Master's Thesis

Environmental Management

Macroinvertebrate communities along an elevational gradient of 28 alpine lakes in Hohe Tauern National Park, Austria

Submitted by

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Abstract

Alpine lakes are among the most remote and extreme habitats. They support very specific compositions of aquatic organisms and have undergone little historical alteration by humans. Their specific water chemistry and environmental setting renders them susceptible to subtle changes in climate. For these reasons, they constitute ideal sentinels for climate change. High mountain lakes are known to be impacted by the effects of climate change already. Thus, it is crucial to understand the specific and regional drivers for the structure of communities inhabiting alpine lakes, e.g. those of macroinvertebrates. For this study, 28 lakes within Hohe Tauern National Park, Austria, between altitudes of 2,000 and 2,700 m a.s.l. were sampled in 2018. Quantitative sampling of littoral macroinvertebrates was accompanied by measurements of a number of environmental parameters (lake size, habitat types and their extent, pH, chlorophyll, oxygen saturation, nitrate). Our results reveal a high importance of habitat types (sedimented areas, small rocks, sheer rock faces / large boulders) and the interaction of lake size and elevation for macroinvertebrate communities. The more rocky habitats dominated the lake littoral, the lower total abundances and family richness were, while the ratio of *Ephemeroptera*, *Plecoptera* and *Trichoptera* (EPT) abundance by total abundance increased. Additionally, lake size showed a negative effect on coleopteran, chironomid, and total abundances while the EPT ratio increased. Extent of rocky habitat and the interaction of lake size and elevation were strong and displayed significant effects on community composition while elevation, lake size and dissolved oxygen only showed weakly significant effects. Structural parameters, which will not directly be influenced by climate change, were of great importance to macroinvertebrate communities in alpine lakes. However, melting glaciers will create new lakes which can be expected to quickly be colonized by insect macroinvertebrates. Insect fauna in alpine lakes will be of great importance in monitoring the impact of climate change.

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1. Introduction

Alpine lakes are extreme habitats that support very specific species compositions and are among those ecosystems impacted the least by human activities (see e.g. Catalan et al. 2006). Their specific water chemistry and environmental setting makes them susceptible to subtle changes in climate (Beniston et al. 1997; Skjelkvåle and Wright 1998; Thompson et al. 2005). Alpine lakes are thus suited to serve as sentinels for climate change (Adrian et al. 2009) and may reveal early stages of changing conditions in mountain areas. For a long time, benthic communities in alpine lakes have been neglected (Füreder et al. 2006) but recently, more studies have been conducted that deal with macroinvertebrate communities and the ecological state of alpine lakes in Europe (e.g. Bitušík et al. 2006; Čiamporová-Zaťovičová et al. 2010; Hamerlík and Bitušík 2009; Füreder et al. 2006; Marchetto et al. 2008). Climate change has already been shown to affect remote high altitude lakes (Catalan et al. 2009a), underlining the urgency of this matter.

Altitude is a multi-faceted ecological factor that is closely related to other environmental variables and often, these parameters are hard to disentangle (Mendoza and Catalan 2010). With increasing altitude, environmental parameters are changing. Mean annual air temperatures as well as annual minimum temperatures are lower in higher elevations, resulting in a decrease of ice-free days. Due to this circumstance, elevation can be considered a proxy of ice cover duration (Catalan et al. 2009b). The thermocline in alpine lakes is more shallow due to relatively cold epilimnic water temperatures (Luoto and Nevalainen 2013). Dissolved oxygen is known to be of importance to macroinvertebrates (see e.g. Covich and Thorp 2010), even in high-altitude aquatic systems that are thought to be oxygen saturated (Jacobsen et al. 2003). Oxygen is especially interesting against the background of climate change, as rising temperatures are expected to result in changing oxygen availability and, as a consequence, in an alternation of macroinvertebrate assemblages (Luoto and Nevalainen 2013). Being set in remote environments with short vegetation periods, productivity in and around alpine lakes is naturally low. This leads to oligotrophic or ultraoligotrophic lake conditions, unless there is a considerable amount of land use or tourism within the catchment.

Chlorophyll and nitrate are accordingly low in high-alpine lakes. PH values can be low due to atmospheric acidification. Most lakes however, are set in calcareous catchments which buffers acid deposition (Füreder et al. 2006).

As environmental parameters change with the altitudinal gradient, so do macroinvertebrate communities of lakes along this gradient. Macroinvertebrate communities in high-altitude lakes are dominated by insects; especially abundant are Chironomidae (Čiamporová-Zaťovičová et al. 2010; Mendoza and Catalan 2010; Füreder et al. 2006). While Mendoza and Catalan (2010) have found a high abundance of oligochaetes in the Pyreneans, Füreder et al. (2006) also highlight the presence of typical cold-stenothermal insect species (species adapted to cold temperatures) of *Ephemeroptera* (mayflies), *Plecoptera* (stoneflies) and *Trichoptera* (caddisflies), also referred to as EPT-species. It is the cold-stenothermic species (especially *Chironomidae* and *Trichoptera*) in high-altitude lakes that play an important role in monitoring climate change (Čiamporová-Zaťovičová et al. 2010). Lake size (either expressed as lake area or depth), tropho-dynamic state, acid-base-balance (represented by pH) , ice-cover duration, organic matter and fine substrate presence have been found to be among the most influential environmental parameters on macroinvertebrate community composition and distribution in high altitude lakes (Catalan et al. 2009b; Mendoza and Catalan 2010). Marchetto et al. (2008) single out two environmental parameters (geology and lake shape) as most influencing concerning the composition of biotic communities. Macroinvertebrate taxa along the elevational gradient rather respond in incidence rather than abundance, meaning that with increasing elevation, the number of taxa decreases while abundances show little response (Mendoza and Catalan 2010). However, the response of macroinvertebrates to altitude is not the same across groups. Diving beetles in mountain lakes are mainly predacious and decrease in species richness with increasing elevation due to harsh environmental conditions and lack of food (Čiamporová-Zaovičová and Čiampor 2011). Gathering chironomids dominate in high mountain lakes (Hamerlík and Bitušík 2009), with chironomid species preferences differing between rocky and sandy littorals (Catalan et al. 2009b; Rieradevall et al. 1999; Reuss et al. 2014). Plecopterans are sensitive to water pollution and need water bodies with high oxygen levels to survive. *Planariidae* (planarians), *Halacaridae* (water mites), *Perlodidae* (stoneflies) and *Diamesinae* (non-biting midges, a subfamily of chironomids) have been found to be positively related to altitude (Mendoza and Catalan 2010). Čiamporová-Zaťovičová et al. (2010) observed that non-insect macroinvertebrate fauna did not seem to be affected in species richness by increasing elevation. A pattern that has become obvious in studies that deal with the elevational gradient of macroinvertebrate communities, is the change of species compositions and abundances. Major changes in community composition have been found between elevations below the tree line and higher altitudes (Heegaard et al. (2006) as well as decreasing taxa diversity with increasing altitude (Čiamporová-Zaťovičová et al. 2010). In contrast, richness may also be highest in intermediate elevations (Füreder et al. 2006). There is indication for an ecological threshold between 2,500 and 2,600 m a.s.l., above which abundances and richness strongly decrease (Füreder et al. 2006; Mendoza and Catalan 2010). Čiamporová-Zaťovičová et al. (2010) however, found the highest abundance at an altitude of around 1,900 m with decreasing numbers in two lakes above and below this elevation. However, the response of biota and the specific combination of environmental conditions differ greatly on a regional level (Catalan et al. 2009a). Many studies have not assessed the entire elevational gradient, making general implications hard to single out. It is also important to recognize the regionality of macroinvertebrate communities and their response to changing environmental parameters with increasing elevation. Many of the previous results may thus be context dependent, highlighting the need for additional data.

In this study, we hypothesize that community composition of lake macroinvertebrates changes along the elevational gradient. Overall macroinvertebrate diversity and abundances are expected to decrease with increasing elevation, especially marked by the expectedly largest groups *Chironomidae* and *Oligochaeta*. Presence of larger predators, such as diving beetles, is expected to decrease with increasing elevation. EPT occurrence on the other hand is expected to increase with higher altitudes, especially in comparison with other groups. We further hypothesize that increasing habitat diversity has a positive effect on overall taxa richness. Our main goal is finding patterns in changing macroinvertebrate communities of alpine lakes along the elevational gradient within Hohe Tauern National Park.

2. Material and Methods

2.1. Study sites

Hohe Tauern National Park (47°04'19.2"N; 12°39'53.7"E), the research area of this study, is one of the largest protected areas in central Europe and extends over 1,856 ha. There are more than 500 mountain lakes (between 35 and 270,000 sqm) within the National Park (Nationalpark Hohe Tauern, 2019). Twenty-eight lakes between altitudes of 2,000 and 2,700 m were sampled from beginning of July to beginning of August 2018 (see Fig. 1 and Tab. S 1). Lakes are located in different areas of the National Park or at the National Park border to include a wide range of conditions. Lakes were ice-free at the time of sampling.

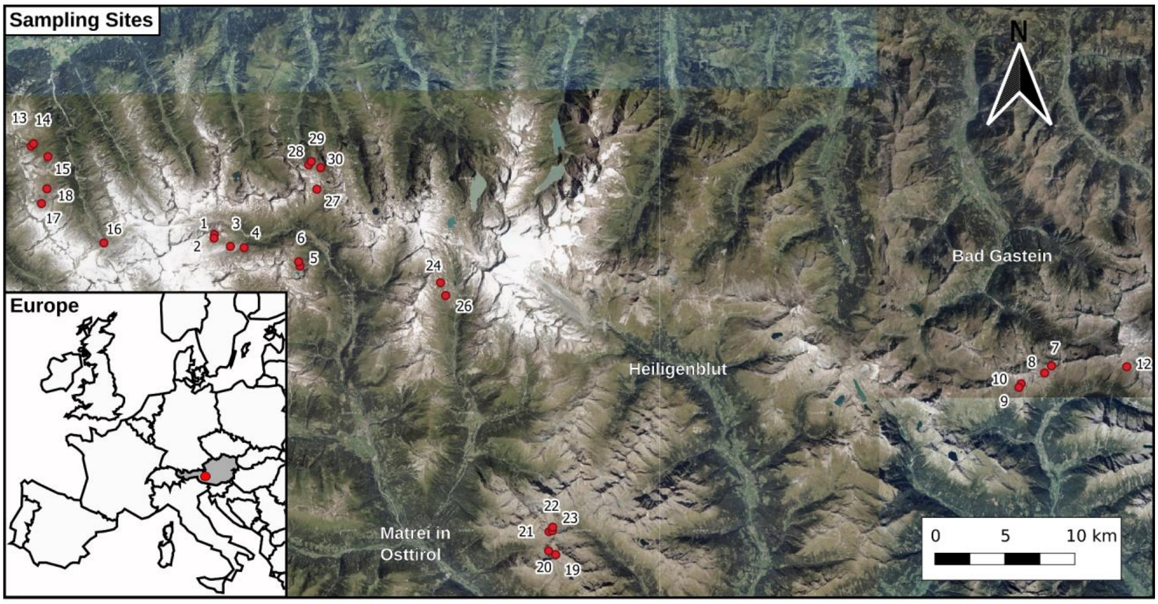

Fig. 1: Studied lakes in Hohe Tauern National Park. Sampled lakes are marked with red dots, the map of Europe gives the location of Austria (grey area) and Hohe Tauern National Park (red dot). Lakes in quotation marks did not have official names and were named by the sampling team. 1 – "Innergeschlöss 2", 2 – "Innergeschlöss 3", 3 – "Gletscherplateau", 4 – Salzbodensee, 5 – "See nahe Löbbensee", 6 – Löbbensee, 7 – Kleiner Tauernsee, 8 – Grüneckersee, 9 – "Schneefeldsee", 10 – "Plattensee", 12 – "Großes Elend", 13 – "See neben Seebachsee", 14 – Seebachsee, 15 – Foisskarsee, 16 – Sulzsee, 17 – "Obervorderjaidbachsee", 18 – "Untervorderjaidbachsee", 19 – Barrenlesee, 20 – "Kleiner Barrenlesee", 21 – Gartlesee, 22 – "Leibnitzkopfpfütze", 23 – "Debantsee", 24 – Schwarzseele, 26 – "Murmelblubber", 27 – "Elisabethsee", 28 – Plattachsee, 29 – "Kleiner Plattachsee", 30 – Langsee. (©Basemap.at, altered)

2.2. Sampling of macroinvertebrates

Macroinvertebrate samples were collected from the littoral of the lakes. Brauns et al. (2016) developed guidelines for standardized sampling of macroinvertebrates in lakes. For each lake, habitat types were assessed and classified into, sediment, small rocks (up to 20 cm x 15 cm x 5 cm), and large boulders/sheer rock faces. The extent of these three habitat types in the littoral was then estimated.

A total area of one square meter was sampled for each lake. A hand net with a sharp frame (25 cm in width) and 500 µm mesh-size was used for sampling. Mixed samples were taken, covering each habitat type proportional to its extent in the lake. For habitats covering 1-10 % of the lake, a standardized area of 0.1 sqm was sampled. In sediment, the first 2-5 cm were scooped into the net by swiping it swiftly through the ground. When sampling large boulders or rock faces, a metal spatula was used to scrape off the macroinvertebrates and collect them in the net. Macroinvertebrates were brushed off small rocks using a toothbrush over water-filled trays. Their dimensions were measured and total surface area was calculated, assuming a suitable geometric form (ellipsoid or cuboid).

Samples were presorted in the field and preserved in 4 % formalin to be taken to the laboratory. After 3-4 weeks, all samples were rinsed in tap water and transferred to 70 % ethanol for further storage. Determination was performed using a stereomicroscope (OLYMPUS SZX16) to the lowest taxon possible, with the assistance of different determination keys (Bährmann and Müller 2011; Glöer 2017; Lubini et al. 2012; Schaefer 2018; Waringer and Graf 2004; Sundermann et al. 2007; Jansson 1969; Jäch 2006).

2.3. Measurement of environmental parameters

Lake size was determined by aerial photograph in Google Earth Pro (2018) . Environmental water parameters were measured with a multi-parameter probe (EXO2 YSI): water temperature (°C), pressure (mm Hg), dissolved oxygen (% saturation), conductivity (µS/cm), pH, nitrate (mg/l), turbidity (FNU), blue-green algae pycocyanin (µg/l), chlorophyll (µg/l) and maximum depth (m). Measurements for lakes 1-18 were taken from a boat at the deepest point of the lake. The probe measured every

10 seconds while being lowered into the water. Sampling in lakes 19-28 was done without a boat. In these cases, the probe was held into the water either from a rock or by wading into the lake. No data for maximum depth was gathered for lakes 19-28. For further analysis, probe data from the surface to 1.2 m depth was averaged. This depth was chosen according to recommendations for maximum sampling depth of macroinvertebrates in lakes by Brauns et al. (2016). Two data loggers were planted in lakes 1-18 respectively in the previous year and were recovered in 2018. Data loggers measured water temperature at about half a meter depth in six-hour intervals. Data from loggers in lakes 2, 4 and 16 were not available due to missing or defect loggers. Ice-free days were deduced from available logger data, assuming an ice-cover at water temperatures below 2 °C. Zooplankton data from the first 18 lakes was additionally gained by samples taken during field work. Zooplankton samples were analyzed by Dr. Steven Wickham from Salzburg University and kindly provided for testing in this study.

2.4. Statistical Analysis

Plecoptera (stoneflies), *Tricladida* (flatworms) and adult *Coleoptera* (beetles) could be determined to species level (Tab. S 2). *Hemiptera* (true bugs), *Veneroida* (molluscs) and larval *Coleoptera* were determined to genus level. Identification of other groups was restricted by difficulties due to early larval stages or complex taxa. Consequently, *Diptera* (true flies), *Trichoptera* (caddisflies) and *Trombidiformes* (mites) were determined to family and *Oligochaeta* (worms) as well as the individual of *Hirundinea* (leeches) were determined to subclass level. Since most groups could not be identified to species level, statistical analysis was done at family level for the majority of macroinvertebrates. Abundance data from these groups will be called “total abundances” in the following. Community analysis did not include *Oligochaeta* and *Hirudinea* to maintain comparability by only analyzing groups determined to the same level. Family richness and Shannon Index were calculated for groups determined at least to family level. Habitat diversity was calculated with the Shannon Index for the habitat types, using their relative extent per lake. All explanatory variables were tested for colinearity with Pearson’s product-moment correlation test (see Tab. S 3). Variables that showed colinearity were selected for regression analysis according to their ecological importance. Hence, pressure, conductivity, temperature, turbidity, cyanobacteria, latitude and longitude were omitted from further analysis. Maximum depth, zooplankton richness, Shannon index of zooplankton and number of ice-free days were only available for 18 lakes or less and never showed significances when tried in modelling. Consequently, elevation, lake size, the extent of rocky habitats (small rocks and sheer rock faces combined), dissolved oxygen, nitrate, chlorophyll, pH and habitat diversity as well as the interaction of elevation and lake size were fitted as explanatory variables in the models.

Probe measurements at lake 22 ("Leibnitzkopfpfütze") were deficient which led to their exclusion in the regression models. Separate analyses were done additionally for abundances of *Coleoptera*, *Trichoptera*, *Chironomidae* and *Oligochaeta* because abundance and presence at sampling sites was high enough to allow for separate analyses of these groups. Abundance, family richness, Shannon index as well as separate analyses of *Chironomidae* and *Limnephilidae* were done using a generalized linear model with quasipoisson error distribution and a log link. For oligochaetes, a generalized linear model with quasipoisson distribution and a log link was used after removing a single outlier with an exceptionally large number of individuals (2,238 individuals in lake 3). Due to low overall abundances, *Coleoptera* data was transformed into presence-absence data and then analyzed using a generalized linear model with binomial distribution and a logit link.

The effect of the environmental variables on community composition was investigated calculating Bray-Curtis dissimilarities of abundance data. A permanova (function Adonis in the R package vegan) was applied with 9999 permutations. Non-metric multidimensional scaling (NMDS) was used to illustrate the differences in community structure graphically.

All data was analyzed using R, Version 3.4.2 (R Core Team 2017) and the package "vegan" (Oksanen et al. 2018). Graphs were done with "ggplot2", "colortools" and "faraway" packages (Wickham 2016; Sanchez 2013; Faraway 2016).

3. Results

3.1. Lake characterization and physio-chemical parameters

Lake sizes varied strongly with the majority of lakes smaller than three hectares (mean = 1.65 ha, SE = 0.57). The three largest lakes span from 4.86 ha to 12.82 ha. Proportion and presence of lake substrate types (sediment, small rocks and large rock faces) differed among lakes (see Tab. S 4). Lakes held between 10 and 100 % rocky habitats (sum of small rocks and sheer rock faces), with a mean of 66.15 % (SE = 6.11).

In situ measurement of lake water temperature with the probe revealed temperatures between 2.4 and 18.0 °C, with a mean of 10.8 °C (SE = 0.77). Data logger showed high temperature amplitudes throughout the year. Temperatures in "Gletscherplateausee" for example, jumped from 0 to 22 °C within a month. In general, thawing and warming of lakes after the long ice-covered period was a quick event. Most lakes showed summer maxima between 15 and 20 °C. Number of ice-free days from June 2017 to June 2018 were between 55 and 157 (mean = 105.5, SE = 8.43). Probe measurements showed dissolved oxygen contents to be high, with a mean of 78.4 % (SE = 0.88), a minimum of 68.8 % and a maximum of 88.9 %. PH values varied between 8.0 and 10.9 (mean = 9.2, SE = 0.14) and nitrate had a mean of 0.6 mg/L (SE = 0.11), peaking at 1.9 mg/L. Chlorophyll values were generally low with a mean of 1.2 µg/L (SE = 0.36) and a minimum of 0.3 µg/L. Lake #3 (Gletscherplateausee) clearly stood out with a value of 10.3 µg/L.

Chlorophyll showed a very high significance for oligochaete abundance in the GLM, which was suspected to be due to exceptionally high chlorophyll values in lake #3. The model was run additionally without the outlier to ensure validity. Results changed in the way that chlorophyll was not significant anymore for oligochaete abundance. Due to the high impact, this single lake had on our results, lake #3 was omitted from regression modelling for oligochaete abundance.

3.2. Community Composition

A total of 17,978 macroinvertebrates were collected. No taxon occurred in all 28 lakes. Chironomids were the most common and the most abundant taxa, followed by oligochaetes (see Fig. S 5 & Fig. S 6). *Pisidium* sp. (pea clams) only occurred in two lakes in large numbers and were absent from the other lakes.

Tab. 1 and Fig. S 7 illustrate results of generalized linear modelling for total macroinvertebrate abundances. Lake size had a negative effect on total abundance. Abundance is generally lower in lakes with a higher percentage of rocky habitats (compared with sediment) (Fig. S 6). Contrarily, dissolved oxygen had a significant positive relationship with total macroinvertebrate abundance. The interaction between elevation and lake size had a very significant impact on abundance such that lake size had a positive effect on abundance at increasing elevations in small (< 0.15 ha) and medium sized lakes (0.15 – 1 ha), while abundance in large lakes was generally lower and slightly decreased with increasing elevation (Fig. S 7d). The share of rocky habitats in the littoral has a negative influence on family richness (Tab. 1, Fig. S 8). None of the variables significantly affected Shannon diversity at family level (Tab. S 9). The ratio of EPT abundances by total abundance is significantly influenced by lake size (positive effect, Tab. 1 & Fig. S 10a) and shows a highly significant relationship with the share of rocky habitats (positive effect, Tab. 1 & Fig. S 10b). The interaction of lake size and elevation has a significant effect on the EPT ratio (Tab. 1). The model was additionally tested with absolute abundances of EPT-taxa instead of the ratio, but only the share of rocky habitats showed a tendency for a positive relationship in this case (df = 1, 17, F = 3.12, P = 0.095, data not shown).

Tab. 1: Results of generalized linear modelling (GLM) , applying quasipoisson distribution and a log link for total abundance, family richness and the ratio of Ephemeroptera, Plecoptera, Trichoptera (EPT) abundance by total abundance of macroinvertebrates in alpine lakes of Hohe Tauern National Park (Austria). Each variable used up 1 df, significant values are printed in bold. Residual degrees of freedom: 26

	Total Abundance		Family Richness		EPT/Total Abundance	
	F	P	F	P	F	P
Elevation	0.59	0.45	1.53	0.233	0.004	0.950
Lake Size	6.92	**0.018**	0.22	0.643	7.16	**0.016**
Rocky Habitats	15.34	**0.001**	8.68	**0.009**	29.35	**<0.001**
Habitat Diversity	1.45	0.245	4.35	0.052	0.03	0.861
Dissolved Oxygen	5.23	**0.035**	1.82	0.195	0.21	0.649
Nitrate	2.87	0.109	0.001	0.969	4.13	0.058
Chlorophyll	0.80	0.385	1.53	0.232	0.64	0.434
pH	2.14	0.162	0.16	0.695	0.44	0.518
Elevation:Lake Size	8.54	**0.010**	0.63	0.444	5.25	**0.0350**

The percentage of rocky habitats and the interaction between elevation and lake size showed very significant effects on community composition (Tab. 2, Fig. 2). Furthermore, elevation, area, nitrate and dissolved oxygen significantly influenced macroinvertebrate community composition in the studied lakes (Tab. 2).

Tab. 2: Results of permanova, applying Bray-Curtis dissimilarities and running 9999 permutations to investigate the effect of environmental variables on macroinvertebrate community composition in alpine lakes of Hohe Tauern National Park (Austria). Significant values are printed in bold.

	Community Comparisons	
	R2	P
Elevation	0.0714	**0.0475**
Lake Size	0.0677	**0.0402**
Rocky Habitats	0.1496	**0.0015**
Habi. Div.	0.013	0.7513
Dis. Oxygen	0.0671	**0.0494**
Nitrate	0.0395	0.1856
Chlorophyll	0.0234	0.4798
pH	0.0138	0.7075
Elevation:Lake Size	0.1142	**0.0052**

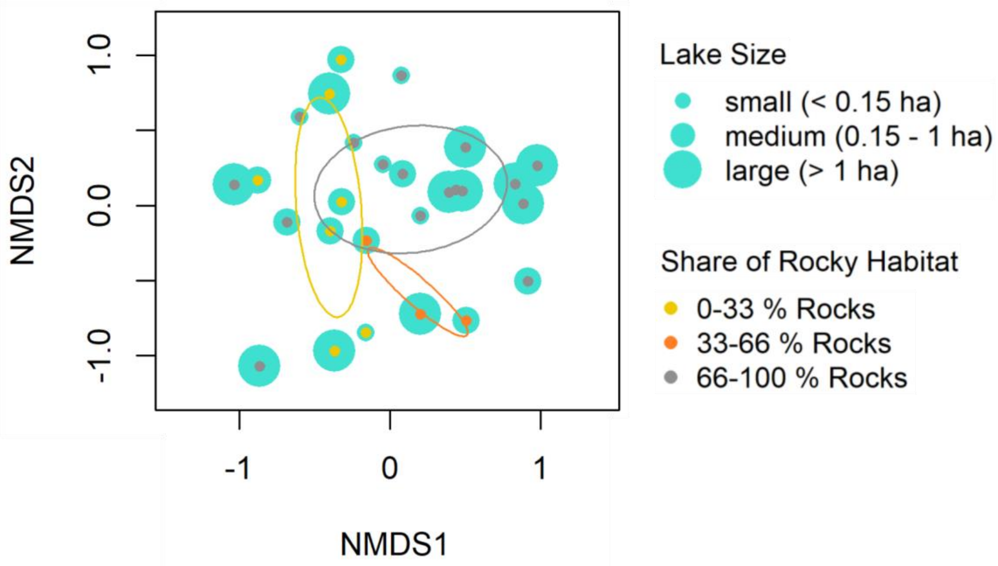

Fig. 2: Non-metric multidimensional scaling (NMDS), illustrating similarity in macroinvertebrate community composition of alpine lakes, lake sizes (different sizes of dots) as well as share of rocky habitats (different colors). Yellow, orange and grey circles display location of centroids for their respective class in rocky habitats.

3.3. Specific Groups

Groups with high abundances and a high presence in sampling sites were further investigated separately.

Chironomidae, the group with the highest abundance across the study, was present in 25 of the 28 lakes. The percentage of rocky habitats in the littoral had a negative effect on chironomid abundance (Tab. 3, Fig. S 11b). The interaction of elevation and lake size had a highly significant effect on chironomids as well (Tab. 3). Lake Size and nitrate negatively influenced chironomid abundance (Tab. 3, Fig. S 11a).

All ***Trichoptera*** in our samples belonged to the family *Limnephilidae*. They were the third most common group encountered in sampled lakes: 486 individuals were found at 21 sampling sites. Only few individuals had already reached final larval stages – most were still too young to be determined to lower taxa. In six lakes, trichopteran cases were discovered but no larvae were found. None of the tested variables showed a significant effect on trichopteran abundance (Tab. S 12).

Two ***Coleoptera*** families were found in the samples: Dytiscidae and Helophoridae. With 187 individuals at 12 sampling sites, Dytiscidae were distinctly more common than Helophoridae (9 individuals at 3 sampling sites). There was evidence that area and pH had a significant, negative effect on Coleoptera presence, whereas dissolved oxygen showed a slight tendency towards a positive effect (Tab. 3, Fig. S 13).

Oligochaeta, the second largest group in abundance, had a similarly high presence as chironomids (22 out of 28 lakes). Nitrate had a significant, negative impact on oligochaetes (Tab. 3 , Fig. S 14).

Tab. 3: Results of generalized linear modelling (GLM) , applying quasipoisson distribution and a log link for Chironomidae abundance and Oligochaeta abundance and applying binomial distribution and a logit link for Coleopteran presence in alpine lakes of "Hohe Tauern" National Park (Austria). Each variable used up 1 df, significant values are printed in bold. Residual degrees of freedom: 26

	Chironomidae		Coleoptera		Oligochaeta	
	F	P	F	P	F	P
Elevation	0.9	0.355	36.2	0.275	0.03	0.87
Lake Size	8.48	**0.0097**	30.56	**0.018**	0.04	0.835
Rocky Habitats	12.71	**0.002**	20.15	0.527	1.44	0.247
Habi. Div.	1.466	0.243	28.09	0.151	1.69	0.212
Dis. Oxygen	4.31	0.053	25.08	0.083	0.04	0.85
Nitrate	2.75	0.116	23.79	0.258	4.71	**0.045**
Chlorophyll	0.75	0.399	21.32	0.116	0.56	0.465
pH	2.54	0.129	15.94	**0.02**	0.11	0.747
Elevation:Lake Size	8.4	**0.01**	15.75	0.663	0.15	0.704

4. Discussion

The generally high abundances of chironomids and oligochaetes that were found align with results of several studies on high mountain lakes (Čiamporová-Zaťovičová et al. 2010; Füreder et al. 2006; Hamerlík et al. 2006; Fjellheim et al. 2009). Abundances of other groups were very low in our samples.

Elevation did not show any significant effects on abundance, family richness or Shannon index in our models. Since analysis was only done on family level, possible effects of elevation may be masked by the rather low taxonomic resolution of our data. However, an impact of elevation on community composition was found in our dataset. Increasing elevation is generally reflected in harsher conditions and shorter ice-free periods for lakes. Thus, communities in lakes of higher altitude may be increasingly dominated by cold-stenothermal and semi-terrestrial species (Hamerlík et al. 2017). Cold stenothermal species, like *Hydroporus foveolatus* that was present in the studied lakes, are thought to be important indicators for the expected upward shift of geographical species ranges due to climate change (Oertli et al. 2008). An increase in abundance along elevations of up to 2,600 m a.s.l. with a following decrease in higher altitudes was observed by other studies (Hamerlík and Bitušík 2009; Füreder et al. 2006). A similar trend can be seen in our data set, as abundances seem to strongly decrease in lakes above 2,600 m a.s.l. This relationship however was never significant in our data due to low sample numbers above 2,600 m a.s.l. Temperatures in lakes above that threshold are thought not be warm enough to support large communities, especially because availability of food resources is restricted to short time periods in summer so that only few, well-adapted species survive (Čiamporová-Zaťovičová et al. 2010; Füreder et al. 2006).

Chironomid, coleopteran as well as total abundances had a negative relationship with **lake size** and were significantly lower in large than in small lakes. Contrary to Hamerlík et al. (2017) who found an increase of chironomid and macroinvertebrate taxa richness with increasing lake area, our results did not show a relationship between family richness and lake size. Decreasing abundances with increasing lake size seem to be rooted in the fact that larger lakes experience higher wave action (Johnson et al. 2004). Exposure to wind and thus higher water movement in lakes leads to harsher living conditions for macroinvertebrates (Johnson et al. 2004; Brauns et al. 2007; Tolonen et al. 2001). This may have a reducing effect on abundances and lead to the observed community shift with changing lake size. Another explanation for this shift may be a larger lake-terrestrial interface in smaller lakes which provides more opportunities for semi-terrestrial species to thrive (Hamerlík et al. 2017). Statistical analysis of community composition and total abundance did not only reveal a significant effect of lake size, but also a very significant effect of the **interaction of lake size with elevation** on macroinvertebrate communities. While small (< 0.15 ha) and medium sized lakes (0.15 – 1 ha) showed increasing total abundances with increasing elevation, macroinvertebrate abundances in large lakes (> 1 ha) slightly decreased (see Fig. S 7d). Conditions become harsher with increasing elevation, leading to higher wave action, especially in larger lakes. This may not only reduce abundances in large lakes, but also result in a shift towards more adapted and robust species. Our data for small and medium sized lakes only shows abundances of macroinvertebrates in elevations up to 2,500 m a.s.l. The decrease in elevations above that, which has been observed by other authors (Hamerlík and Bitušík 2009; Füreder et al. 2006), may still occur in lakes this size even though not reflected in our data. However, the observed increase of abundances in small and medium sized lakes with increasing altitudes may be due to the fact that small water bodies warm up and thaw faster than large ones, creating a more favorable environment for macroinvertebrates and a longer ice-free period. Increasing abundances may be due to a few very well adapted species that thrive in the absence of competitors. With ongoing climate change, ice-free periods in high altitude lakes are expected to increase and abundances in large lakes may rise. Presence of cold-stenothermal species will probably be negatively affected.

Oligochaete abundance related negatively to **nitrate** concentrations. Increased nitrate levels indicate nutrient input by grazing cattle or sheep. Livestock or their excrements were observed in about half of the lakes. Grazing presence was tested in an additional model as an explanatory variable, yielding similar statistical results as nitrate. This variable was left out of the final model because presence of grazing cattle or sheep was judged subjectively during field work and is thus not as reliable as in-situ measurements of nitrate. It is uncertain why oligochaete abundance reacted the way it did to nitrate concentrations. The expected relationship would be an increase of oligochaetes with increasing nutrient input. A possible explanation may be that the oligochaete species present were highly specialized in the oligotrophic conditions of these lakes and reacted sensitive to a change in nitrate content.

The ratio of EPT-species abundance (species of *Ephemeroptera*, *Plecoptera* and *Trichoptera*) by total macroinvertebrate abundance is positively affected by lake size. EPT species do not seem to be negatively affected by increasing lake size or stronger wave action, as they are more mobile than chironomids and are able seek cover easily in periods of strong winds or, in the case of case-bearing caddisflies, carry their refuge with them. Increasing numbers of EPT species with increasing lake size are a known phenomenon (Hamerlík et al. 2006). The observed effect on EPT/total ratio may partially be explained by the significantly decreasing chironomid abundances.

Community composition changed with increasing amount of **dissolved oxygen** in the water. Total abundances decreased with increasing oxygen content while chironomid and coleopteran abundances displayed only a tendency to decrease. Oxygen content is known to have an impact on macroinvertebrate communities (Rossaro et al. 2007) and although often overlooked, slight changes in oxygen content may affect macroinvertebrate communities even in highly oxygen-saturated alpine environments (Madsen et al. 2015; Jacobsen et al. 2003). Increasing oxygen content may be an indicator for reduced productivity of a lake and consequently low food resources for macroinvertebrates. This circumstance may explain the negative relationship between dissolved oxygen and abundances in our samples. Especially for the predominantly predacious diving beetles (which posed the majority of Coleopterans found), a lack of food in oligotrophic lakes will create unfavorable living conditions (Čiamporová-Zaovičová and Čiampor 2011) and thus lead to a decrease in abundance. Oxygen availability in alpine lakes is speculated to increase with ongoing climate warming, as summer stratification and mixing depth are expected to change (Luoto and Nevalainen 2013). Small, shallow mountain ponds that hold a considerable amount of algae and detritus provide favorable living conditions for water beetles (Čiamporová-Zaovičová and Čiampor 2011) – a circumstance that may explain the positive relationship between Coleopteran abundance and chlorophyll-a values of the studied lakes.

Our data showed a negative relationship of coleopteran abundance with **pH**. PH in lakes is mainly determined by the predominant bedrock within the catchment. Benthic communities in mountain lakes with high alkalinity, like the lakes that were sampled, have not been studied exhaustively (Fjellheim et al. 2000). However, Kownacki et al. (2006) found pH to be the main separating gradient of macroinvertebrate communities of small boreal lakes. Regarding species richness of macroinvertebrates in alpine lakes, optimum pH levels are suggested to be between 6 and 7 with pH values higher than 7 resulting in a decrease in species richness (Fjellheim et al. 2000). Even though a direct conclusion from richness to abundances cannot be drawn, this fact may indicate that abundances of coleopterans decreased with increasing pH values in our samples due to their surpassed optimum.

The amount of rocky **habitats** played a vital role in determining abundances, family richness and community composition of the studied lakes. A difference in community composition between habitat types was observed in our data, which is in accordance with other studies (Reuss et al. 2014; Heino 2000). In small, oligotrophic lakes, habitat structure is more important in shaping macroinvertebrate communities than water chemistry (Heino 2000). Considering the high share of chironomids on total abundance, it is not surprising that chironomid abundances drove the effects of most variables on total abundance. The higher the share of rocky habitats was in our study, the lower total and chironomid abundances were. Research on chironomid communities in alpine lakes has shown that rocks support the lowest taxa richness while sediment has higher richness (Reuss et al. 2014), which complies with our results of decreasing overall family richness with increasing share of rocky habitats in the littoral.

It seems that in our study, differences in total abundance are mostly due to chironomid habitat preference for sediment. Chironomids found in sandy littoral may be highly specialized to those habitat types. Most rocky habitats consisted of sheer rock faces or large boulders and exposition of these habitats to wind can be considered very high, especially compared to sandy patches that were often nested in between large boulders. Rocky habitats mainly consisted of large boulders and interstitial space was thus very small. This harshness of hard substrates and reduced interstitial space could explain lower abundances and family richness in rocky habitats. Additionally, sandy habitats may be more favorable in terms of nutrient storage, possibly explaining higher abundances and family richness in those sedimented areas. The largest biomass in lakes is generally found in gently sloped areas with accumulations of fine sediment (Tolonen et al. 2005). This corresponds to our results of high abundances in lakes with a higher share of sedimented littoral. On the contrary, the EPT ratio showed a strongly significant, positive relationship to the amount of rocky littoral, reflecting their preference for those habitats. This is probably due to a combination of decreasing chironomid abundance and an actual increase in EPT abundances in rocky habitats. The latter was observed in our data by the tendency of trichopteran and total EPT abundances to increase with increasing share of rocky habitats.

Another group with high abundances, Oligochaeta, were mainly observed in sediment littoral. This coincides with findings of other studies, that report oligochaete preference for sandy habitats (Rieradevall et al. 1999; Cai et al. 2011). Rieradevall et al. (1999) mention the preference of *Pisidium* species to be in fine sediments. In our study, the two lakes with large *Pisidium* abundances indeed showed 50 % and 90 % sediments, respectively (see Fig. S 6, *Sphaeriidae*).

Habitat types are considered to be a major influencing variable on community composition of macroinvertebrates (Brauns et al. 2007). This is reflected in our results, as community composition significantly changed with changing share of rocky littoral. The number of habitats has a significant impact on species richness of macroinvertebrates in mountain ponds (Martinez-Sanz et al. 2012). This corresponds to the tendency of a positive relationship between family richness and habitat diversity in our models.

5. Conclusion

Unlike initially hypothesized, we did not find strong effects of elevation per se on communities and macroinvertebrate groups. However, potential differences may have been masked by rather low taxonomic resolution. Mendoza and Catalan (2010) have already noted that elevation itself is described by many different variables. The effect of lake size was dependent on elevation, as small and medium sized lakes showed increasing abundances with increasing elevation, while macroinvertebrate abundances in large lakes slightly decreased. Lake and habitat structure seemed to be of great importance for macroinvertebrate communities, as the most obvious effects were produced by habitat type. Increasing amount of rocky habitat lead to changing community composition. Only the ratio of EPT species had an evidently positive relationship with rocky habitats. Opposed to our hypothesis, not so much habitat diversity but rather habitat type seems to be of great importance to macroinvertebrates in alpine lakes. Chemical parameters only showed weak significances or tendencies in regression analyses.

Estimating the effects of climate change in high-altitude ecosystems is related to a high degree of uncertainties in the future (Beniston et al. 1997). Alpine lakes are very sensitive to shifts in climate, especially lakes between 1,500 and 2,000 m a.s.l. are thought to be highly affected (Thompson et al. 2005). A general upwards movement of species ranges is anticipated to go along with climate change (Hodkinson & Jackson 2005). Insect fauna can be expected to be most influenced by this effect, because they are highly dependent on altitudinal levels as opposed to non-insect fauna (Čiamporová-Zaťovičová et al. 2010). Variables that showed great importance in our study were of structural nature (habitat type and lake size) and will not transform greatly with climate change. However, melting glaciers with ongoing climate warming will increase sizes of adjacent lakes and create new lakes. These can be expected to be colonized quickly by flying insect macroinvertebrates as their adult stages live terrestrial and have high dispersal abilities. Insect fauna will thus be of great importance in further monitoring the impact of climate change on alpine lakes.

6. References

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Supplementary Information

Tab. S 1: List of sampled lakes in "Hohe Tauern" National Park, valleys the lakes are located in, sampling date and elevation in meters above sea level (m a.s.l.). Lakes in quotation marks did not have official names and were named by the sampling team.

Number	Lake Name	Valley	Elevation	Date
1	„Innergeschloess 2"	Innergeschloess	2,550	31.07.2018
2	„Innergeschloess 3"	Innergeschloess	2,520	31.07.2018
3	„Gletscherplateau"	Innergeschloess	2,235	01.08.2018
4	Salzbodensee	Innergeschloess	2,138	01.08.2018
5	„See nahe Löbbensee"	Innergeschloess	2,233	02.08.2018
6	Löbbensee	Innergeschloess	2,226	02.08.2018
7	Kleiner Tauernsee	Seebachtal	2,310	17.07.2018
8	Grüneckersee	Seebachtal	2,307	17.07.2018
9	„Schneefeldsee"	Seebachtal	2,474	18.07.2018
10	„Plattensee"	Seebachtal	2,441	18.07.2018
12	„Grosses Elend"	Seebachtal	2,510	19.07.2018
13	„See neben Seebachsee"	Obersulzbachtal	2,083	25.07.2018
14	Seebachsee	Obersulzbachtal	2,083	25.07.2018
15	Foisskarsee	Obersulzbachtal	2,132	25.07.2018
16	Sulzsee	Obersulzbachtal	2,193	24.07.2018
17	„Obervorderjaidbachsee"	Obersulzbachtal	2,412	26.07.2018
18	„Untervorderjaidbachsee"	Obersulzbachtal	2,274	26.07.2018
19	Barrenlesee	Leibnitzbachtal	2,727	06.08.2018
20	„Kleiner Barrenlesee"	Leibnitzbachtal	2,511	06.08.2018
21	Gartlesee	Leibnitzbachtal	2,570	07.08.2018
22	„Leibnitzkopfpfütze"	Leibnitzbachtal	2,650	07.08.2018
23	„Debantsee"	Leibnitzbachtal	2,486	07.08.2018
24	Schwarzseele	Dorfer Tal	2,601	08.08.2018
26	„Murmelblubber"	Dorfer Tal	2,316	08.08.2018
27	„Elisabethsee"	Felbertal	2,361	09.08.2018
28	Plattachsee	Felbertal	2,199	10.08.2018
29	„Kleiner Plattachsee"	Felbertal	2,199	10.08.2018
30	Langsee	Felbertal	2,229	10.08.2018

Tab. S 2: List of all orders or subclasses, the lowest taxon they were determined to, total abundances across the study, the number of sampling sites they were present in and the number of taxa within each order/subclass that were determined for macroinvertebrates in alpine lakes of Hohe Tauern National Park.

Order / Subclass	lowest taxon determined	Total Abundance	# Sampling Sites	# Taxa determined
Coleoptera (adult)	Species	42	7	5
Coleoptera (juvenile)	Genus	155	12	5
Diptera	Family	11,925	25	6
Hemiptera	Genus	9	2	1
Plecoptera	Species	23	5	3
Trichoptera	Family	534	21	1
Tricladida	Species	22	5	1
Trombidiformes	Family	44	2	1
Veneroida	Genus	142	4	1
Oligochaeta	Subclass	5,080	22	1
Hirudinea	Subclass	1	1	1

Tab. S 3: Table of correlations between measured variable in the lakes of Hohe Tauern National Park according to Pearson's product-moment correlation test. Only significant correlations are listed.

Parameter 1	Parameter 2	P	r
pressure	elevation	<0.0001	-0.7808
pressure	pH	0.0297	-0.4187
conductivity	Dissolved oxygen	0.0038	0.5374
temperature	Dissolved oxygen	0.0312	0.4155
temperature	Nitrate	0.0013	-0.5858
turbidity	Nitrate	0.0128	0.4728
Cyanobacteria	Nitrate	0.0129	0.4723
Cyanobacteria	turbidity	0.0348	0.4076
Cyanobacteria	pH	0.0021	0.5660
cyanobacteria	chlorophyll	0.0398	0.3979
GPS E	Elevation	0.0178	0.4524
GPS E	Temperature	0.0102	-0.4860
GPS E	GPS N	0.0004	-0.6348
GPS E	Nitrate	0.0364	0.4045
GPS N	Elevation	<0.0001	-0.7138
GPS N	conductivity	0.0067	-0.5091
GPS N	nitrate	0.0028	-0.5524

Tab. S 4: List of estimated habitat coverage (given in percent) in the littoral of sampled lakes of Hohe Tauern National Park. Habitat types are sheer rock (large boulders and sheer rock faces), small rocks (up to 20 cm x 15 cm x 5 cm) and sediment.

Number	Name	Sheer Rock [%]	Small Rocks [%]	Sediment [%]
1	„Innergeschloess 2“	48	2	50
2	„Innergeschloess 3“	10	20	70
3	„Gletscherplateau“	60	20	20
4	Salzbodensee	19	1	80
5	„See nahe Löbbensee“	30	0	70
6	Löbbensee	70	10	20
7	Kleiner Tauernsee	79	0	21
8	Grüneckersee	100	0	0
9	„Schneefeldsee“	44	44	12
10	„Plattensee“	99	0	1
12	„Grosses Elend“	18	2	80
13	„See neben Seebachsee“	20	20	60
14	Seebachsee	25	25	50
15	Foisskarsee	10	0	90
16	Sulzsee	10	90	0
17	„Obervorderjaidbachsee“	10	5	85
18	„Untervorderjaidbachsee“	86	4	10
19	Barrenlesee	100	0	0
20	„Kleiner Barrenlesee“	10	10	80
21	Gartlesee	70	28	2
22	„Leibnitzkopfpfütze“	50	30	20
23	„Debantsee“	10	75	15
24	Schwarzseele	30	50	20
26	„Murmelblubber“	30	60	10
27	„Elisabethsee“	30	40	30
28	Plattachsee	70	30	0
29	„Kleiner Plattachsee“	33	34	33
30	Langsee	35	60	5

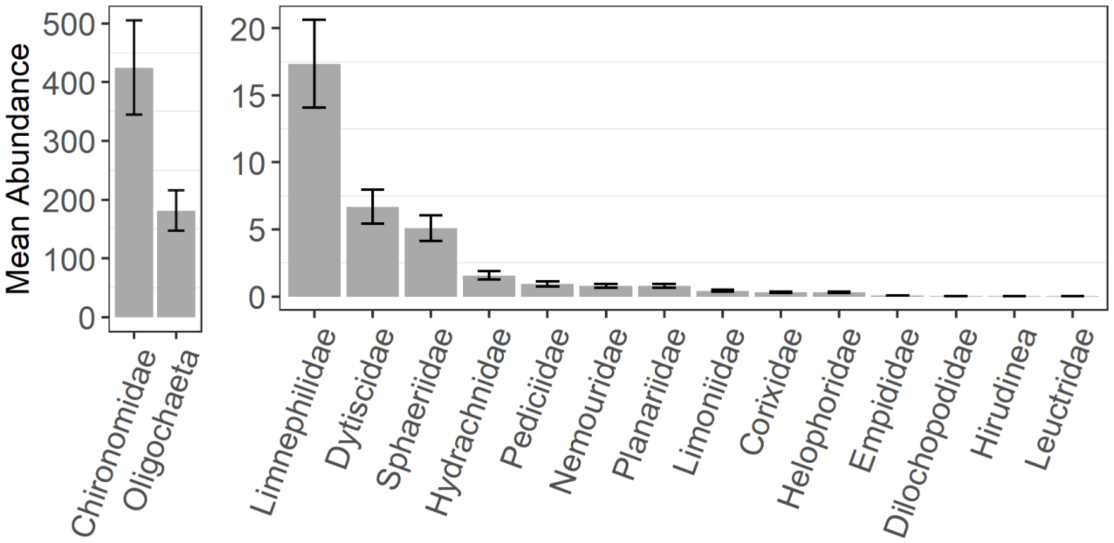
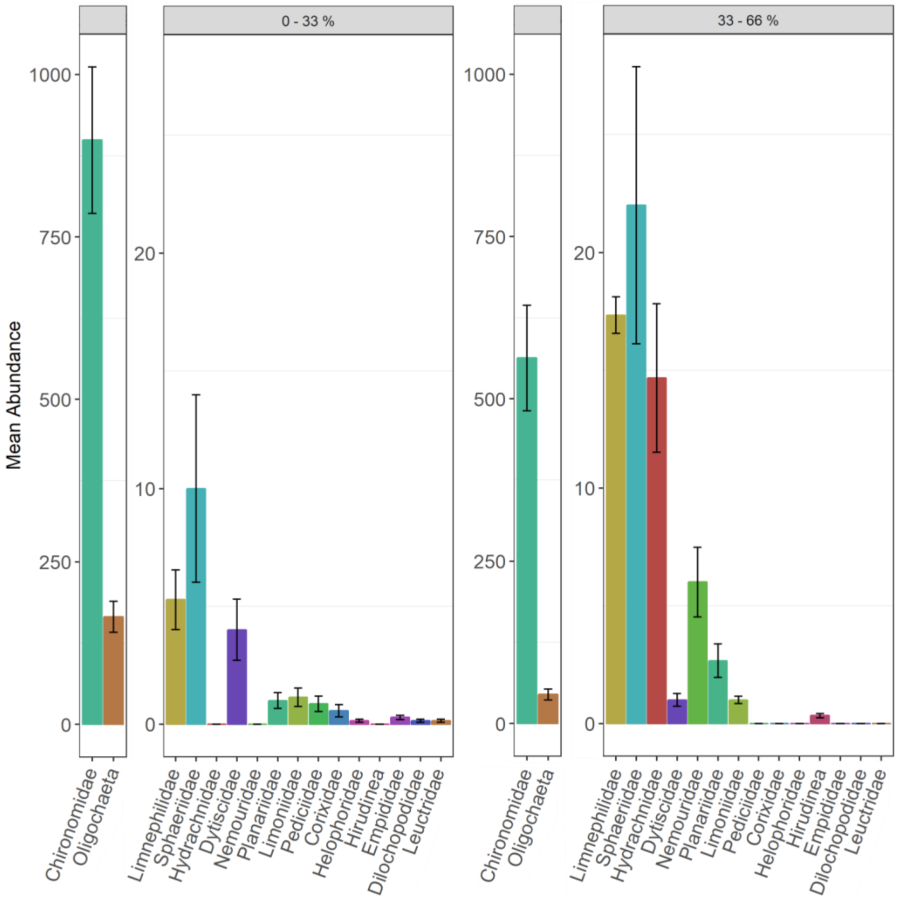


Fig. S 5: Mean abundances of families/subclasses across the study of macroinvertebrates in alpine lakes of Hohe Tauern National Park. Standard error is given by error bars. Due to large differences in abundance, chironomids and oligochaetes are displayed on a different scale.



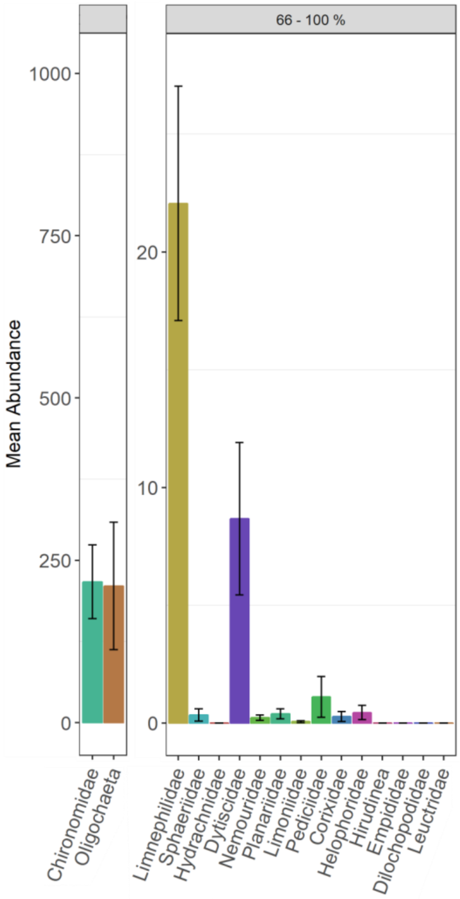


Fig. S 6: Mean abundances of families/subclasses across the study of macroinvertebrates in alpine lakes of Hohe Tauern National Park, grouped by share of rocky habitat (given in percent on top of graphs). Standard error is given by error bars. Due to large differences in abundance, chironomids and oligochaetes are displayed on a different scale.

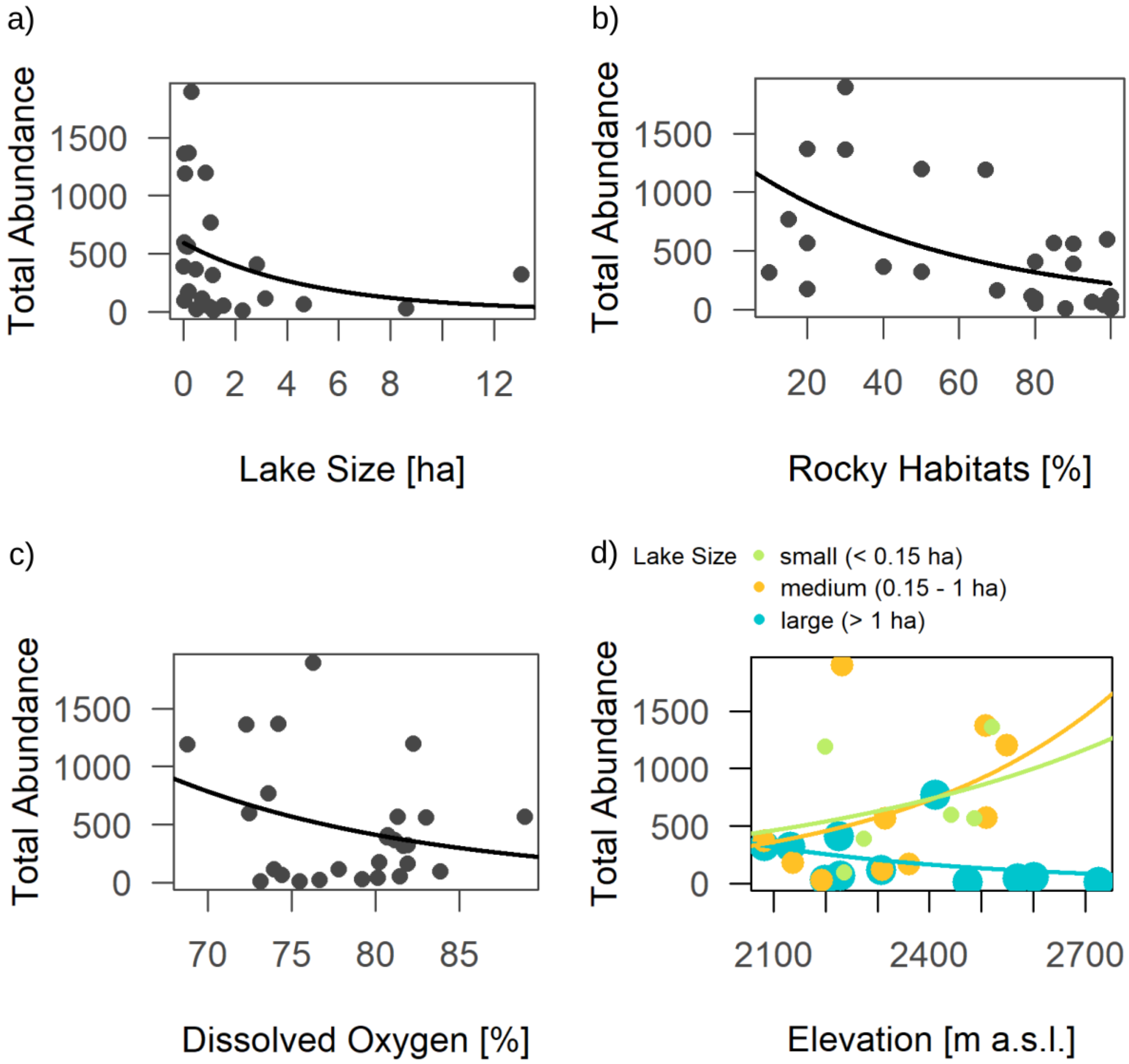


Fig. S 7: Generalized linear regression with quasipoisson distributions and log-links between total macroinvertebrate abundances in alpine lakes and a) lake size (F=6.92, P=0.018, n=27); b) percentage of rocky habitats (F=15.34, P=0.001, n=27); c) dissolved oxygen (F=5.23, P=0.04, n=27) and d) the interaction of elevation and lake size (F=8.54, P=0.010, n=27), where lake size is visualized by different colors and sized of the dots.

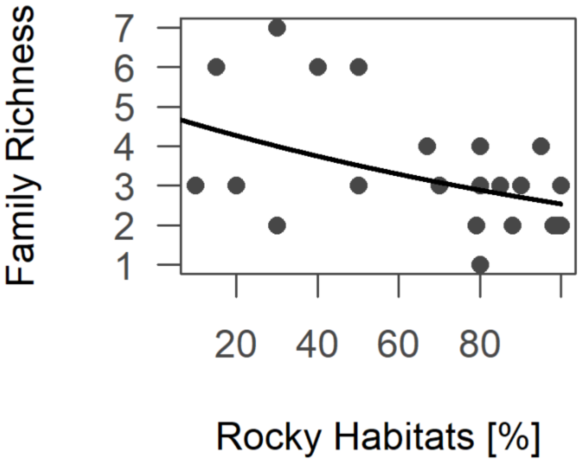


Fig. S 8: Generalized linear regression with quasipoisson distribution and log-link between total family richness in alpine lakes and percentage of rocky habitats in the lakes (F=8.68, P=0.009, n=27).

Tab. S 9: Results of generalized linear modelling (GLM), applying quasipoisson distribution and a log link for the Shannon index on family level of macroinvertebrates in alpine lakes of Hohe Tauern National Park (Austria). Each variable used up 1 df, significant values are printed in bold. Residual degrees of freedom: 26

	Shannon Index	
	F	P
Elevation	1.06	0.317
Lake Size	1.57	0.227
Rocky Habitats	1.28	0.274
Habi. Div.	0.16	0.698
Dis. Oxygen	0.63	0.439
Nitrate	1.84	0.193
Chlorophyll	0.29	0.595
pH	0.22	0.644
Elevation:Area	1.56	0.227

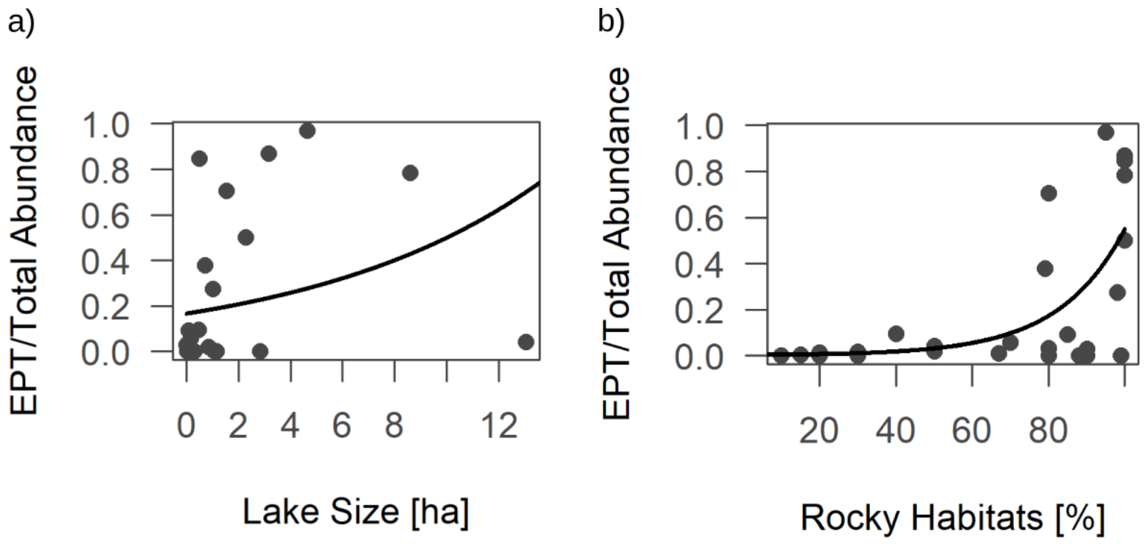


Fig. S 10: Generalized linear regression with quasipoisson distribution and log-link between the ratio of EPT (Ephemeroptera, Plecoptera, Trichoptera) abundance by total abundance in alpine lakes and a) lake size (F=7.16, P=0.016, n=27) and b) percentage of rocky habitats (F=29.35, P=<0.001, n=27).

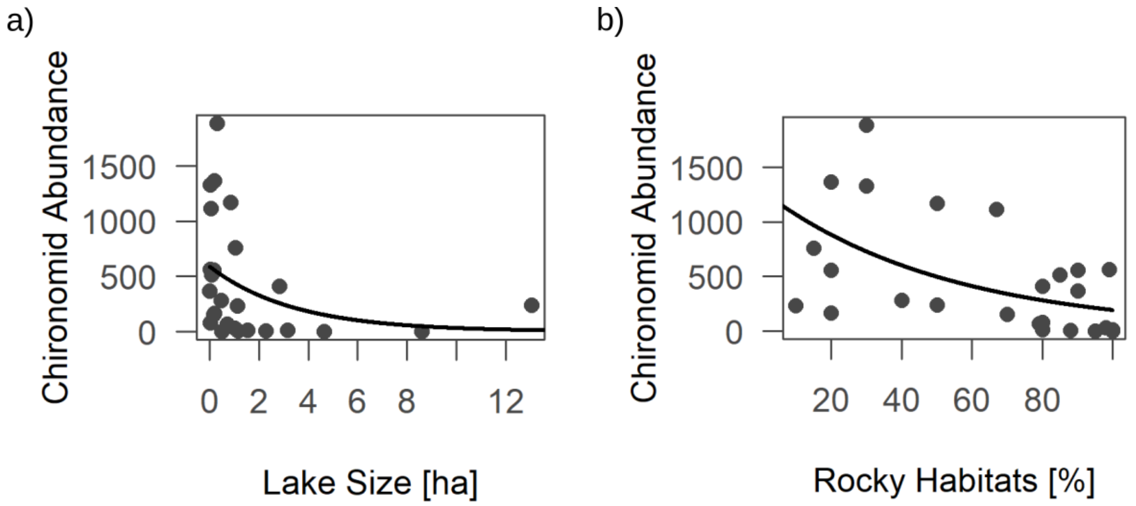
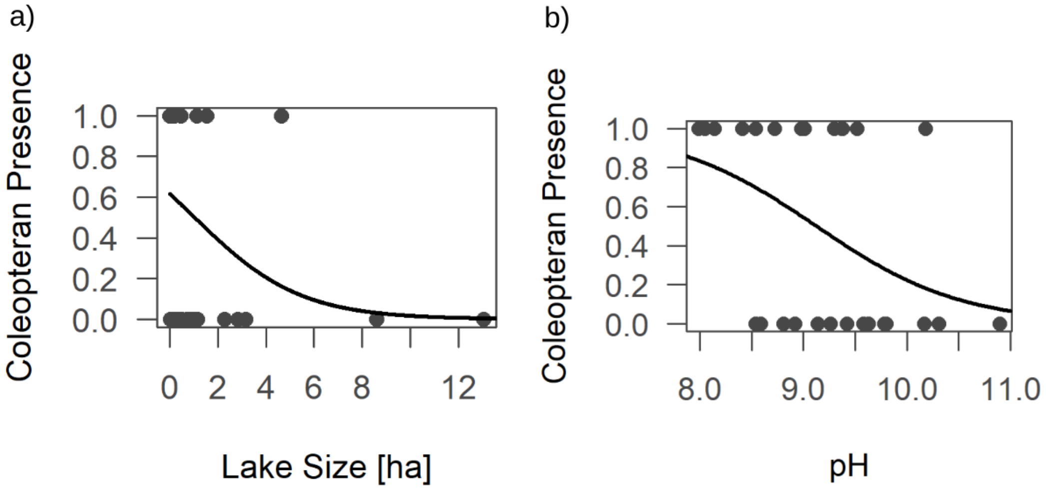


Fig. S 11: Generalized linear regression with quasipoisson distribution and log-link between chironomid abundances in alpine lakes and a) lake size (F=8.48, P=0.0097, n=27) and b) percentage of rocky habitats (F=12.71, P=0. =27).

Tab. S 12: Results of generalized linear modelling (GLM), applying quasipoisson distribution and a log link for trichopteran abundances in alpine lakes of Hohe Tauern National Park (Austria). Each variable used up 1 df, significant values are printed in bold. Residual degrees of freedom: 26

	Trichoptera	
	F	P
Elevation	0.01	0.932
Lake Size	1.02	0.326
Rocky Habitats	3.76	0.069
Habi. Div.	0.20	0.662
Dis. Oxygen	0.27	0.609
Nitrate	0.49	0.495
Chlorophyll	0.54	0.471
pH	0.28	0.607
Elevation:Area	0.05	0.821



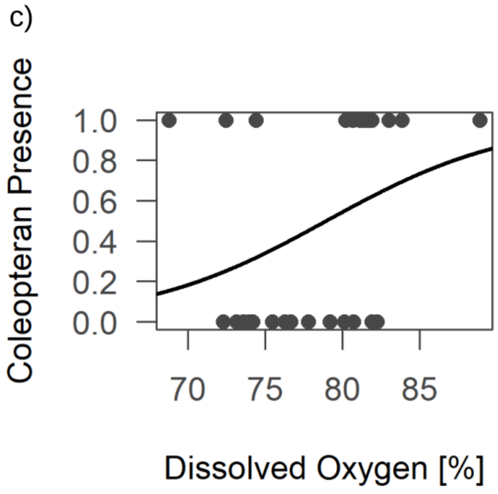


Fig. S 13: Generalized linear regression with binomial distribution and logit-link between coleopteran presence in alpine lakes and a) lake size (F=30.56, P=0.018, n=27); b) pH (F=15.94, P=0.02, n=27) and c) dissolved oxygen (F=25.08, P=0.083).

1 = coleopterans were present,

0 = coleopterans were absent.

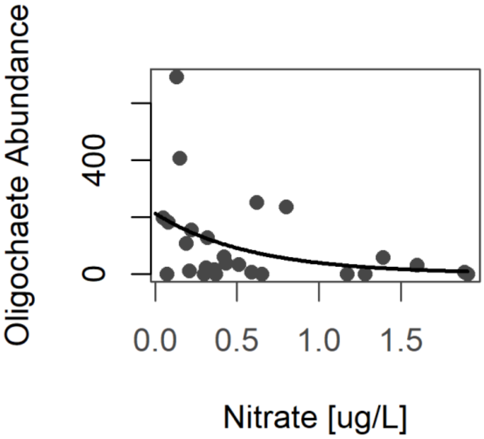


Fig. S 14: Generalized linear regression with quasipoisson distribution and log-link between oligochaete abundances and nitrate in alpine lakes (F=4.71, P=0.045, n=27).

Declaration

Herewith, I declare that this thesis has been completed independently and unaided and that no other sources other than the ones given here have been used.

The submitted written version of this work is the same as the one electronically saved and submitted on CD. The written version is rating relevant.

Furthermore, I declare that this work has never been submitted at any other time and anywhere else as a final thesis.

July 29, 2019