



RESEARCH
PAPER

Environmental harshness and global richness patterns in glacier-fed streams

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ABSTRACT

Aim To test for a possible effect of environmental harshness on large-scale latitudinal and elevational patterns in taxon richness of macrofauna in arctic and alpine glacier-fed streams.

Location Svalbard (79° N), Iceland (65° N), Norway (62° N), Switzerland and Italy (46° N), France (43° N), New Zealand (43° S) and Ecuador (0°), covering an elevational gradient from sea level to 4800 m a.s.l.

Methods We gathered data from 63 sites along 13 streams and created an index of glacial influence (the glacial index, GI) as an integrative proxy for environmental harshness. The explicative power of the GI, environmental variables, latitude and elevation on taxon richness was tested in generalized linear models. Taxon richness along geographical gradients was analysed at standardized levels of GI in contour plots. Beta diversity and assemblage similarity was calculated at different GI intervals and compared with a null-model.

Results Overall, taxon richness decreased exponentially with increased GI ($r^2 = 0.64$), and of all included factors, GI had the highest explicative power. At low values of GI we found that local taxon richness varied along the coupled gradients of latitude and elevation in a hump-shaped manner. However, this pattern disappeared at high values of GI, i.e. when environmental harshness increased. Beta diversity increased, while similarity among assemblages decreased towards high GI values.

Main conclusions In our study system, the number of taxa able to cope with the harshest conditions was largely independent of the regional taxon pool, and environmental harshness constituted a 'fixed' constraint for local richness, irrespective of latitude and elevation. Contrary to expectations, we found that beta diversity was highest and similarity lowest among the harshest sites, suggesting that taxon richness was not solely driven by niche selection based on environmental tolerances, but also stochastic ecological drift, leading to dispersal-limited communities.

Keywords

Aquatic macroinvertebrates, benthic communities, dispersal limitation, geographical gradients, glacial rivers, niche selection, large-scale patterns, similarity, taxon richness.

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INTRODUCTION

Some of the most prominent large-scale geographical patterns in species richness and composition of natural communities are those along latitudinal and elevational gradients, often resembling each other (Lomolino, 2001; Gaston & Spicer, 2004). Several climatic factors such as mean temperature

run more or less parallel along latitudinal and elevational gradients, and climate (including energy) is undoubtedly a prime factor determining the distribution of life on earth (Currie, 1991; Whittaker *et al.*, 2001). However, the mechanism by which, for example, temperature relates to taxonomic richness is still debated (Currie *et al.*, 2004; Clarke & Gaston, 2006).

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1 Taxonomic richness is usually lower in harsh (e.g. cold or dry)
2 than in more benign (warm or wet) habitats (Currie *et al.*,
3 2004), perhaps because 'stressful' habitats such as hot springs,
4 salt flats and mountaintops are relatively rare and scattered
5 (Whittaker *et al.*, 2001). Richness is even further reduced in
6 ephemeral or intermittent environments (Williams, 1987;
7 Vincent & James, 1996). Still, even though disturbance is one
8 form of environmental harshness, according to the 'intermediate
9 disturbance hypothesis' (Connell, 1978) species richness is
10 expected to peak at intermediate levels of environmental distur-
11 bance. Hump-shaped relationships between species richness
12 and disturbance have been demonstrated in a number of eco-
13 systems, including streams (Townsend *et al.*, 1997), but this
14 pattern seems to be more the exception than the rule (Mackey &
15 Currie, 2001).

16 In harsh environments, the composition of local communi-
17 ties is expected to be predictable and similarity among commu-
18 nities high, due to deterministic niche selection filtering out
19 many species from the regional pool that cannot tolerate such
20 conditions (Chase, 2007). In contrast, in benign habitats where
21 most taxa can tolerate conditions, ecological drift produces
22 dispersal-limited communities with low similarity among local
23 communities (Leibold *et al.*, 2004; Chase, 2007). Thus, as envi-
24 ronmental harshness affects taxon richness at a local scale and
25 similarity among sites, broad-scale geographical patterns may
26 also depend on environmental harshness.

27 Arctic and alpine ecosystems are examples of harsh environ-
28 ments that cover about 8% of the terrestrial surface of our
29 planet, within a truly global distribution from 80° N to 67° S and
30 reaching elevations of more than 6000 m in the tropics (Chapin
31 & Körner, 1996). In spite of obvious differences in seasonality
32 between arctic and lower-latitude alpine systems, these are often
33 classified together as having comparable and harsh climatic con-
34 ditions, in particular low mean temperature (Körner & Paulsen,
35 2004; Nagy & Grabherr, 2009). Taxonomic diversity in arctic and
36 alpine communities varies and is shaped by the interaction of
37 many factors, including local environmental gradients (e.g.
38 topography, soil substratum), historical factors (e.g. glacial
39 history, species migration and evolution), disturbances (e.g. cli-
40 matic fluctuation and seasonality) and biotic interactions (e.g.
41 herbivore pressure, food web complexity) (Chapin & Körner,
42 1996; Nagy & Grabherr, 2009), with direct implications for
43 alpine ecosystem function (Dangles *et al.*, 2011, and references
44 therein). Even though there are local and regional differences in
45 taxon richness among arctic and alpine ecosystems, the observed
46 decrease in species richness of fungi, plants and animals within
47 arctic and alpine life zones has been attributed, at least in part,
48 to increasingly harsh environmental conditions (Gardes & Dahl-
49 berg, 1996 and references therein).

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50 Glacier-fed streams formed by ice-cold meltwater are
51 examples of arctic-alpine ecosystems that are expected to be
52 particularly similar across wide gradients in latitude and eleva-
53 tion (Ward, 1994), due to the very similar and environmentally
54 harsh nature of this habitat (Ilg & Castella, 2006). The usually
55 low richness of taxa (Milner *et al.*, 2001a) and functional traits
56 (Ilg & Castella, 2006) of the macroinvertebrate fauna in reaches

near the glaciers is believed to be limited, in particular, by low
water temperature, hydrological instability and disturbance of
the stream bed (Milner *et al.*, 2001a). The environmental harsh-
ness of a specific stream site is highly dependent on its distance
from the glacier and the size of the glacier delivering the melt-
water. Utilizing this simple and deterministic harshness gradient
in a globally distributed ecosystem, glacial streams provide an
excellent model system to explore how environmental harshness
interplays with large-scale geographical patterns in taxonomic
richness.

For this meta-analysis, we compiled data from the literature
on macroinvertebrate assemblages and environmental variables
at 63 sites along 13 glacier-fed streams, spanning wide gradients
in latitude (from 79° N and 43° S to the equator) and elevation
(from sea level to 4800 m a.s.l.). We created an index of glacial
influence (GI) (combining glacier size with distance from the
glacier terminus) and used this as an integrative proxy for envi-
ronmental harshness, allowing us to decouple harshness from
the spatial gradients and compare latitudinal and elevational
richness patterns at distinct levels of environmental harshness.
By using an ecosystem occurring at different elevations along
latitudes, we are dealing with inevitably linked latitudinal and
elevational gradients.

The overall objective of our study was to search for and deter-
mine the drivers causing large-scale spatial patterns in local
taxonomic richness of the macrofauna in an extreme ecosystem,
i.e. glacier-fed streams, and more specifically, we tested for a
possible effect of environmental harshness on any such large-
scale patterns. To our knowledge, whether richness patterns
along geographical gradients are influenced by environmental
harshness has yet to be demonstrated. Our a priori hypothesis
was that taxon richness would increase monotonically from
high- to low-latitude streams following the general latitudinal
pattern in local taxonomic richness (e.g. Gaston & Spicer, 2004),
including stream invertebrates (Vinson & Hawkins, 2003; Hof
et al., 2008), and that this relationship would disappear at
increasing levels of environmental harshness (Fig. 1). We did not
have sufficient data to test for true elevational patterns in
GI-standardized taxon richness within latitudes. However, as
glaciers are generally located at higher elevations at lower lati-
tudes this implies that taxon richness was expected to increase
monotonically from low to high elevations as well, simply
reflecting the latitudinal pattern. We further hypothesized that
high environmental harshness would be followed by a decrease
in beta diversity and an increase in mean assemblage similarity
among sites. This should be due to filtering out of most taxa
from regional species pools except for a few cosmopolitan taxa
able to cope with the harsh conditions.

MATERIALS AND METHODS

Data compilation

We compiled all available studies that provided data on macro-
invertebrate fauna, latitude, elevation, distance from glacier,
glacier size, maximum water temperature (T_{max}), stream water

conductivity and stream bed instability measured as the bottom component of the Pfanckuch index (Pfanckuch, 1975) from at least three stream sites at varying distances from the glacier. We included only streams with several study sites because we wanted to test whether the longitudinal distribution of taxon richness was dependent on glacier size. Few studies provide detailed data for groups of organisms other than macroinvertebrates, and the environmental variables were selected because they are given in most studies and because of their supposed importance for the distribution of macroinvertebrates in glacial streams (Castella *et al.*, 2001; Milner *et al.*, 2001a). Further, T_{max} was used instead of T_{mean} or T_{min} because it is the temperature measure applied in the conceptual model for the distribution of fauna in glacier-fed streams by Milner *et al.* (2001a). Data on T_{max} were obtained from either continuous logging during at least three 5-day periods in early summer, mid-summer and early autumn (European and north Atlantic streams), from 1 to 2 months of logging during March–April (Ecuadorian streams), or at least four spot measurements (New Zealand streams). Conductivity data represent mean values based on three to six spot measurements. The Pfanckuch index is a fairly constant site characteristic (Brittain *et al.*, 2001; Cadbury *et al.*, 2010). Seven of the 13 streams included (Brittain *et al.*, 2001; Gíslason *et al.*, 2001; Lods-Crozet *et al.*, 2001; Maiolini & Lencioni, 2001; Snook & Milner, 2001) were the same as those used in an analysis of effects of in-stream factors by Castella *et al.* (2001), but we added two streams in New Zealand (Milner *et al.*, 2001b), one more in Switzerland (Burgherr & Ward, 2001) and three in Ecuador (Jacobsen *et al.*, 2010; Jacobsen & Dangles, unpublished data).

We did not include sites below lakes or major non-glacial tributaries, as these may modify benthic communities considerably (Milner *et al.*, 2001a; Knispel & Castella, 2003). These criteria gave us data from 63 sites in 13 streams, with 3 to 10 sites per stream. All streams were represented by sites very close to the glacier (50–300 m), while the most distant sites included varied

more (1.5–11.0 km). Streams covered a latitudinal gradient from 79° N (Svalbard) and 43° S (New Zealand) to the equator (Ecuador), and an elevational range from sea level to 4800 m a.s.l.

To reduce the confounding effect from varying sampling protocols and taxonomic resolution of macroinvertebrates among studies, we counted family-level richness (Chironomidae sub-family). Moreover, none of the studies provided consistent species-level, or even genus-level, identification. Many families of freshwater macroinvertebrates have very wide or even cosmopolitan distributions (Jacobsen *et al.*, 1997), and it was expected that a large proportion of the fauna in our glacier-fed streams would be shared among regions.

Data analysis

Several measures of glacial influence at specific stream sites have been applied in the literature, including distance from the glacier terminus, percentage meltwater contribution to discharge, and percentage glacial cover of the catchment. None of these measures per se are believed to influence macroinvertebrate distribution (Milner *et al.*, 2001a), and their relationships with natural communities are likely to be indirect through other variables such as water temperature, water chemistry (conductivity), and streambed stability. We did not have data on percentage meltwater contribution to discharge or percentage glacial cover of catchment in this dataset. However, glacier size should influence meltwater discharge, and thus longitudinal distribution of in-stream conditions and community composition (Castella *et al.*, 2001). Therefore, we analysed local taxon richness in relation to an index integrating these two parameters. To obtain a standardized measure of glacial influence, and thus an integrated proxy for environmental harshness, we created an index combining glacier size with distance from the glacier terminus in the dimensionless measure:

$$GI = \frac{\sqrt{\text{Size}}}{\text{Dist} + \sqrt{\text{Size}}} \quad (\text{for size} > 0)$$

where GI is the glacial index, Size is the extension of the glacier in km² and Dist is the distance of the study site in km from the glacier's terminus. At maximum glacial influence (zero distance from the glacier snout) GI = 1, and it decreases exponentially towards zero with increasing distance from the glacier (Fig. S1 in Supporting Information).

Generalized linear models (GLMs) with a log link function were used to test for the effect of T_{max} , conductivity, Pfanckuch index, GI, latitude and elevation on taxon richness. We recognize that spatial coordinates such as latitude and elevation are arbitrary surrogates that may relate to richness merely if they are collinear with environmental variables (Currie *et al.*, 1999; Willig *et al.*, 2003) and therefore should not be considered in most analyses (Hawkins & Diniz-Filho, 2004). Nevertheless, our purpose was to compare the explicative power of three directly acting, small-scale, in-stream factors (T_{max} , conductivity and the Pfanckuch index), with that of a more indirect measure of glacial influence (GI index), and that of large-scale geographical vari-

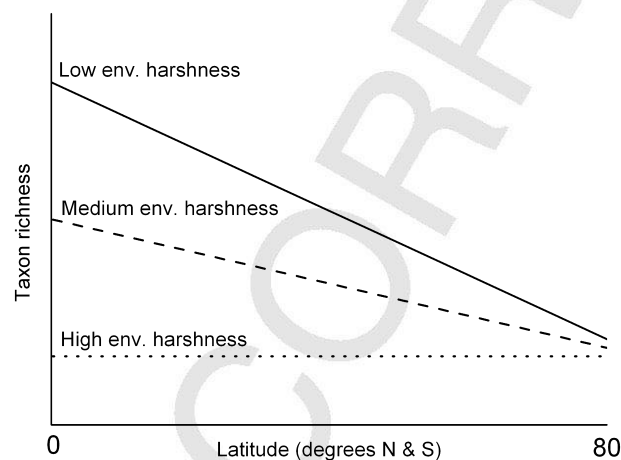


Figure 1 Conceptual diagram showing how three levels of environmental harshness are expected to influence a monotonic richness pattern along a latitudinal gradient.

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ables (latitude and elevation). Here, we therefore regard latitude and elevation as proxies for a possible regional taxon pool effect on local richness of glacial streams. All predictor variables were log-transformed. It was not necessary to remove sites with missing values because the GLM procedure handled the unbalanced design through the calculation of type III sum of squares. To avoid collinearity, a pair-wise regression matrix of all predictors was constructed.

Highly correlated predictors ($r > 0.6$, *sensu* Fernández *et al.*, 2006) such as elevation and latitude or elevation and glacier size were never included in the same model. Nevertheless, we chose to treat elevation and latitude separately in the analysis and plots because the effect that they have on taxon richness may imply different mechanisms. For each model, we included the effect of each factor alone and their interaction. We also included a term 'site' in our analysis to allow within-site comparisons while controlling for variation resulting from unmeasured site-specific parameters. Site was treated as a random effect in all analyses by means of the generalized linear mixed model function (glmmPQL; MASS library for R). This ensured that the correct degrees of freedom were used in the different analyses. The more parsimonious model was identified using the Akaike information criterion (AIC). We used the likelihood ratio test (LRT) to find the difference between the initial models and the reduced models, dropping an 'effect' term. All analyses were performed using the mass library for R (R Development Core Team, 2009, version 2.10.1). Note that we preferred using linear models rather than nonlinear ones (e.g. generalized additive models) because coefficients of linear models are easily comparable between studies and interactions can easily be tested. To graphically represent spatial patterns in taxon richness, we used contour plots performed with Statistica® version 9 (Statsoft).

Variability in taxonomic composition among sites was analysed at five different intervals of environmental harshness: GI = 0.0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8 and 0.8–1.0. For each of these five groups, we calculated a simple measure of beta diversity or species turnover as γ/α , where γ is the total number of taxa at seven sites (which was the smallest number of sites in any of the five groups) randomized 10,000 times, and α is the mean number of taxa per site in the group (Tuomisto, 2010). We also calculated the mean value of Sørensen's similarity index (based on presence/absence data) on all pair-wise combinations in each of the five groups. Because similarity indices are biased by the number of taxa in the different communities (Wolda, 1981), and because taxon richness varied considerably along the GI gradient, we developed an additional null-model approach where mean similarities within groups were calculated on randomized selections of taxa from the entire dataset. This approach, which is quite similar to the one applied by Chase (2007), allowed us to test the hypothesis of whether within group similarity differed from the one expected from a purely random distribution.

RESULTS

The compiled data used in the analysis are found in Appendix S1. Even though the specific longitudinal pattern in local taxon

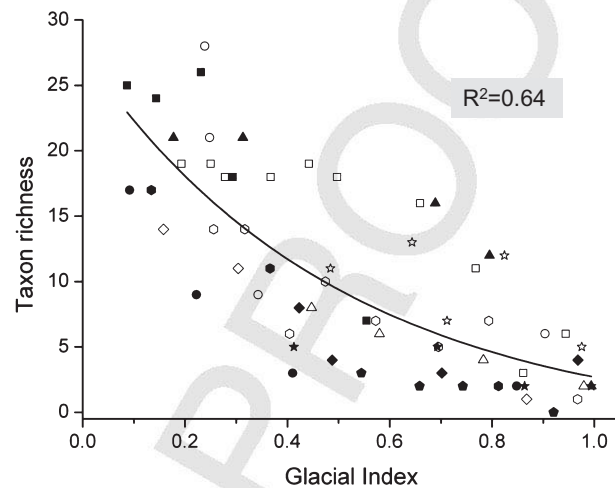


Figure 2 Local taxon richness of macroinvertebrates in glacier-fed streams as a function of the glacial index. The regression line is an exponential model, shapes represent different glaciers (see Appendix S1) Glacier15, open diamond; Glacier14, closed hexagon; Antisana, open hexagon; TAI, open circle; Fox, open triangle; Waiho, closed diamond; CON, closed square; Roseg, open square; MUT, closed triangle; BRI, open star; LEI, closed circle; WJO, closed star; BAY, closed pentagon.

richness varied considerably among the 13 streams, all (except for Waiho in New Zealand) showed a clear increase in taxon richness within the first few kilometres from the glacier (Fig. S2, Appendix S1). The steepness of this increase within each stream, expressed as the slope of a linear regression of taxon richness versus log distance from the glacier, was inversely related to glacier size ($r^2 = 0.69$) (Fig. S3). The GI explained 64% of the variability in local taxon richness, following an exponential fit (Fig. 2). Overall, local taxon richness was correlated with GI ($r = -0.78$; $P < 0.0001$), T_{\max} ($r = 0.54$; $P = 0.0002$), the Pfanckuch index ($r = -0.49$; $P = 0.0002$), distance to the glacier ($r = 0.44$; $P = 0.0003$) and glacier size ($r = -0.39$; $P = 0.0015$), but not with latitude, elevation or conductivity ($P > 0.05$). GI correlated significantly with T_{\max} ($r = -0.66$; $P = 0.0002$) and the Pfanckuch index ($r = 0.55$; $P = 0.0002$).

These results were largely supported by the GLMs (Table 1). Of the six explanatory factors considered in the GLM analysis (see Materials and Methods), GI had by far the most significant effect on taxon richness ($\Delta AIC = 80.0$, $P < 0.001$). The GLM also identified T_{\max} , the Pfanckuch index and their interaction as significant predictors of taxon richness ($P < 0.05$, Table 1). No significant effect of sites was found, indicating that our patterns were globally little affected by site-specific variables not accounted for. We found a hump-shaped relationship between local taxon richness and latitude and elevation, but this pattern disappeared at high values of GI, i.e. when environmental harshness increased (Figs 3 & 4). Taxon richness at similar values of GI was higher in all four streams in the European Alps than in the three Ecuadorian streams.

Many taxa were shared between regions, e.g. 58% of the families found in Ecuadorian streams were also found in central

Table 1 Results of the generalized linear model's (GLM's) deviance analysis on taxon richness in the 63 glacier-fed stream sites.

Effect	Terms included in the initial model (+ interactions)	AIC	ΔAIC	LRT	P-value
GI	Lat, GI, Cond, Pfan	349.2	80.0	8.981	< 0.001
T_{\max}	T_{\max} , Cond, Pfan, Lat	276.2	3.4	2.054	0.017
$T_{\max} \times \text{Pfan}$	T_{\max} , Cond, Pfan, Lat	275.0	2.2	1.431	0.039
Lat \times Cond	T_{\max} , Cond, Pfan, Lat	276.1	3.3	2.021	0.019

AIC is the Akaike information criterion for the initial model after removal of the 'effect' term. ΔAIC corresponds to the difference between the AIC of the initial model and that of the reduced model. The likelihood-ratio test (LRT) and associated P-value test the hypothesis that the suppression of the 'effect' term provides no better fit than the initial model. For each model, we included the effect of each factor alone and their interaction. Only significant results of the GLM analysis are shown. GI = glacial index; Lat = latitude; Pfan = Pfankuch index; Cond = water conductivity; T_{\max} = maximum water temperature.

Europe (Pyrenees and Alps), while 85% of the families in New Zealand were found in Ecuador and 54% in central Europe. Most of the families occurring in the poorer streams in Svalbard and Iceland were also found in the other regions (83–100%). Neither beta diversity nor mean assemblage similarity followed the expected pattern (Fig. 5). Beta diversity increased, while similarity decreased at higher values of GI ($F_{4,296} = 15.9$, $P < 0.001$, ANOVA; GI-groups 0.0–0.2 and 0.2–0.4 significantly different from groups 0.4–0.6, 0.6–0.8 and 0.8–1.0, $P < 0.05$, Turkey test). All observed mean similarities were significantly higher than expected by the random null-model ($P < 0.05$, t -test).

DISCUSSION

The GI as a proxy for environmental harshness

The strong relationship between local taxon richness and GI (Fig. 2) showed that the index performed well and should be taken into account or standardized in comparative analyses of driving factors for taxon richness across geographical gradients. Even though GI is supposed to reflect environmental disturbance (and it was in fact correlated with the Pfankuch index), we should not necessarily expect a unimodal relationship between taxon richness and GI, as otherwise predicted by the 'intermediate disturbance hypothesis' (Connell, 1978; Townsend *et al.*, 1997) because glacial streams may not include the most stable sites, and thus not cover the entire disturbance gradient.

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The GI alone explained more total variability in local taxon richness than the model based on T_{\max} and stream bed instability (Pfankuch index) and was the most important effect comparing models in the GLMs. This was surprising considering that these factors are generally regarded as those directly regulating communities in glacial streams (Milner *et al.*, 2001a). There may be at least three explanations for this finding. First, in addition to the effects of T_{\max} and stream bed instability, GI probably integrates the effects of other factors that we have not considered here (e.g. turbidity, suspended solids, substrate type). Second, the lower explanatory power of the in-stream variables could be related to the quality of the data. T_{\max} and conductivity are

elusive parameters in that reliable mean, maximum and minimum values are difficult to obtain. The Pfankuch index is subjectively derived from a score sheet, and values may therefore not be fully consistent among studies. Third, even though T_{\max} is provided and used as a predictive parameter in most studies on glacial stream ecology, it may not be the temperature metric with the most ecological relevance; mean or mean maximum temperature could prove more important. Likewise, the Pfankuch index may not be measuring the most relevant components of disturbance that actually act upon benthic communities, such as for instance fluctuations in near-bed shear stress or in available food resources.

The GI appears to be a simple and useful measure of environmental harshness in glacier-fed streams that may be used in future and ongoing long-term studies on the effects of glacial retreat (Oerlemans, 2005; Vuille *et al.*, 2008) on alpine streams (Brown *et al.*, 2007; Milner *et al.*, 2009). However, data were sparse. To improve the geographical coverage of data, future studies should particularly focus on systems in the subtropics (e.g. Central Asia, southern Andes) and tropics (northern Andes, eastern Africa).

Maximum richness at temperate latitudes

Based on data from seven glacial streams, Castella *et al.* (2001) and Milner *et al.* (2001a) found an increase in taxon richness from Svalbard to the French Pyrenees. They saw this as an expression of the general latitudinal pattern in taxon richness observed for many organisms (e.g. Gaston & Spicer, 2004), including stream invertebrates (Vinson & Hawkins, 2003; Hof *et al.*, 2008), with local richness reflecting the regional taxon pool (Caley & Schluter, 1997; Fox *et al.*, 2000). They explained the increase in taxon richness from high- to mid-latitude (and mid-elevation) glacial streams by a low regional species pool due to recent glaciations and geographical isolation at high latitudes (Iceland and Svalbard are islands). In addition, speciation is probably also low at high latitudes due to low temperature and evolutionary time (Rohde, 1992, 1999) and high climatic variation (Kozak & Wiens, 2007). However, in the studies by Castella

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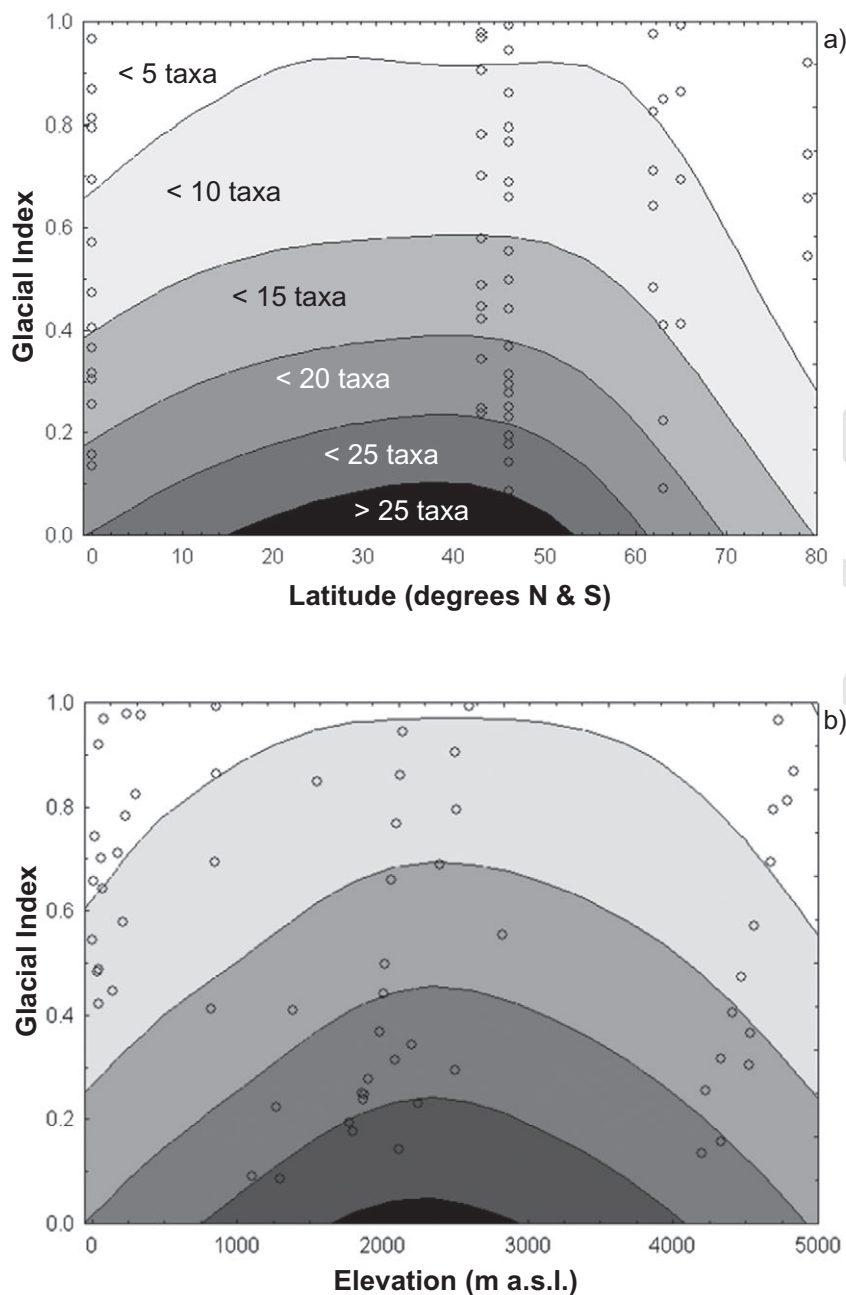


Figure 3 Contour plots showing how local taxon richness of macroinvertebrates in glacier-fed streams (surface, grey shading) vary with latitude and the glacial index (a), and elevation and the glacial index (b). A spline fit was used to produce the contour lines. Data points denote single stream sites.

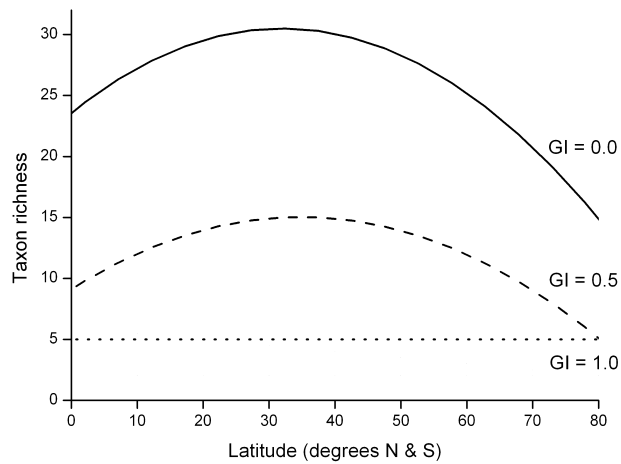
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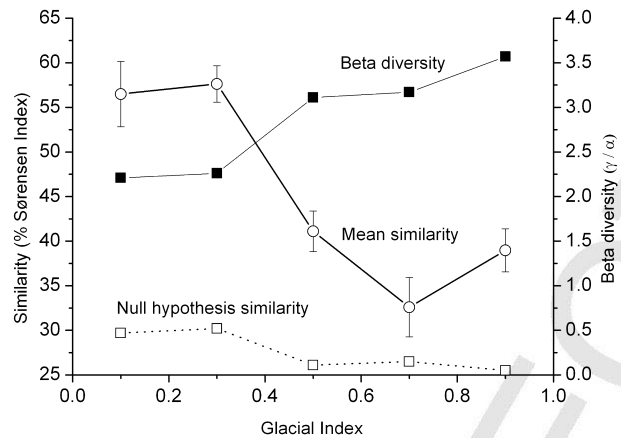
1 *et al.* (2001) and Milner *et al.* (2001a), latitude was paralleled by
2 a gradient in glacier size, with the largest glaciers at the northern
3 end of their range and smaller glaciers at the southern end; the
4 Alps and Pyrenees. Consequently, the latitudinal pattern in
5 taxon richness of stream fauna could have been influenced by a
6 gradient in environmental harshness, in addition to the latitudi-
7 nal one.

8 By extending the latitudinal and elevational range to the
9 tropics and standardizing the environmental harshness through
10 GI we found that the relation between taxon richness and lati-
11 tude and elevation was hump-shaped rather than monotonic.
12 Within latitudes, hump-shaped relationships between species
13 richness and elevation have been shown for a number of taxo-

14 nomic groups in defined regions, such as birds in the tropical
15 Andes (Rahbek, 1997), small mammals on Borneo (Md. Nor,
16 2001), plants in the Himalayas (Grytnes & Vetaas, 2002), ants
17 in the western USA (Sanders, 2002), and, to some degree, stream
18 macroinvertebrates in Ecuador (Jacobsen, 2008). Such patterns
19 have often been interpreted as being caused by a stochastic distri-
20 bution of taxa within geometric constraints from 'hard
21 boundaries', leading to a mid-elevational maximum denomi-
22 nated mid-domain effect (MDE), with no other ecological
23 factors driving the observed patterns (Colwell & Lees, 2000).
24 However, MDE null models have been seriously questioned,
25 mainly due to internal logical inconsistencies and artefacts
26 (Currie & Kerr, 2008, and references therein). We regard the
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1 **Figure 4** Maximum taxon richness at three different levels of
 2 environmental harshness (index of glacial influence GI = 0.0, 0.5
 3 and 1.0) along the latitudinal gradient. The figure is based on the
 4 data extracted from the contour plot in Fig. 3(a).

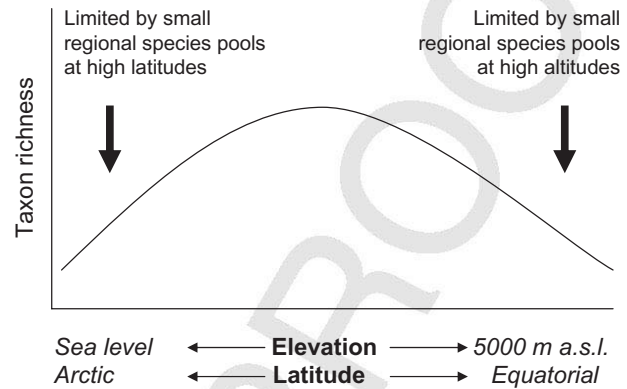


5 **Figure 5** Beta diversity (γ/α), observed mean assemblage
 6 similarity (Sørensen index) and the expected similarity under a
 7 random null model among sites at five different intervals of
 8 environmental harshness: GI = 0.0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8
 9 and 0.8–1.0. Error bars denote SE.
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12 MDE as irrelevant to this study because the relationship between
 13 taxon richness and elevation found here is an inter-latitudinal
 14 relationship produced by the fact that a standard ecosystem like
 15 pro-glacial streams moves to higher elevations when moving
 16 from the arctic to the equator. Pro-glacial streams cover rela-
 17 tively narrow elevational ranges within latitudes; for instance in
 18 the European Alps such streams are found from 1320 m a.s.l.
 19 (Robinson *et al.*, 2001) to 2830 m a.s.l. (Maiolini & Lencioni,
 20 2001). At present we do not have sufficient data density to test
 21 for GI-standardized elevational patterns in taxon richness
 22 within latitudes.

23 The elevational richness pattern found here is thus linked to
 24 the latitudinal pattern, showing a peak at mid-latitudes. Such
 25 patterns deviating from the common maximum richness in the

Harshness and richness in glacier-fed streams



26 **Figure 6** A conceptual diagram showing how local taxon
 27 richness of macroinvertebrates in glacier-fed streams varies along
 28 parallel gradients in latitude and elevation, with maximum
 29 richness at north-temperate latitudes and mid-elevations, and
 30 richness limited at both high latitudes and elevations by low
 31 regional taxon richness.
 32

33 tropics have been reported before (Currie *et al.*, 1999), but
 34 usually for quite well-defined taxonomic groups such as amphipods
 35 and crayfish (France, 1992), copepods (Reid, 1994), galling
 36 insects (Price *et al.*, 1998) and sawflies (Kouki, 1999), and in
 37 studies covering incomplete latitudinal gradients on, for
 38 example, marine algae (Rivadeneira *et al.*, 2002) and cave fauna
 39 (Culver *et al.*, 2006). However, our latitudinal hump-shaped
 40 pattern is unusual considering that stream macroinvertebrates
 41 comprise a taxonomically diverse assemblage.

42 Between mid-latitude and the polar regions, the general
 43 increase in richness with decreasing elevation (Jacobsen, 2004)
 44 is apparently surpassed by the generally negative relationship
 45 between richness of stream macroinvertebrates and latitude
 46 (Jacobsen *et al.*, 1997). In contrast, glaciers at low latitudes are
 47 situated at such extreme elevations that the elevational effect
 48 seems to overrule that of latitude. Year-round nocturnal freezing
 49 of the stream and/or low oxygen availability may be a limiting
 50 factor for biodiversity in glacial systems at extreme elevations in
 51 the tropics (Jacobsen *et al.*, 2003; Jacobsen, 2008). Hence, there
 52 seem to be unbalanced relationships between latitude, elevation
 53 and taxon richness of macroinvertebrates in glacial streams over
 54 wide latitudinal gradients (Fig. 6).
 55

Low similarity and dispersal-assembled communities in harsh glacial streams

56 The hump-shaped latitudinal pattern in taxonomic richness in
 57 glacier-fed streams was lost at high levels of environmental
 58 harshness, i.e. taxon richness of the sites closest to the glaciers
 59 varied only slightly along the latitudinal gradient. Consequently,
 60 even though environmental harshness decreased taxonomic
 61 richness over the entire latitudinal gradient, the relative effect
 62 was greatest in the richest streams at mid-latitudes. Hence, in
 63 our system, the number of taxa able to cope with extreme
 64 conditions was largely independent of the regional taxon pool, and
 65
 66

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1 environmental harshness seemed to constitute a 'fixed'
2 constraint for taxonomic richness, irrespective of latitude and
3 elevation.

4 Consequently, we expected beta diversity to be negatively
5 related and assemblage similarity positively related to environ-
6 mental harshness, even when analysing across regions as done
7 here. Our results may have been affected by possible differences
8 among studies in the thoroughness and timing of sampling.
9 Likewise, a higher level of taxonomic resolution (species level)
10 could potentially reveal other patterns. It is worth noting that
11 patterns in mean similarities at different levels of harshness
12 might have been different had the analyses been performed on
13 quantitative faunal data. Nevertheless, our finding that beta
14 diversity, even at the family level, was highest and assemblage
15 similarity lowest among the harshest sites closest to the glaciers
16 was in contrast to expectations (Chase, 2003). There could be
17 several explanations for this. First, even though assemblages at
18 the harshest sites close to the glaciers could mainly be driven by
19 niche selection (Chase, 2007, and references therein), the envi-
20 ronments at these sites may not be as similar as we think.
21 Second, instead of representing multiple stable equilibria, which
22 should be more likely in systems with large regional species
23 pools, low rates of connectivity, high productivity and low dis-
24 turbance (Chase, 2003), the harshest sites might be non-
25 equilibrium, temporally unstable assemblages. Third, pro-glacial
26 reaches indeed seem to select for certain species traits such as
27 cylindrical and streamlined shape, small body size, clinging
28 behaviour, omnivory and short life cycles (Ilg & Castella, 2006;
29 Füreder, 2007; Milner *et al.*, 2009), and some glacial stream-
30 dwelling species can be denoted as habitat specialists which are
31 very characteristic to pro-glacial reaches on specific continents
32 (Milner *et al.*, 2001a). However, the families and subfamilies to
33 which these species belong (as analysed here) are certainly not
34 restricted to glacial streams and occur on most continents. In
35 addition, many more taxa that are common in non-glacial
36 streams lower down (perhaps possessing some of the same func-
37 tional traits) are often found in pro-glacial reaches as well, but
38 their occurrence here is rather sporadic. Based on the limited
39 number of data available we tentatively suggest that pro-glacial
40 streams may not be driven by competition (Flory & Milner,
41 1999) and/or niche-selection based on environmental tolerances
42 alone, but also stochastic ecological drift due to low dispersal
43 into and among sites located at such extreme geographical posi-
44 tions as pro-glacial streams, leading to dispersal-limited com-
45 munities (Leibold *et al.*, 2004; Chase, 2007).

46 Glacial streams could serve as an ideal system to conduct
47 experimental and long-term studies to understand more about
48 the relative importance of niche-selection versus dispersal in
49 determining communities, and the occurrence of multiple stable
50 equilibria or/and temporally unstable communities in harsh
51 environments.

52 ACKNOWLEDGEMENTS

53 The funding by a WWF-Novozymes grant 2008 to D.J. and an
54 Ecofondo grant no. 034-ECO8-inv1 to O.D. is greatly appreci-
55

ated. We thank John Brittain, Peter Burgherr, Emmanuel Cas-
tella, Bruno Maiolini and Alexander Milner for additional
unpublished data, and Patricio Andino, Rodrigo Espinosa,
Ladislav Hamerlik, Jesper Köhl and Signe Vie for technical
support with invertebrate sampling in the Ecuadorian streams.
The comments by Fabien Anthelme, Peter Burgherr and Nathan
K. Lujan on an early version, and by two anonymous referees
and editors Janne Soininen and David Currie on a later version
greatly improved the paper.

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SUPPORTING INFORMATION

7

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

Figure S1 The glacial index (GI) as a function of distance from
the glacier in the 13 study streams.

Figure S2 Taxon richness as a function of distance from the
glacier in the 13 study streams.

Figure S3 The slope of linear regressions of taxon richness
versus log distance from the glacier as a function of glacier size
for the 13 study streams.

Appendix S1 Compiled data on geographical information,
environmental variables and taxon richness of macroinverte-
brates in glacier-fed streams.

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Editor: Janne Soininen

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