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ORIGINAL RESEARCH

Patagonian deglaciation: aquatic macroinvertebrate biodiversity in proglacial and paraglacial ponds

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Abstract

Glacier retreat is rapidly transforming cryospheric landscapes with new pond networks establishing in deglaciated landscapes. However, our understanding of the aquatic biodiversity within these rapidly evolving landscapes has been limited, especially in southern Patagonia despite having the largest temperate icefields globally. We examined the aquatic macroinvertebrate diversity in paraglacial forest and proglacial ponds at the snout of the Exploradores Glacier (Southern Patagonia, Chile) and assessed the environmental factors influencing taxonomic richness and community composition. Alpha and estimated gamma diversity were significantly higher in periglacial forest ponds compared to proglacial ponds. Clear differences in macroinvertebrate community composition were recorded between paraglacial and proglacial ponds. Taxonomic turnover explained most of the variation in community composition with Trichoptera and Diptera taxa constituting a greater proportion of taxonomic richness in proglacial ponds, while Coleoptera and Hemiptera taxa represented a higher proportion of taxa in paraglacial forest than proglacial ponds. When taxa-environment relationships were examined, a significant negative association was recorded between dissolved oxygen and taxonomic richness. Sodium concentrations were also found to be negatively associated with LCBD. This study provides vital evidence that ponds formed naturally due to deglaciation can support a wide diversity of aquatic macroinvertebrates, and as glacial retreat continues and landscapes transition from glacial to paraglacial, pond habitats represent increasingly important freshwater habitats at the landscape scale. Future research is critical to advance understanding of proglacial and paraglacial pond networks to provide the underpinning information needed to raise awareness to support the conservation of these unique habitats.

Keywords Beta-diversity · Environment relationships · Freshwater conservation · Glacial habitats · Ponds

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Extended author information available on the last page of the article

Introduction

Understanding how climate change, and particularly glacier retreat, affect freshwater biodiversity patterns in cryospheric environments represents an emerging but growing challenge (Losapio et al. 2025). Currently, 10% of the earth's land surface is covered by glaciers, but recent estimates have highlighted a global decline of glacier mass loss of 259 ± 28 Gt $^{y-1}$ between 2003 and 2009 (Gardner et al. 2013), with losses predicted to increase considerably by 2100 (Clarke et al. 2015). Glacier loss is a primary threat to freshwater biodiversity in crysopheric regions worldwide, but only recently has ecological interest in post glacial environments increased (Cauvy-Fraunié et al. 2019). However, to date almost all studies have focussed on lake (Feiner et al. 2016; Miserendino et al. 2023) and river systems (Pitman et al. 2021; Brown et al. 2018; Lencioni 2018; Cauvy-fraunie et al. 2015) with very few examining pond habitats.

Highly specialised communities and endemic species are often recorded from glacial lotic systems (Muhlfeld et al. 2020; Lencioni and Marziali 2005), and glacier retreat has been shown to cause alterations to macroinvertebrate composition associated with reductions in specialised stenothermal species in lotic systems (Wilkes et al. 2023; Muhlfeld et al. 2011). While increased deglaciation and warmer water temperatures can result in a loss of stenothermal specialists, some studies have recorded an overall increase in macroinvertebrate diversity within deglaciating rivers, as the changing environmental conditions (e.g., increasing water temperatures, higher resource availability) facilitate the upstream colonisation of different, more generalist macroinvertebrate taxa (e.g., Ephemeroptera, Plecoptera and Trichoptera: Milner et al. 2001; Jacobsen et al. 2014; Miserendino et al. 2018). As a result, alpha diversity (reach scale) among glacial rivers will likely increase but gamma diversity (regional scale) may decrease due to the loss of specialist macroinvertebrate taxa (Miserendino et al. 2018).

As glaciers retreat, supra-glacial ponds often form on or adjacent to glacier termini (Lencioni et al. 2021). Over time new ponds form as glaciers continue to retreat, and the older ponds may become isolated and increasingly distant from the influence of the glacier and its meltwater. Within Patagonia, these older paraglacial ponds are often surrounded by forest landscapes (Manzo et al. 2019), reflecting the low altitude and maritime climate (Wilson et al. 2018), whilst in other glacial environments such as the European Alps, they can be situated in poorly vegetated catchments (Catalan et al. 2009). Recent research on glacial ponds in alpine environments have found them to support limited biodiversity, often being dominated by one or two taxa such as Chironomidae larvae, reflecting the harsh environmental conditions present (Chertoprud et al. 2017; Gobbi and Lencioni 2021; Lencioni et al. 2021; Debiasi et al. 2022). However, other studies have reported that high-altitude/glacial ponds can provide unique habitats that support diverse macroinvertebrate fauna including Hemiptera, Coleoptera and Trichoptera (Oertli et al. 2008; Hill et al. 2021).

Ponds located within paraglacial landscapes may experience less harsh environmental conditions that enable more complex ecological communities to develop (Wissinger et al. 2016), although research on these ponds has been limited. Hamerlik et al. (2014) examined the biodiversity of high-altitude ponds and lakes in the Tatra Mountains, Slovakia, and found that ponds supported a similar regional diversity to high altitude lakes, but a lower local diversity. In the same study, high altitude ponds also recorded greater species turnover than lakes, attributed to the high environmental heterogeneity recorded among the high-altitude ponds (Hamerlik et al. 2014). While the effects of deglaciation on macroinvertebrate communities in streams have been studied (Brighenti et al. 2019), to the best of our knowledge no studies have examined the environmental conditions and macroinvertebrate communities in ponds as the landscape transitions from a glacial to paraglacial environment.

In line with global trends, glaciers in the Andes have retreated and thinned significantly since the end of the Little Ice Age (LIA: 1400–1850). In Southern Patagonia (45°–55°S), which contains the largest concentrations of ice mass in the southern hemisphere, ice extents since the LIA maximum have been reduced by 10% since the start of the 21 st Century, which is equivalent to a loss of 0.47 km^2 a^{-1} (Carrivick et al. 2024). This trend has accelerated over recent decades with geodetic measurements for this region revealing glacial losses of 0.78 ± 0.25 m w.e. per year between 2000 and 2018 (Dussaillant et al. 2019). This reduction in glacial extent is in response to climatic warming and spatially variable changes in precipitation (Villalba et al. 2003; Garreaud et al. 2013) and has given rise to new and extensive paraglacial environments. These environments, in many cases, have been occupied by glacial lakes which have formed in the over-deepened basins left behind by the retreating ice. In 2016, it was estimated that a total of 3,889 glacial lakes had developed in Southern Patagonia impounded by either moraine-, rock-bar- or ice-dams (Wilson et al. 2018). However, there are also many supra-glacial ponds that have established on the surface of the termini of Patagonian glaciers in response to enhanced melting. Given that lake abundance scales with size (Cael and Seekell 2016), small temporal or permanent pools and ponds may be an order of magnitude more abundant.

With glacier retreat in Southern Patagonia predicted to continue into the future (Bravo et al. 2021) and given the paucity of ecological information on glacial and post-glacial lentic waterbodies globally, this study aims to examine the aquatic macroinvertebrate diversity supported in paraglacial forest and proglacial ponds at the Exploradores glacier snout (Patagonia, Chile). Specifically, we sought to (i) quantify the macroinvertebrate richness supported in proglacial ponds and paraglacial forest ponds, (ii) examine the compositional variation in proglacial ponds and paraglacial forest ponds and (iii) assess the environmental factors influencing taxonomic richness and community composition.

Methods

Study area

An outlet of the Northern Patagonian Icefield, Exploradores Glacier (46.528°S, 73.184°W; Patagonia, Chile) is located in the Aysén Region of Chilean Patagonia and has a surface area of approximately 85.9 km^2 (RGI 7.0 Consortium, 2023). Unlike other glaciers in the surrounding area that have responded to recent climate change by retreating considerably (Minowa et al. 2021), the terminus of Exploradores Glacier has retreated only marginally and instead has exhibited static downwasting of ~ 0.5 m a^{-1} since 2000 (Dussaillant et al. 2019; Irarrazaval et al. 2022). This thinning has resulted in the development of numerous glacial lakes/ponds both on the surface and along the periphery of the glacier snout that are increasing in both size and number (Fig. 1). This study focusses on ponds (defined here as lentic waterbodies between 1 m^2 and 2 ha: Pond Conservation Group 1993) located near to or on the snout of Exploradores Glacier which extends at a low gradient ($< 1°$) down to

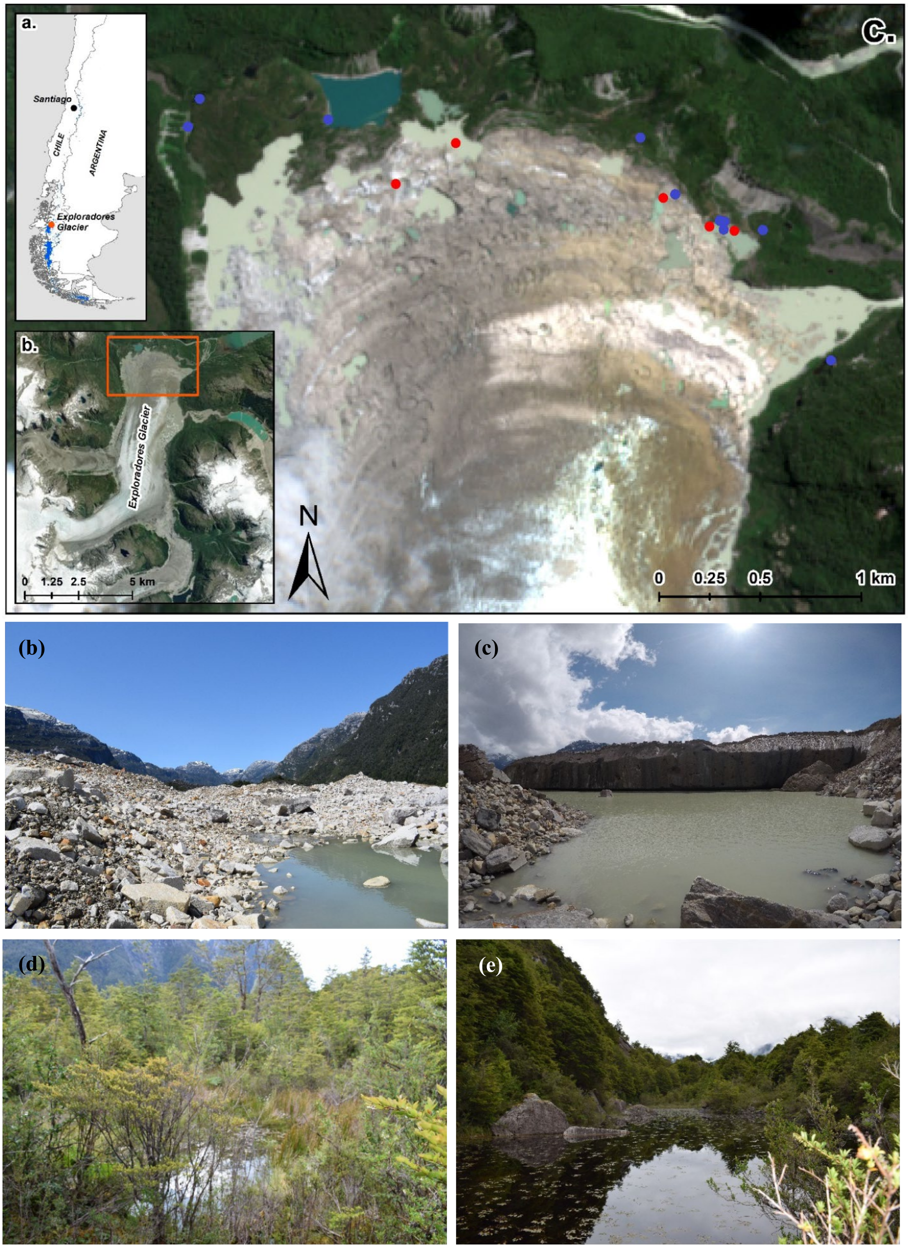

Fig. 1 Location of the 20 surveyed paraglacial forest (15) and proglacial ponds (5) across the Parc Nacional Laguna San Raphael and its location in relation to Chile (a) (blue circles = paraglacial forest ponds, red circles = proglacial pond). Photos of proglacial (b and c) and paraglacial forest ponds (d and e) sampled in this study (photos taken in January 2020 by Matthew J Hill).

~150 m.a.s.l. The glacier snout terminates adjacent to a large terminal moraine that is now extensively vegetated by native forest comprised of Southern Beeches including *Nothofagus antartica*, *N. dombeyi* and *N. nitida* (Luebert and Pliscoff 2019). The wider Exploradores basin exists in a cold temperate and humid climate with mean annual air temperatures of 9.1 °C (Bañales-Seguel et al 2020). Air temperatures on the glacier snout itself rarely fall below 0 °C (Irarrazaval et al 2022). This area is also characterised by large amounts of year-round precipitation, with annual totals of 2,000-3,000 mm (Aniya et al. 2007). The 20 ponds chosen were selected based on their accessibility and to ensure a wide gradient of connectivity and age as possible (Fig. 1). All ponds were formed naturally, perennial (holding water throughout the year) and were located 150–230 m.a.s.l. The ponds studied were divided into two groups (i) paraglacial forest ponds (n = 15), located in forested areas directly surrounding the Exploradores glacier, and (ii) proglacial ponds (n = 5), located at the snout of the glacier. The uneven sample number among proglacial and paraglacial ponds represents the dynamic nature of glacial retreat, and is representative of the deglaciating landscape studied here. Environmental and macroinvertebrate data collection in each study ponds was undertaken at the same time in January 2020.

Environmental data collection

At each pond site, pH, conductivity, dissolved oxygen and water temperature were recorded using a YSI ProDSS muli-parameter probe. Total nitrogen (TN) and total phosphorus (TP) were analyzed by digestion of unfiltered samples, using potassium persulfate followed by colorimetric analysis (APHA 2005). Dissolved silica (dSi) was analyzed using a modified molybdo-silicate method, with metal-sulfide as the reducing agent (following methodology described by Strickland and Parsons 1968). Alkalinity was determined by titration with HCl to colorimetric endpoint (APHA 2005). Major ions were analyzed by a DionexTM ICS-5000 ion chromatograph with eluent generation. In addition, altitude (m.a.s.l) and surface area (m^2) were recorded. A visual estimation of the percentage of pond margin overhung (shaded) by trees, percentage coverage of submerged, emergent and floating macrophytes, percentage coverage of different substrates (sand, clay/silt, decomposing leaves and twigs, coarse organic debris, gravel, pebbles and glacial till) was made at each pond site. In addition, water samples (2 × 265 ml) were taken at each pond site using a syringe, with filtration in the field (Nitrocellulose 0.45um pore size) and maintained cool/shaded until transport to the laboratory. Pond connectivity (the number of other waterbodies within 500 m of the pond) was calculated using aerial imagery (Google Earth 2022).

Macroinvertebrate data collection

Aquatic macroinvertebrate (larvae and adults) sampling was undertaken following the Freshwater Habitats Trust Pond Survey methods (Biggs et al. 1998). At each site, aquatic macroinvertebrates were sampled for a total of three minutes using a sweep technique with a standard pond net (1 mm mesh bag). The three minutes sampling time was divided equally between all mesohabitats present in each pond (e.g., submerged macrophytes, woody debris, emergent macrophytes, floating macrophytes, decomposing leaves, open water). However, where one mesohabitat dominated the pond, sampling time was further divided to reflect this (see Biggs et al. 1998). Complete access for some ponds was not possible, so mesohabitats were characterised based on accessible sections of those ponds. In addition, an inspection of surfaces that could not be sampled with the pond net (e.g., under large rocks and boulders) was undertaken for a total 60 s to ensure all available habitats were sampled for aquatic macroinvertebrates. Macroinvertebrate samples from each mesohabitat were pooled to create one sample per pond site, placed into plastic zip lock bags and preserved in the field in 70% ethanol. Samples were stored in a cold room prior to processing. In the laboratory, macroinvertebrate samples were processed and identified to the lowest possible taxonomic classification, with most taxa identified to family or genus level (Hamada et al. 2019; Domínguez & Fernández 2009; Stark et al. 2009). Macrozooplankton, principally Cladocera, were included, since they were larger than most early instar insect invertebrates (esp. Chironomidae), and where present were often dominant.

Statistical analysis

All statistical analyses were undertaken in the R environment (R Development Core Team 2025). Analysis was undertaken using species-abundance data, and one proglacial pond site was removed from the multivariate and regression analyses outlined below as it recorded 0 species.

Environmental characteristics

Preliminary Shapiro-Willk tests were undertaken to test for normality in the environmental data (Shapiro–Wilk test results are presented in Table S1). Mann–Whitney U or One-Way ANOVA tests were undertaken to examine the statistical differences in environmental characteristics between proglacial and paraglacial forest ponds (Table S1). Variation in environmental characteristics (based on the Euclidean distance) between proglacial and paraglacial forest ponds were visualised using Non-metric Multidimensional Scaling (NMDS), using the *metaMDS* function in the vegan package. To examine if differences in environmental conditions were statistically significant, a permutational analysis of variance (PERMANOVA) was undertaken using the function *adonis2* in the vegan package. Heterogeneity of environmental conditions within paraglacial forest and proglacial ponds were quantified by calculating the homogeneity of multivariate dispersions using the *betadisper* function in vegan, and statistically compared using a One-Way Analysis of Variance (ANOVA). Prior to environmental NMDS, PERMANOVA and homogeneity of multivariate dispersion analysis, environmental characteristics were standardised (where each environmental parameter recorded a zero mean and unit variance).

Alpha and gamma diversity

Alpha diversity is defined here as the total taxonomic richness within each pond sample site (Hill et al. 2022). To account for differences in sample size, rarefaction was undertaken using the function *rrarefy* in the vegan package to generate an expected taxonomic richness for each site (Oksanen et al. 2025). *Rrarefy* generates a randomly rarefied community value for each sample site based on a given sample size (Oksanen et al. 2025), which in this study was based on 100 individuals. Preliminary analyses indicated that the taxonomic richness data did not follow a normal distribution (Shapiro–Wilk test: $W = 0.895$, $p = 0.034$), and as a result Mann–Whitney U tests were employed to examine the statistical differences in alpha diversity (taxonomic richness) and rarefied richness between proglacial and paraglacial forest ponds. Gamma diversity is defined here as the total number of aquatic macroinvertebrate taxa recorded among proglacial and paraglacial forest pond sites. Estimated gamma diversity was calculated based on the Chao2 estimator using the *specpool* function in the vegan package, which uses the number of uncommonly occurring taxa in a sample to estimate the number of undiscovered species (see Oksanen et al. 2025). If there was no overlap in the estimated gamma diversity 95% confidence intervals for proglacial and paraglacial forest ponds, the differences were considered significant ($p < 0.05$).

Macroinvertebrate community composition

Differences in aquatic macroinvertebrate composition between proglacial and paraglacial forest ponds were visualised using NMDS, using the *metaMDS* function in the vegan package. The Bray Curtis dissimilarity index was employed for the macroinvertebrate NMDS. To examine if differences in macroinvertebrate composition were statistically significant, PERMANOVA was undertaken using the function *adonis* in the vegan package. Heterogeneity of macroinvertebrate composition within paraglacial forest and proglacial ponds was quantified by calculating the homogeneity of multivariate dispersions using the *betadisper* function in vegan and statistically compared using a One-Way ANOVA. Indicator Value Analysis was undertaken to identify indicator macroinvertebrate taxa associated with paraglacial forest or proglacial ponds using the function *multipatt* in the indicspecies package (De Caceres et al. 2024). Indicator value analysis measures the association between a taxa and a ‘group’ and is a product of two components: *specificity* (the uniqueness of a taxa to a given group of sites) and *fidelity* (the extent to which a species occurs across all sites in a group) (Legendre 2024).

Total beta-diversity (defined here as the variation in macroinvertebrate composition among the studied ponds sites), and the contribution of species replacement and richness difference were calculated for the entire dataset (based on the Baselga family, Jaccard based indices), and for paraglacial forest and proglacial ponds separately using the *beta.div.comp* function in the adespatial package (Dray et al. 2022). The Local Contribution to Beta Diversity (LCBD) metric quantifies the ecological uniqueness of each site, with high values for a given site indicative of high dissimilarity to other sites in the region (Hill et al. 2021). The Local Contribution to Beta Diversity (LCBD: based on the Hellinger distance, and Baselga Jaccard indices) was calculated for each site across the entire dataset and for paraglacial forest and proglacial ponds separately, and were statistically tested using random, independent permutations within the community matrix (Legendre & Cáceres 2013). The function *beta.div* and *beta.div.comp* in the adespatial package were used to calculate LCBD (Legendre & De Cáceres 2013).

Species-environment relationships

Prior to redundancy and regression-based analysis, the covariance of all environmental variables was assessed using Pearsons correlation coefficients. One independent variable was removed from further analysis where any two were correlated $\rho \geq 0.70$, with the most ecologically meaningful variable retained. This resulted in several correlated variables being removed: Magnesium, Potassium, Calcium, Sulphate, Chloride, dissolved silica, pond connectivity, percentage coverage of pebbles, altitude, depth, emergent macrophyte and percentage of water overhung. Variance Inflation Factor analysis (VIF: using the function *vif* in the car package; Fox, et al. 2021) was undertaken to minimise multicollinearity among the remaining environmental variables. Using a stepwise procedure, VIF values were calculated for each environmental variable, with the variable with the highest value being removed. The procedure was repeated until all VIF values were 5 or less (Hill et al. 2022) with alkalinity, Total Nitrogen, Conductivity, and water temperature subsequently removed. pH, TP, Fluoride, Sodium, dissolved oxygen, surface area, margin overhung, percentage coverage of sand substrate, percentage coverage of leaf substrate, percentage coverage of submerged substrates were all retained and used in subsequent analyses. Furthermore, the spatial autocorrelation of the macroinvertebrate community structure from the sample ponds was assessed using correlograms, based on Moran I statistics of Euclidean macroinvertebrate distance matrices in relation to geographic distance, using the *correlog* function in the pgirmess package (Giraudoux et al. 2022).

Redundancy analysis (RDA) was used to examine the association between the ten retained environmental variables and macroinvertebrate community composition (Hellinger transformed), using the function '*ordiR2step*' in vegan package to identify the significant ($p < 0.05$) environmental variables influencing macroinvertebrate communities. Regression analysis was undertaken to examine the association of environmental variables with a number of community metrics. Prior to any regression-based analyses, outliers (those values of a given variable that were three times the interquartile range; White et al. 2021) were identified and removed, resulting in three total phosphorus values, and three surface area and percentage coverage of sand values being removed. The response of taxonomic richness was examined in relation to the individual effect of each environmental variable (pH, TP, Fluoride, Sodium, dissolved oxygen, surface area, margin overhung, percentage coverage of sand substrate, percentage coverage of leaf substrate, percentage coverage of submerged substrates) via independent statistical models, each testing a unique dependent-independent pairwise combination ($n = 10$, 1 dependent and 10 independent). Running individual dependent-independent regression models ensured that the models were not overfitted (White et al. 2017). To determine the optimal statistical function for each environmental variable, the independent variable was modelled via linear, exponential, logarithmic and quadratic statistical functions and the model exhibiting the lowest AIC was considered to be the optimal structure (Johnson and Omland 2004; Fornaroli et al. 2019). Once the optimal statistical function was determined for each environmental variable, pairwise regression analysis was undertaken for all dependant and independent variables in their optimal structure (linear, quadratic, logarithmic or exponential). The proportion of statistical variation explained (R^2) and significance of each dependant-independent regression model ($n = 10$) was determined. To examine the relationship between LCBD and each environmental variable the same regression-based procedure undertaken for taxonomic richness was followed (see above). The same regression-based procedure was also followed to examine the relationship between LCBD and taxonomic richness, and if there was an association between the distance of the pond to the glacial snout and taxonomic richness or LCBD.

Results

Environmental conditions

Environmental characteristics among paraglacial forest and proglacial ponds were clearly separated in the NMDS biplot and were found to be statistically different (PERMANOVA $F_{1,15}=2.498$, $R_2=0.14$, $p<0.05$; Fig. 2a). Paraglacial forest ponds (4.96) recorded a higher average distance to group centroid than proglacial ponds (4.0) for environmental characteristics, although this was found to be not statistically significant (ANOVA $F_{1,15}=1.757$, $p>0.05$; Fig. 2c).

The percentage of decomposing leaves and twigs substrate ($W=47.5$, $p<0.05$), total nitrogen ($W=56.5$, $p<0.01$), temperature ($W=52$, $p<0.05$) and the % coverage of submerged ($W=59$, $p<0.01$) and emergent macrophytes ($W=51.5$, $p<0.05$) were all significantly higher in paraglacial forest ponds compared to proglacial ponds, while dissolved

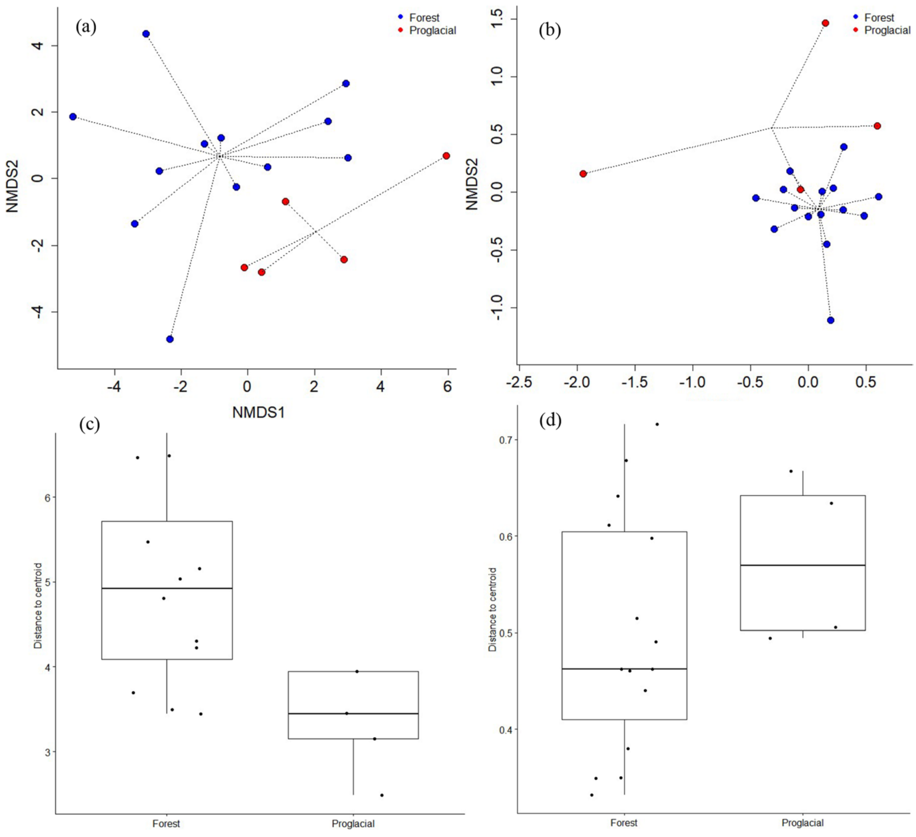

Fig. 2 Non-metric Multidimensional Scaling (NMDS) biplots of dissimilarity in environmental conditions (Euclidean distance) (**a**); and macroinvertebrate community composition (Bray Curtis dissimilarity) (**b**) between proglacial and paraglacial forest ponds, and boxplots of multivariate dispersion distances for (**c**) environmental conditions and macroinvertebrate community composition (**d**) from paraglacial forest and proglacial ponds (Boxes show 25th, 50th, and 75th percentiles and whiskers show 5th and 95th percentiles)

oxygen ($W = 8$, $p < 0.05$), Floride (ANOVA $F_{1,15} = 4.71$, $p = 0.05$) and the substrate % of glacial till ($W = 18$, $p < 0.05$) were significantly higher in proglacial ponds (Table S2; Fig. 3). No significant difference ($p > 0.05$) in the 22 other physicochemical parameters were recorded between paraglacial forest and proglacial ponds.

Macroinvertebrate taxonomic richness

In total, 49 taxa from 14 orders were recorded across the ponds studied. More taxa were recorded from paraglacial forest ponds (observed total: 42) compared to proglacial ponds (observed: 27 taxa). Estimated gamma diversity (based on the Chao 2 estimator) was found to be similar ($p > 0.05$) in paraglacial forest (estimated gamma: 50, 95% CI: 37.07–62.49) to proglacial ponds (estimated gamma: 51, 95% CI: 20.54–81.59). Diptera (total taxa: 12, proportion of total richness: 25%) Coleoptera (total taxa: 12, proportion of total richness: 25%), Trichoptera (total taxa: 7, proportion of total richness: 14%), and Odonata (total taxa: 3,

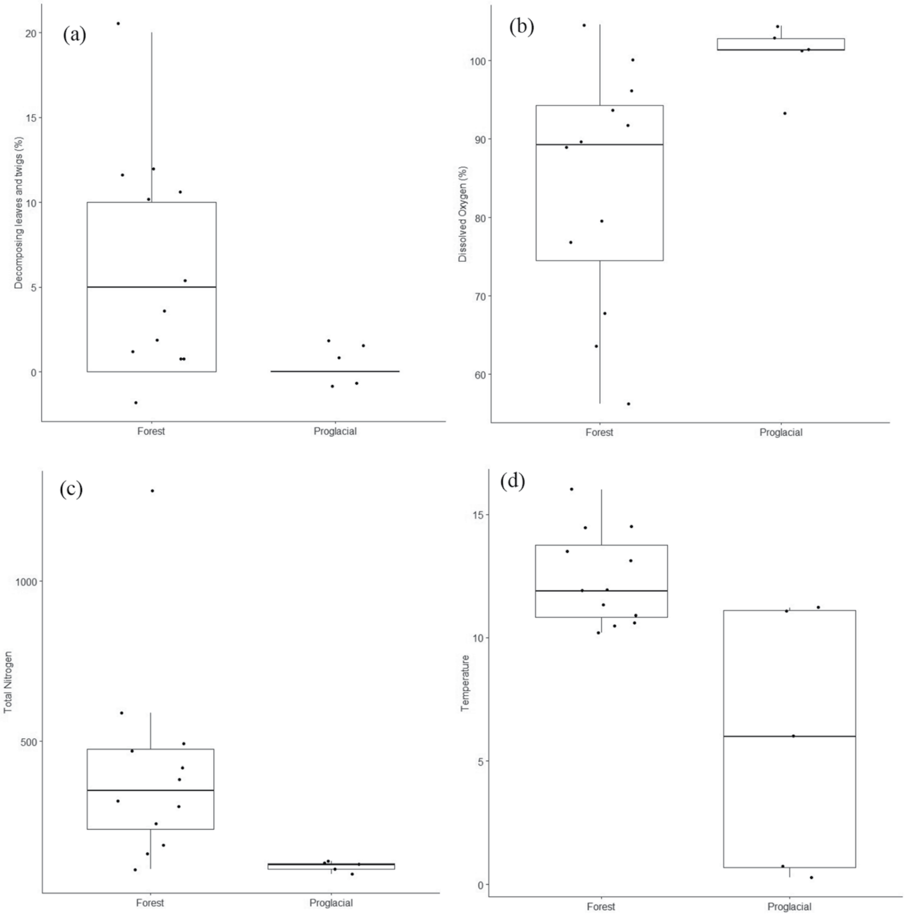

Fig. 3 Median values of decomposing leaves and twig substrate (**a**), Dissolved oxygen (**b**), Total Nitrogen (**c**) and water temperature recorded from paraglacial forest and proglacial ponds. Boxes show 25th, 50th, and 75th percentiles and whiskers show 5th and 95th percentiles

proportion of total richness: 6%) constituted the greatest proportion of total taxonomic richness recorded across the study sites. The most abundant macroinvertebrate taxa across the study sites were: *Simocephalus expinosa* (total: 1163), *Ceriodaphnia dubia* (total: 1002), Chironomidae 1 (total: 969), and Chironomidae 3 (total: 780, see supplementary material Table S3 for the abundances of all recorded macroinvertebrates).

On average, macroinvertebrate richness was significantly higher in paraglacial forest ponds (median: 14 taxa) than glacial ponds (median: 10 taxa; $w=69.5$, $p<0.01$; Fig. 4a). In addition, rarefied richness was also significantly higher in paraglacial forest (median richness: 6) ponds compared to proglacial (median richness: 3) ponds ($w=64.5$, $p<0.05$; Fig. 4b). The greatest taxonomic richness was recorded from a paraglacial forest pond (24 taxa), with five paraglacial forest ponds supporting > 15 taxa, while all glacial ponds supported less than 14 taxa. Trichoptera (paraglacial forest pond: 10% proglacial pond 11%), and dipteran taxa (paraglacial forest pond: 28%, proglacial pond: 33%) constituted a greater proportion of taxonomic richness in proglacial than paraglacial forest ponds, while Coleoptera (paraglacial forest pond: 24%, proglacial pond: 18%) taxa represented a higher proportion of taxa in paraglacial forest than proglacial ponds (Fig. S1a). Actively dispersing taxa dominated glacial ponds (actively dispersing: 22 taxa (81%), passively dispersing: 5 taxa (19%)), whilst a greater number of passively dispersing taxa were recorded from paraglacial forest ponds (actively dispersing: 31 taxa (74%), passively dispersing: 11 taxa (26%): Fig. S1b).

Macroinvertebrate community composition

Glacial ponds were widely distributed throughout the NMDS biplot (stress: 0.16), while paraglacial forest ponds were clustered together (Fig. 2b). Differences in macroinvertebrate composition between paraglacial forest and proglacial ponds were found to be significant (PERMANOVA, $F_{1,17}=1.709$, $R_2=0.091$, $p<0.05$). Multivariate dispersion was similar for macroinvertebrate composition among paraglacial forest (distance to centroid: 0.499) and proglacial ponds (distance to centroid: 0.575, ANOVA $F_{1,17}=1.298$, $p=0.271$), although greater variability in multivariate dispersion was recorded among paraglacial forest ponds (Fig. 2d).

Proglacial and paraglacial forest ponds each recorded a moderate beta-diversity (proglacial ponds: 0.44, paraglacial forest ponds: 0.32), and when all ponds were considered together (0.35; Table 1). Turnover explained the majority of the variation in community composition when all sites were considered together (turnover: 89%, nestedness: 11%) and when proglacial ponds (turnover: 95%, nestedness: 5%) and paraglacial forest ponds (turnover: 88%, nestedness: 12%) were considered separately (Table 1). When turnover and nestedness pairwise comparisons were examined, turnover was the dominant contributor to the dissimilarity between proglacial and paraglacial forest ponds (average turnover: 0.70 (89%), average nestedness: 0.09 (10%)). In total, seven taxa (14% of total taxa recorded) were unique to proglacial ponds, 22 taxa (45%) were unique to paraglacial forest ponds and 20 (41%) taxa were shared (please see Table S4 for full list of unique and shared taxa among proglacial and paraglacial forest ponds). Chironomidae (Chironomidae 2, stat: 0.556, $p=0.038$) was identified as an indicator taxon for paraglacial forest ponds, while no macroinvertebrate taxa were identified as indicator taxa for proglacial ponds. Across the entire dataset, one proglacial pond and one paraglacial forest pond recorded significant LCBD

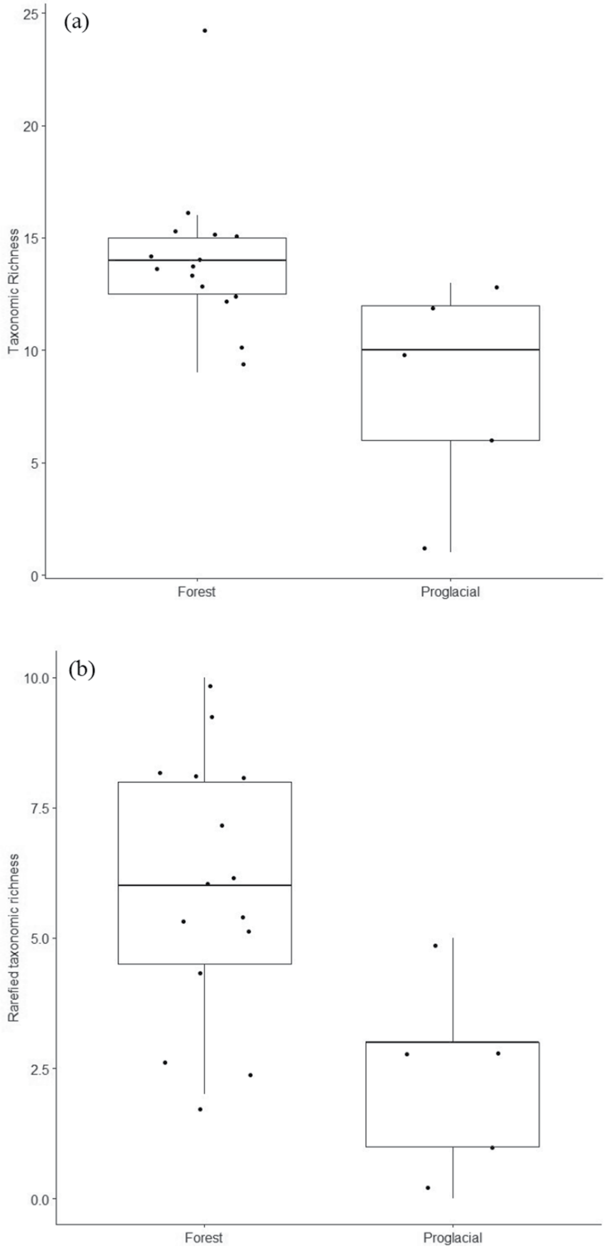

Fig. 4 Median macroinvertebrate taxonomic richness (**a**) and rarefied taxonomic richness (**b**) recorded from paraglacial forest and proglacial ponds. Boxes show 25th, 50th, and 75th percentiles and whiskers show 5th and 95th percentiles

values ($p < 0.05$). On average, proglacial ponds (median: 0.074) recorded higher LCBD values compared to paraglacial forest ponds (median: 0.043; Fig. 5), although no significant differences in LCBD values were recorded ($w = 16$ $p = 0.185$).

Table 1 Relative contribution of species turnover and nestedness to total beta-diversity (based on the Baselga-Jaccard dissimilarity) when all sites were considered together, and among proglacial and paraglacial forest ponds separately

	Total beta diversity	Turnover	Nestedness
Proglacial ponds	0.44 (100%)	0.42 (95%)	0.02 (5%)
Paraglacial forest ponds	0.32 (100%)	0.28 (88%)	0.04 (12%)
All ponds together	0.35 (100%)	0.31 (89%)	0.04 (11%)
Proglacial ponds v paraglacial forest ponds	0.79 (100%)	0.70 (89%)	0.09 (11%)

The contribution of turnover and nestedness to total beta-diversity between proglacial and paraglacial forest ponds is also presented. Percentage contribution is presented in parentheses

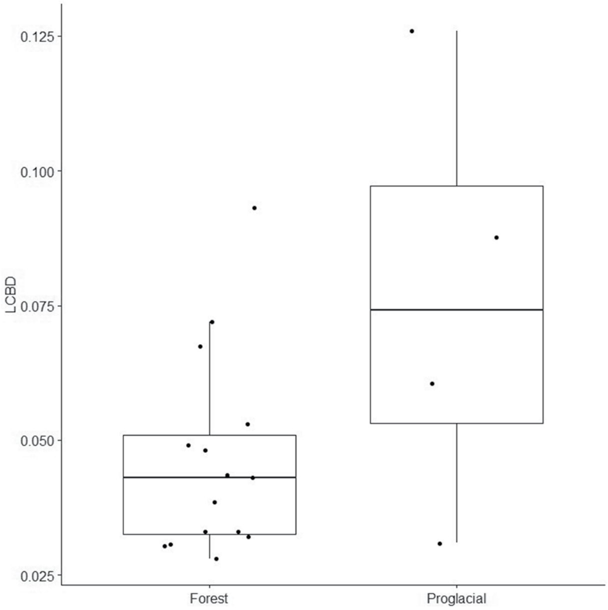

Fig. 5 Median Local Contribution to Beta Diversity (LCBD) values for paraglacial forest and proglacial ponds. Boxes show 25th, 50th and 75th percentiles and whiskers show 5th and 95th percentiles

Species-environment relationships

Preliminary analysis indicated that there was no spatial autocorrelation for taxonomic richness or LCBD at any spatial scale (See Fig. S2 for mantel correlograms). Regression analyses indicated a significant negative association between dissolved oxygen and taxonomic richness (adjusted $R^2=0.1947$, $F_{1,14}=4.626$, $P<0.05$ – linear function; Fig. 6a). A negative association was recorded between LCBD and Sodium (adjusted $R^2=0.2275$, $F_{1,14}=5.418$, $P<0.05$—logarithmic function; Fig. 6b. No significant associations were recorded between taxonomic richness or rarefied richness, and the distance of the pond to the glacial snout (Supplementary Material Table S5). Redundancy analysis indicated that none of the measured environmental variables were significantly associated with pond macroinvertebrate community composition.

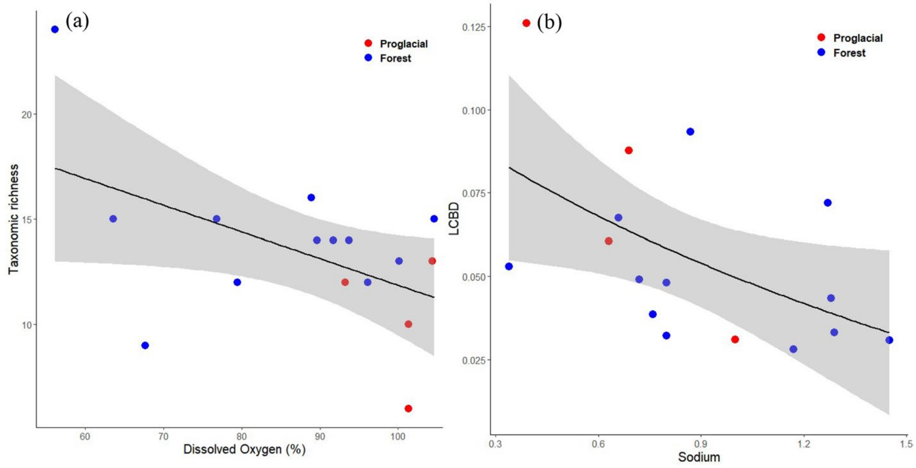

Fig. 6 Association between taxonomic richness and (**a**) dissolved oxygen, and and between LCBD and Sodium (**b**)

Discussion

Deglaciation is predicted to increase over the coming decades (Clarke et al.2015), and as a result new paraglacial landscapes will become established. Ponds are common habitats across paraglacial landscapes (Lencioni et al. 2021) and likely to become more abundant, yet limited research has examined their biological communities (Laske et al. 2021; Wissinger et al. 2016). This study sought to characterise the aquatic macroinvertebrate communities supported in paraglacial forest and proglacial ponds adjacent to the Exploradores Glacier snout, with results demonstrating differences in the macroinvertebrate communities among ponds connected to the glacial snout (proglacial ponds) and ponds located in the paraglacial landscape (paraglacial forest ponds).

Macroinvertebrate richness among proglacial and paraglacial forest ponds

At both a landscape (gamma) and local (alpha) scale, taxonomic richness was found to be higher in the paraglacial forest ponds than the proglacial ponds in this study. While there are no other similar pond studies to compare these findings with from other recently deglaciated environments, the results are not unexpected. Proglacial ponds are recently formed (primary succession) and are often located in highly stressed/biologically challenging environments that probably limit their suitability for most macroinvertebrate taxa (Hamerlik et al. 2014). For example, during the summer months proglacial ponds are subjected to large water level fluctuations and may dry, while in the winter months they may freeze over. These ponds are often highly turbid, can experience extreme fluctuations in water chemistry and temperature, support limited physical habitat complexity and macrophytes, and are largely unproductive due to their limited soil development, low organic matter availability and small catchments (Gobbi and Lencioni 2021). Some of the proglacial ponds in this study were closely connected to the snout of the glacier and regularly experience inputs of broken ice falling into the pond. The paraglacial forest ponds provided more stable environmental conditions as they were broadly unaffected by the glacier directly, with lower fluctuations in water chemistry, higher productivity, habitat complexity and macrophyte coverage, which increases the availability of suitable ecological niches for aquatic macroinvertebrates (Jara et al. 2023; Epele et al. 2021; Netto et al. 2012).

However, other studies have found that the newly formed proglacial ponds can provide important habitats for macroinvertebrates, particularly early aerial colonisers including Chironomidae and some Coleoptera (Gobbi and Lencioni 2021; Lencioni 2018). In this study, Dipteran taxa and Trichoptera constituted a greater proportion of the taxonomic richness than the paraglacial forest pond richness. Similarly, in a study of high-altitude glacial ponds in the Tatra mountains of central Europe, the most diverse invertebrate groups recorded were Chironomidae and Trichoptera (Novikmec et al. 2015). There is often a limited presence of predators in these ponds, and where organic material is available (either through algal growth or wind-blown terrestrial plant inputs), abundant resources may be exploitable by Diptera and Trichoptera, with numerous species within these invertebrate groups adapted to cold environments (Martel-Cea et al. 2021). In addition, during summer months warmer water temperatures can occur in the shallow proglacial ponds, which create ideal breeding conditions for Chironomidae (Hagvar et al. 2016).

Macroinvertebrate community composition among proglacial and paraglacial forest ponds

This study found significant differences in macroinvertebrate assemblages between proglacial and paraglacial forest ponds, which were almost entirely explained by species replacement, supporting previous findings from glacial lentic systems (Hamerlik et al. 2014; Hill et al. 2021). Large spatial environmental gradients were recorded among the ponds in this study, which provided large ecological niches to support a wider range of taxa, thus promoting high species replacement via environmental filtering (Hamerlik et al. 2014). Although not measured here, the temporal (daily, seasonally and inter-annually) environmental variability in glaciated landscapes is likely to be more extreme than other biomes, which may impose a strong environmental filter for proglacial and paraglacial pond aquatic macroinvertebrate communities (Wissinger et al. 2016). However, the high beta diversity and species replacement among the proglacial and paraglacial forest ponds may also reflect the relative isolation of the ponds, which can be particularly high in glaciated landscapes reflecting the distinctive topographic barriers (Hamerlik et al. 2014; Hyseni et al. 2021).

Previous research in glaciated environments has shown that such early-stage lentic systems are often colonized by cold-tolerant and actively dispersing generalists such as Chironomidae (Debiasi et al.2022; Gobbi and Lencioni 2021; Martel-Cea et al. 2021). There is often a limited presence of predators in these ponds, and reduced competition, and as a result available resources may be readily exploitable by early colonisers. Additionally, the dominance of actively dispersing taxa in proglacial ponds we recorded, likely reflects their reliance on periodic recolonisation by these fauna, as the periodic freezing of the ponds in winter months (and the harsh winter environmental conditions) probably displaces macroinvertebrates from these ponds during these months (Gobbi and Lencioni 2021; Hamerlik et al. 2014). In contrast, paraglacial forest ponds likely represent more stable communities due to their disconnection from the glacial snout, which can increase thermal stability, extend the biological activity period, and promote the establishment of aquatic macrophytes which have been shown to enhance pond biodiversity through increased niche availability and food web complexity (Hinden et al. 2005; Hassall et al. 2011). This is reflected in our study with several taxa being found to be unique to paraglacial forest ponds, notably from Coleoptera orders which can require more stable environmental conditions. However, care is needed when interpreting these results as the uneven number of sample ponds in each group may have influenced the compositional patterns recorded.

Environmental drivers of proglacial and paraglacial forest pond macroinvertebrate communities

Several environmental factors were identified to be significantly associated with taxonomic richness and LCBD among the studied ponds. In this study, dissolved oxygen was found to be an important correlate of taxonomic richness. A negative association was recorded between dissolved oxygen and taxonomic richness in this study, contrasting sharply with studies that have examined ponds in lowland temperate and mediterranean environments which have found a positive association between dissolved oxygen and taxonomic richness (Lamelas-López et al. 2021; Hill et al. 2019). Many macroinvertebrates are directly reliant on dissolved oxygen for respiration, as they frequently possess gills or other underwater respiratory structures and often require high dissolved oxygen concentrations to survive (Croijmans et al. 2021; Lancaster and Downes 2013). In this study, the proglacial ponds often recorded a supersaturation of dissolved oxygen. This is likely caused by glacial meltwater and low productivity (Irvine-Fynn and Hodson 2010; Craig et al. 1992), and the negative association between dissolved oxygen and taxonomic richness may be more reflective of the wider harsh glacial conditions (e.g., rapidly fluctuating environmental conditions) limiting macroinvertebrate communities in proglacial ponds.

Sodium was also found to negatively influence ecological uniqueness (LCBD). High sodium levels in cryospheric freshwaters likely reflects glacially derived mineral inputs via weathering (Litaor 2022; Salerno et al. 2016; Sertic Peric et al. 2015), and could act as an abiotic filter of sensitive macroinvertebrate species. Sodium plays a key role in osmoregulatary processes of freshwater species, and excess sodium could negatively influence macroinvertebrate taxa due to increased energy expenditure and challenges with maintaining osmotic balance (Scheibener et al. 2016). Similar findings have also been recorded from glacier-fed streams and lakes, where conductivity, and water chemistry serve as key environmental filters for macroinvertebrate communities (Sertic Peric et al. 2015; Scotti et al. 2019; Fureder et al. 2006; Lods-Crozet et al. 2012).

Interestingly, no significant associations were recorded between taxonomic richness (or rarefied richness), and the distance of the pond to the glacial snout. This suggests that in lowland glacial landscapes the influence of glaciers on pond conditions and macroinvertebrate communities may be limited to the glacial snout itself. Once ponds have become hydrologically disconnected from the glacial snout, even if in close proximity to the glacier, their environmental conditions can temporally stabilise, macrophyte communities can colonise and environmental conditions can be established that supports a wide range of macroinvertebrate taxa. However, among lotic systems glaciers can have an extended influence, as a result of the longitudinal connectivity of rivers (Milner et al. 2001). Positive correlations have been demonstrated between taxonomic richness and the distance to the glacial snout, reflecting the gradual decrease in the influence of glaciers (and therefore increasingly suitable and stable environmental conditions, in particular temperatures) on the lotic environment downstream (Lencioni 2018; Jacobsen and Dangles 2012; Kuhn et al. 2011).

Conclusion

Understanding how freshwater biodiversity may respond and adapt within deglaciating environments is an increasing challenge. This study has shown that ponds formed as a result of deglaciation can support a wide diversity of aquatic macroinvertebrates, although proglacial ponds, located at the glacier snout, support a lower taxonomic richness than paraglacial forest ponds that are more isolated, and therefore have more suitable and stable physicochemical conditions (e.g., higher aquatic macrophyte coverages). Our study demonstrates the dynamic nature of pond macroinvertebrate communities in deglaciating landscapes, and that paraglacial forest ponds that are isolated from the glacier can support complex communities. As glacial retreat continues and landscapes transition from glacial to paraglacial, pond habitats will become increasingly important in supporting aquatic biodiversity at the landscape-scale. Future research is critically needed in these novel habitats to advance understanding of the spatial and temporal dynamism and succession of pond networks to provide the underpinning information needed to support biodiversity in these rapidly changing environments.

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Author contribution Matthew J. Hill: Conceptualisation, Methodology, Formal Analysis, Writing – original draft, Writing – review and editing, Visualisation. Ryan Wilson: Conceptualisation, Methodology, Formal Analysis, Writing—original draft, Writing – review and editing. Luis Uribe: Methodology, Writing – review and editing. Brian Ried: Conceptualization, methodology, Writing – review and editing. Pedro Pedreros: Writing – review and editing. Kate L. Mathers: Writing – review and editing, Paul J. Wood: Writing – review and editing.

Data availability The data generated in this study is stored by the authors and is available upon request.

Declarations

Competing interests The authors declare no competing interests.

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