.

<table>
<thead>
<tr>
<th>Altitude (m.a.s.l)</th>
<th>Area (m²)</th>
<th>Depth (average cm)</th>
<th>Conductivity (µS cm⁻¹)</th>
<th>pH</th>
<th>Dissolved oxygen (%)</th>
<th>Temperature (°C)</th>
<th>Pond connectivity</th>
<th>Hydrological connectivity</th>
<th>Taxon Richness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>2663</td>
<td>1548</td>
<td>27.39</td>
<td>6.59</td>
<td>6.83</td>
<td>111</td>
<td>9.86</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>Median</td>
<td>2667</td>
<td>925</td>
<td>26</td>
<td>3.9</td>
<td>7.06</td>
<td>108</td>
<td>9</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>Std. Error</td>
<td>8.49</td>
<td>624</td>
<td>3.1</td>
<td>1.22</td>
<td>0.23</td>
<td>2</td>
<td>0.84</td>
<td>1</td>
<td>0.91</td>
</tr>
<tr>
<td>Min</td>
<td>2560</td>
<td>51</td>
<td>9.75</td>
<td>1.7</td>
<td>5.26</td>
<td>99</td>
<td>3.4</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Max</td>
<td>2706</td>
<td>11055</td>
<td>56.75</td>
<td>16.3</td>
<td>8.55</td>
<td>142</td>
<td>15.5</td>
<td>18</td>
<td>8</td>
</tr>
</tbody>
</table>
Table 3 – Significant predictors of taxonomic richness and functional alpha diversity resulting from regression analyses. The statistical function used for each significant environmental variable are presented in parenthesis.

<table>
<thead>
<tr>
<th>Variable</th>
<th>F value</th>
<th>P value</th>
<th>adjusted R²</th>
<th>Directional response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxonomic Richness</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pond connectivity</td>
<td>4.83</td>
<td>0.04</td>
<td>0.19</td>
<td>+</td>
</tr>
<tr>
<td>(Exponential)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Permanence</td>
<td>8.01</td>
<td>0.01</td>
<td>0.30</td>
<td>+</td>
</tr>
<tr>
<td>(Linear)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface area</td>
<td>15.19</td>
<td>&lt;0.01</td>
<td>0.47</td>
<td>+</td>
</tr>
<tr>
<td>(Logarithmic)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Functional Diversity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


Table 4 – Significant predictors of variation in taxonomic and functional community composition resulting from redundancy analyses.

<table>
<thead>
<tr>
<th>Variable(s)</th>
<th>F value</th>
<th>P value</th>
<th>Adj. R²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Taxonomic composition</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total beta</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>3.78</td>
<td>0.004</td>
<td>0.15</td>
</tr>
<tr>
<td>Depth</td>
<td>2.26</td>
<td>0.012</td>
<td>0.06</td>
</tr>
<tr>
<td>Conductivity</td>
<td>2.12</td>
<td>0.018</td>
<td>0.06</td>
</tr>
<tr>
<td>Turnover</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>3.69</td>
<td>0.002</td>
<td>0.16</td>
</tr>
<tr>
<td>Conductivity</td>
<td>2.51</td>
<td>0.018</td>
<td>0.08</td>
</tr>
<tr>
<td>Depth</td>
<td>0.22</td>
<td>0.044</td>
<td>0.06</td>
</tr>
<tr>
<td>Nestedness</td>
<td>None</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><strong>Functional composition</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total beta diversity</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Permanence</td>
<td>6.51</td>
<td>0.004</td>
<td>0.26</td>
</tr>
<tr>
<td>Depth</td>
<td>4.79</td>
<td>0.004</td>
<td>0.15</td>
</tr>
<tr>
<td>Temperature</td>
<td>4.88</td>
<td>0.006</td>
<td>0.13</td>
</tr>
<tr>
<td>Turnover</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth</td>
<td>3.69</td>
<td>0.002</td>
<td>0.14</td>
</tr>
<tr>
<td>Permanence</td>
<td>3.29</td>
<td>0.044</td>
<td>0.12</td>
</tr>
<tr>
<td>Nestedness</td>
<td>Permanence</td>
<td>6.03</td>
<td>0.010</td>
</tr>
</tbody>
</table>
Figure Captions

Figure 1 - Location of the 17 ponds in the Macun Cirque, Swiss National Park, Switzerland. Pond ‘P3’ was not sampled as it was dry during the field visit and not shown on the map.

Figure 2 - Photos of Macun ponds sampled in this study (photos taken July 2019).

Figure 3 - Moran’s I statistics (correlograms) for (a) taxonomic richness and (b) functional diversity among Alpine ponds in the Macun Cirque. Distance classes are in kilometres. A red circle indicates a significant value.

Figure 4 - RDA ordination of site plots for (a) taxonomic total beta diversity, (b) taxonomic turnover, (c) functional total beta diversity (d) functional turnover and (e) functional nestedness resultant of the Macun pond macroinvertebrate community. Only significant environmental parameters are presented. The taxonomic nestedness resultant-component had no significant associations with any variables and is therefore not presented.
Figure 1 - Location of the 17 ponds in the Macun Cirque, Swiss National Park, Switzerland. Pond ‘P3’ was not sampled as it was dry during the field visit and not shown on the map.

21x18mm (300 x 300 DPI)
Figure 2 - Photos of Macun ponds sampled in this study (photos taken July 2019).

194x145mm (300 x 300 DPI)
Figure 3 - Moran’s I statistics (correlograms) for (a) taxonomic richness and (b) functional diversity among Alpine ponds in the Macun Cirque. Distance classes are in kilometres. A red circle indicates a significant value.

30x54mm (300 x 300 DPI)
Figure 4 - RDA ordination of site plots for (a) taxonomic total beta-diversity, (b) taxonomic turnover, (c) functional total beta-diversity (d) functional turnover and (e) functional nestedness resultant of the Macun pond macroinvertebrate community. Only significant environmental parameters are presented. The taxonomic nestedness resultant-component had no significant associations with any variables and is therefore not presented.

30x54mm (300 x 300 DPI)