Title: Functional diversity and community assembly of river invertebrates show globally consistent responses to decreasing glacier cover

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Abstract: Global change threatens invertebrate biodiversity and its central role in numerous ecosystem functions and services. Functional trait analyses have been advocated to uncover global mechanisms behind biodiversity responses to environmental change, but the application of this approach for invertebrates is underdeveloped relative to other organism groups. From an evaluation of 363 records comprising >1.23 million invertebrates collected from rivers across nine biogeographic regions on three continents, consistent responses of community trait composition and diversity to replicated gradients of reduced glacier cover are demonstrated. After accounting for a systematic regional effect of latitude, the processes shaping river invertebrate functional diversity are globally consistent. Analyses nested within individual regions identified an increase in functional diversity as glacier cover decreases. Community assembly models demonstrated that dispersal limitation was the dominant process underlying these patterns, although environmental filtering also was evident in highly glacierized basins. These findings indicate that predictable mechanisms govern river invertebrate community responses to decreasing glacier cover globally.

Introduction: Invertebrates account for >95% of animal biodiversity, playing a major role transferring matter through the web of life [1,2]. Understanding invertebrate functional responses to environmental change is of urgent importance to reduce significant extinction threats [3], and changes to major ecosystem functions given the important role of invertebrates in processes such as carbon cycling, soil fertility and water purification. The increasing availability of globally-representative ecological databases has enabled new insights into large-scale synchrony of functional trait responses of selected animal and plant groups to environmental change [4-8]. Yet, no studies have focused on how environmental change influences the traits and functional diversity (FD) of invertebrates at the global scale.

Quantifying the extent to which invertebrates respond to environmental gradients is vital for understanding community assembly processes, functional responses to global change, and effective ecosystem conservation and management.

Ecologists consider organismal traits central to understanding processes maintaining biodiversity because of consistent responses along environmental gradients, whereas taxonomic responses can be influenced by biogeographical constraints on evolutionary processes and dispersal [9,10]. Here we evaluate community level trait and functional diversity responses of river invertebrates to a gradient of decreasing glacier cover worldwide (Supplementary Figure 1), to elucidate the key processes driving their response to this cryospheric symptom of global environmental change. Glaciers cover ~10% of the Earth's land surface, but the most recent estimates of global glacier change [11] indicate mass loss of 259 ± 28 Gt y^{-1} between 2003 and 2009 with global runoff from glaciers exceeding 1,350 km^3 y^{-1} . Changes in hydrology and river geomorphology caused by glacier loss are expected to have major implications for river ecosystems [12]. Glacier fed rivers can inform our understanding of the ecological processes driving trait and functional diversity responses across large spatial scales for two principal reasons: (i) negative glacier mass-balance in most regions of the world due to climate change [12,13] creates consistent gradients in river habitat conditions characterised by increasing water temperature as ice influence decreases, and more stable river channels driven by reductions in glacial sediment production, less variability in flow regimes and vegetation colonisation of river banks [14]; (ii) broadly similar post-glacial habitats without anthropogenic modifications are found worldwide within confined geographic zones (Arctic and alpine), thereby minimising inter-region dispersal and enhancing speciation amongst metapopulations [15]. In addition, although the effects of glacier retreat on taxonomic biodiversity have been examined [16,17], a unified understanding of river invertebrate traits, FD and assembly processes in response to glacier retreat or other forms of environmental change remains elusive.

Trait information was compiled and standardised from databases of aquatic invertebrates covering Europe, North America and New Zealand. Aquatic invertebrates are used widely for river biomonitoring owing to their high biodiversity and diverse environmental requirements; thus, their functional traits are well described [18] enabling their use as a 'model' group for understanding the effects of decreasing glacier cover on river ecosystems globally. Trait information was integrated with a taxonomic dataset totalling >1.23M individual invertebrates comprised of 113 genera and sub-families, collected from river sites where glacier cover varied widely in the river catchment or over time (Supplementary Figure 1; Supplementary Table 1). Traits that offer resistance or resilience to environmental stress in glacier fed river systems [19] were included, specifically body size, life-cycle length, pupation, adult life-stages, respiration mode, locomotion/substrate attachment, diet and resistance elements. Fuzzy codes were adopted to represent affinities of each taxon to each trait (e.g. 0 = no affinity to 3 = strong affinity) and acknowledge variability of traits at different life stages and in response to varied environmental conditions. Although the rivers in the nine biogeographic zones span different geological ages and climatic zones, similar aquatic environmental change gradients, with higher water temperature and channel stability, were evident as glacier cover decreased (Supplementary Table 2). These parameters are known to be central drivers of taxonomic biodiversity patterns in glacier-fed rivers [20]. We tested the hypotheses that there would be consistent responses to decreasing glacier cover apparent for: (i) individual traits and their combinations, (ii) the distribution and abundance of taxa in functional trait space, and (iii) community assembly processes.

Central to our approach is the concept of the metacommunity, defined as a set of local communities that are linked by dispersal of multiple potentially interacting species [21]. Within this framework, local community structure is analysed as a function of the regional species pool to reveal the processes driving community assembly [22]. The sets of processes involved can be described broadly by four non-exclusive ‘paradigms’: neutral (random loss and gain of species); species sorting (niche-based environmental filtering driven by local habitat heterogeneity); patch dynamics (local species diversity limited by dispersal) and mass effects (niche-based processes distorted by high immigration rates). Most ecological applications assume that species sorting is the dominant paradigm [23], yet this special case only occurs where fitness differences between species are sufficient and dispersal rates are of an optimal, intermediate magnitude to allow efficient tracking of the environment without drowning out niche-based processes [24].

The combination of data on species traits and metacommunity structure underlies the most promising community prediction tools available to date. In the context of dispersal, metacommunity processes are best described as probabilistic species pools [25] yet available models are not capable of fully reflecting this at present [22,26]. We propose a powerful, probabilistic approach (Supplementary Figure 2) in which trait selection and metacommunity processes are integrated via four model components: (i) a uniform model, under which taxa are selected randomly from the species pool; (ii) a pure dispersal model, that weights a taxon’s probability of selection from the species pool as a function of their occurrence at sites at varying distances from the focal site under consideration, predicting abundance as the mean abundance of the taxon throughout the metacommunity; (iii) a pure trait selection model, which selects taxa iteratively from the species pool and predicts abundances until the community (abundance) weighted means of traits exhibited by the generated community closely matches the observed means; and (iv) a mixed model, that combines occurrence probabilities from the dispersal component with abundances from the trait selection component. In all cases, species richness is fixed at observed values. By comparing the ability to explain community structure of the latter three model components relative to the uniform (null) model, we can demonstrate the relative influence of dispersal limitation (patch dynamics), trait selection (species sorting), and both in combination.

Results and discussion: Consistent responses of invertebrate community trait composition occurred across a gradient of decreasing glacier cover globally and Fuzzy Correspondence Analysis (FCA) axis 1 scores increased significantly towards high latitudes (Figure 1). Decreasing glacier cover was associated strongly with: a shift in life cycle length from a predominance of multi-generations per year (multivoltine) to longer generation times spanning one (univoltine) or more (semivoltine) years; an increase in no pupation versus a decrease in aquatic pupation; a decrease in burrowing; increases in coarse particulate organic matter (CPOM) consumption but decreases for fine particulate organic matter (FPOM) feeding. Life cycle shifts suggest that where glacier cover is high, organisms typically develop rapidly in the spring and summer melt seasons before many river flows decrease/cease or where rivers freeze through winter. In rivers with less glacial influence, a tendency towards year-round flow and greater habitat stability [27] can benefit larger organisms with longer life cycles, although the FCA1 variance evident at 0% glacier cover exemplifies that some non-glacial rivers in Arctic and alpine areas retain trait profiles similar to rivers with high glacial cover, implying that they may dewater in late summer or freeze in winter. Shifts in pupation traits with decreasing glacier cover reflect the increasing relative abundance of river insects that undergo incomplete metamorphosis, such as Plecoptera (stoneflies) and Ephemeroptera (mayflies), and more non-insect taxa such as Oligochaeta (worms). Dietary shifts reflect a tendency for sites with low or no glacier cover to have more riparian vegetation supplying litter to rivers, and thus more CPOM for detritivores.

To assess whether trait profiles underpinning the consistent FCA1 responses were attributable to Linnean taxonomic groups (i.e. families, orders) and therefore represented a phylogenetic response, hierarchical cluster analysis of the species *x* trait matrix was undertaken to identify distinct functional groups (FGs). Nine FGs were obtained (Figure 2) and several of these superseded taxonomic identity, being composed of taxa from multiple orders but sharing similar biological trait profiles. For example, FG1 and FG3 were composed of the most common, globally incorporated taxa from the Diptera, Ephemeroptera and Trichoptera, and representatives of Oligochaeta, Ephemeroptera and Plecoptera, respectively. FGs 1 and 3 displayed distinctly different functional strategies associated with differing life cycles, diet, body size and pupation strategies (Supplementary Figure 3). The relative abundance of FG1 decreased ($p < 0.001$; $R^2=0.58$) and FG3 increased ($p=0.004$; $R^2=0.36$) as glacier cover declined (Figure 2), highlighting that specific trait combinations confer different responses to decreasing glacier cover. Many other FGs were globally rare and occurred only in low latitude regions and/or at sites of low glacier cover (Figure 2). For example, FGs consisting of large, obligate predators with relatively long life cycles (e.g. FGs 6, 7 and 8) were recorded only in the Alps, Pyrenees, New Zealand and Norway. This is likely due to strong environmental filters (e.g. colder water temperature, shorter growing season, reduced basal resources) operating on the regional species pool in Arctic and sub-Arctic locations [28].

Our analysis of FD response to decreasing glacier cover focused on Functional Richness (FRic), Functional Divergence (FDiv); Functional Evenness (FEve), Functional Dispersion (FDis) and Functional Entropy (FEnt). Decreasing mean index values illustrated that the realised trait space for invertebrates narrows significantly with increasing latitude (Figure 3). Subsequent analyses to test within-region responses revealed significant increases of FD indices with decreasing glacier cover (Figure 4), with the only exception being FDiv (Supplementary Figure 4). FRic increased significantly with less glacier cover ($p<0.001$; $R^2=0.17$), reflecting a greater diversity of traits. FEve showed more regular distributions of organisms in trait space with decreasing glacier cover ($p<0.001$; $R^2=0.28$), demonstrating greater niche saturation and implying that resistance to new colonisers becomes stronger in more benign habitats [29]. FDis ($p<0.001$; $R^2=0.47$) and FEnt ($p<0.001$; $R^2=0.44$) also increased significantly with declining glacier cover. This indicates that dominant species were located further from the centre (FDis) and further from each other (FEnt) in trait space, suggesting greater competition and/or the opening up of new, distinct niches in more benign habitats. Although significant, FDiv was less related to glacier cover ($p<0.001$; $R^2=0.08$), displaying no strong trends within regions. The random effect structure of the 'best' candidate models suggested that FRic and taxonomic richness were sensitive to variation within regions (Supplementary Table 4). Other FD indices were stable across biogeographic regions, demonstrating lower sensitivity to species pool effects and thus more useful for tracking environmental change in the absence of *a priori* information on the regional species pool [30].

Community assembly modelling indicated that dispersal was the primary mechanism driving invertebrate community response to decreasing glacier cover (Table 1), closely following the patch dynamics paradigm of metacommunity theory [21]. This conclusion was supported by the absence of consistent relationships amongst river environmental variable Principal Coordinates of Neighbourhood Matrix (PCNM) scores and residuals from the dispersal model (Supplementary Figure 6). Compared to uniform and trait-selection models, artificial communities assembled through sampling from the species pool were more similar to observed communities when samples were weighted based on distance between sites where each taxon in the species pool occurred. Constraining the composition of artificial communities by observed community weighted means on the first two synthetic traits (FCA axes in the trait selection model) did not, on average, make null and observed communities any more similar than under the uniform scenario. Even a mixed model including both dispersal (species' occurrences) and trait selection (species' abundances) did not improve on predictions under the pure dispersal model (Table 1; Figure 5; Supplementary Figure 5).

The relationship between glacier cover and the residual similarity described by the dispersal and trait selection models compared with the uniform scenario (random with fixed species richness; Figure 5) suggested that communities are environmentally filtered in highly glacierized basins [19] via processes selecting for, or filtering out, traits associated with FCA1 (voltinism, pupation, diet). However, dispersal limitation exerts a stronger influence that is maintained as glacier cover decreases (Figure 5; Table 1), linked to constraints on inter-basin organismal movement due to mountainous terrain, dendritic river network structure, flow intermittency and habitat fragmentation due to lakes and/or anthropogenic development [31,32]. Our finding that dispersal limitation interferes with species sorting is supported by a growing consensus that organismal movement strongly governs ecological community and functional diversity [24]. One implication is that under scenarios of rapid future environmental change such as a shrinking cryosphere, organisms with only short-distance dispersal ability might not keep pace with habitat shifts in space leading to high rates of reorganisation in ecological network interactions [33]. Dispersal constraints, coupled with movement of superior competitors or predators, make it difficult to extrapolate current findings to future scenarios, potentially raising wider concerns about the efficacy of invertebrate biomonitoring approaches that assume target organisms are free to track changes in the local environment.

Together, these analyses reveal empirical evidence for strong similarities in the forces shaping invertebrate functional traits globally in response to decreasing glacier cover. Trait patterns for riverine invertebrates have been examined previously only across individual continents, and spanning different environmental drivers to our focus on glacier retreat [34,35]; in contrast, our study of invertebrates simultaneously covered three continents and both hemispheres. Functional trait analysis revealed a strong likelihood of latitude-contingent trajectories for predicted community responses to global change [16]. Fuzzy correspondence analysis and FD indices indicated a narrowing of the available and realised functional trait space towards polar regions, with high glacial influence rivers being similar to non-glacial rivers [36]. This was further highlighted by the latitudinal variability in FG patterns across the glacier melt gradient, with higher intercepts and lower slope values for FG1 at higher latitudes (Figure 2). These patterns are supported by plant studies which suggest environmental filtering as a central driver of latitudinal patterns [37]; however, our findings for invertebrates could reflect evolutionary constraints linked to colder conditions and shorter development periods for ectotherms [38]. For example, extremes of low temperature and riverbed freezing typical of rivers with high glacier cover at lower latitudes also influence non-glacial systems at high latitudes and altitudes.

Combining a site specific time-series dataset from southeast Alaska with spatially distributed data collected from other regions of the world demonstrated a strong similarity of taxonomic richness and five functional diversity indices to gradients of catchment glacier cover. These findings support the use of spatial records in studies of rivers to infer community development over time as glaciers retreat. In our spatially distributed studies, there was typically no association between catchment glacier cover and time since deglaciation because ice loss: (i) exposes new segments of river channel that often continue to be glacially influenced for many years afterwards; and (ii) can expose tributaries that have different levels of glacier cover, concurrently [39]. This is generally not the case in terrestrial ecosystems, where ice retreat leads to a decoupling of the land from ice, and thus a direct space-time relationship. Experimental studies have illustrated that invertebrates can develop different community structures quickly in situations where low or no glacier cover conditions are formed in rivers [40], driven by environmental parameters such as water temperature, channel stability and food availability, and if a pool of local colonisers can disperse efficiently.

After accounting for regional variability in responses, functional diversity indices showed consistent relationships with glacier cover, notably increases in the proportion of overall functional space filled (FRic), and a broader profile of traits (FDis) with more regular abundance distributions (FEve). Taxonomic responses to glacier retreat have emphasised the potential for diversity losses with ongoing global environmental change [16,41], whereas we found that FD increased from high glacier cover to zero catchment glacier cover, indicating the potential for functional redundancy amongst these river invertebrate communities [19]. Although our findings could indicate that redundancy can buffer functional process responses if some species are lost, this is unlikely because invertebrates are central to complex ecological networks, moderating functional processes through both top-down and bottom-up interactions. Studying the functional diversity of ecosystems where taxonomic and trait information is available for multiple biological domains will greatly improve our understanding of whole system responses to environmental change.

Biogeographical constraints on taxonomic identity have been suggested as a reason why large-scale comparative studies of ecosystem health should focus on process rates (e.g. production, decomposition) [42]. Our finding that invertebrate traits and FD responded similarly to habitat gradients independent of biogeographical differences illustrates that it is possible to standardize biological community responses to environmental change across large spatial scales where process rate information is unavailable. We expect that the globally consistent trait and FD responses identified in our analysis of rivers will also be evident amongst invertebrate responses to environmental gradients in other ecosystems. Identifying such general patterns and processes will lead to better predictions of invertebrate community and ecosystem functioning responses to environmental change.

Methods

Study sites

We compiled 489 records of freshwater invertebrates collected between 1978 and 2013 from ten different locations in nine biogeographic zones (Supplementary Figure 1; Supplementary Table 1). Macroinvertebrate records from southeast Alaska, USA, were collected from a single river, Wolf Point Creek, in a study that tracked invertebrate response to glacial influence decreasing from 70% to 0%. Other locations included the European Alps (Austria and Italy), French Pyrénées, Greenland, Iceland, New Zealand Alps, Norway western fjords, US Rockies and Svalbard, where samples were collected along gradients of catchment glacier cover arrayed in space. At each location, samples were collected in different years (Supplementary Table 1) but similar protocols [20] were followed including sample collection in the summer melt season, with sites located on main glacier-fed river networks as well as those from tributaries. Sites with low/no glacier cover were fed predominantly from hillslope groundwater tributaries sourced from snowmelt and/or rainfall at baseflow.

The full database consisted of records collected using both hand (Surber, Hess, Stone) and Kick samples. Kick samples are typically considered to be semi-quantitative samples but those used in our study were samples kicked from fixed areas. In two regions (Iceland, European Alps), both types of samples had been collected. This allowed us to consider the effect of sample type, and whilst observations were not made concurrently at the same sites, responses of FCA1 scores, taxonomic richness and abundance to glacier cover were similar within the two regions. In particular, regression analysis of FCA1 scores (which integrate information on trait profiles and abundances, and which underpinned the community assembly modelling) against % glacier cover for Iceland showed no difference between Stone and Kick samples, whilst for the European Alps there was no difference between Surber and Kick sample data (Supplementary Table 7).

The percent glacier cover in each river catchment was determined from topographic maps, digital elevation models (DEM) and aerial photographs, which were used together to delineate catchment and glacier area. For individual sample locations, ArcGIS 10.3 was used to calculate the upstream contributing area from the DEM, and combined with glacier polygons to determine the percent glacier cover within the catchment for the year the samples were collected. More direct methods of quantifying actual meltwater contributions to rivers [41] were not available for all sites and years. Latitude of individual river sites was obtained from Google Earth. In-situ measurements of water temperature, river channel stability (bottom component of the Pfankuch Index; PI) and suspended sediment/turbidity were collected by individual research teams (see primary research papers for measurement protocols). Water temperature data and estimates of channel stability (PI) were collected in the majority of studies and these have previously been shown to be central drivers of biodiversity patterns in glacier-fed rivers [20].

The assembled invertebrate dataset totalled 489 records comprising 1,276,029 individuals. Subsequent refinements of the database excluded records for which the numerically dominant Chironomidae were not identified to subfamily or below. Finer resolution trait data (genus level) are unavailable for the majority of Chironomidae globally [19,43] so trait information was applied at the sub-family level. We also excluded records for which no accurate information was available for catchment glacier cover at the time of sampling, or where streams were influenced by non-glacial disturbances, for example extreme rainfall induced flooding. The final dataset retained for analysis therefore was 363 records comprising 1,230,902 individuals. For each sample, we amalgamated all species level observations typically to genus level (sub-family for Chironomidae, Order for Oligochaeta), resulting in 113 unique taxa.

Using information available in aquatic invertebrate trait databases covering Europe [44], North America [45,46] and New Zealand [47], traits were selected to provide information on phenotypic responses that have been suggested previously as indicators of environmental changes in localised studies of glacier-fed river invertebrate communities [19,40,48]. We avoided ecological traits that described habitat preferences as these typically represent the 'outcome' of biological traits [49]. Trait databases for Europe and New Zealand existed already as fuzzy codes designed to account for trait plasticity, and which allowed relatively easy translation to our selected traits/codings. Continuous measurements (e.g. body length, gape size) provide an alternative approach for invertebrate trait analysis but these datasets were not available at the individual invertebrate level for the samples we collated. North American aquatic invertebrate traits have historically been coded in binary form which do not account for any variability of traits within taxa, so therefore we used a combination of information from European databases where there was clear concordance for genera, and we used our own knowledge and that of North American freshwater ecologists for taxa where information was not readily available. We defined fuzzy codes (0 = no affinity, 1=weak affinity, 2 = medium affinity, 3 = strong affinity) for eight traits (body size, life cycles per year, pupation, adult life stages, respiration mode, locomotion/substrate attachment modes, diet and resistance elements; Supplementary Table 3) based on the existing, yet distinct, trait databases for Europe, North America and New Zealand.

All statistical analyses were carried out in R v3.2.2. Fuzzy Correspondence Analysis (FCA) [50] was used to assess how functional trait composition varied between regions and across the glacier cover gradients, with the relationship between each trait and the FCA scores for axes 1 and 2 (43% and 18% of the overall variance, respectively) assessed using Kendall's correlation coefficients. Taxon abundances were $\log_{10}(x+1)$ transformed and used to create an abundance weighted trait matrix [samples x traits] [50]. FCA was conducted on the [sample x trait] matrix using the *ade4* package [51]. Hierarchical clustering (Ward's method) of the global species pool (based on their trait profiles) was conducted to identify the key functional strategies. A distance matrix was calculated following Pavoine et al. [52] to account for the use of fuzzy coded traits. The number of cluster groups (herein functional groups: FG) was selected based on an iterative procedure that minimised within group dissimilarity and maximised between group dissimilarity. Sixteen clustering scenarios were defined (number of groups: 2 – 18) and multivariate analysis of variance (MANOVA) was used to assess the optimal clustering scenario based on the coefficient of determination. When a significant decrease in the amount of variance explained by additional clusters (<10%) was recorded, the number of clusters at this point was deemed to be the optimal, most parsimonious solution [53] (see Supplementary Table 5 for cluster group constituent taxa).

To describe functional diversity (FD) we calculated a suite of indices (Functional Richness [FRic; proportion of functional space filled by a community], Functional Divergence [FDiv; the proportion of the total abundance that is supported by the species with the most extreme traits], Functional Evenness [FEve; the regularity of abundance distributions in the functional space], Functional Dispersion [FDis; the abundance-weighted deviation of species trait values from the centre of the functional space], Functional Entropy [FEnt; the abundance-weighted sum of pairwise functional distances between species in a community]) [54] using the *dbFD* function from the *FD* package [55] after $\log_{10}(x+1)$ transforming taxon abundances. The first two PCoA axes of the trait abundance matrix were used to calculate FD and we corrected negative eigenvalues using the approach described by Cailliez et al. [56]. To examine geographical trends in FD we averaged absolute latitude and FD indices within regions and fitted general linear models. Using generalized additive mixed models

(GAMM), we then analysed responses of taxonomic richness, FD, the first two FCA axes and the two most abundant FGs to glacier cover at the site-level whilst controlling for a suite of co-variables (region, river basin, site). The Poisson family (log link) was used for taxonomic richness, FRic, FDis and FEnt, the Gaussian family (identity link) for FDiv, FEve and FCA axes, and the binomial family for relative abundances of FGs. Optimal random effects structures were determined by comparing AICs and selecting the most parsimonious model within 2 points of the minimum AIC. For the models with optimal random effects structures, we focused on the R^2 adjusted from the generalised additive model (GAM) part of the mixed model. This measure of goodness-of-fit does not account for random effects but was considered appropriate in this context because we were interested in the globally consistent trends. Although optimal random effects structures were not at the region-level for every index modelled (most notably taxonomic richness and FRic), we show only region-level results in figures to aid interpretation.

To investigate community assembly and metacommunity processes, we constructed four null models with different constraints. Under the 'uniform' model, taxa were picked from the regional species pool at random [22]. Under the 'dispersal' model, occurrences of the k^{th} species at sites $j=1..n$ in the metacommunity and their Euclidean distances (*dist*) from the focal site *i* determine a probability weighting (p_k) for selection of the species from the species pool:

$$p_k = \sum_{j \neq i}^{n} \frac{1}{dist_{ij}}$$

Occurrences at the focal site do not contribute to the probability of taxon selection. For the uniform and dispersal models, species' abundances are predicted as mean observed abundances across the metacommunity. Under the pure 'trait selection' model, taxa presences are sampled from the species pool at random and iteratively assigned predicted abundances until the community weighted mean (*CWM*) for the g^{th} trait satisfies $CWM_{pick}=CWM_{site}\pm T$, where *T* is a threshold (2.5%) to reduce computational intensity. We used CWMs of the first two FCA axes, which cumulatively described 61 % of the overall variance in traits and were related strongly to shifts in voltinism, pupation, burrowing habit, and diet traits across the gradient of glacier cover. Thus 'selection' was made on synthetic traits (FCA axes) for computational efficiency. The mixed model combines dispersal-based occurrences with trait-based abundances. In all cases, 1000 samples of *s* (species richness) taxa were taken from the species pool with *s* fixed at the observed value for each site, i.e. fixed row sums as recommended by [57]. This approach is equivalent to a non-parametric version of Shipley's [22] Community Assembly by Trait Selection (CATS) model, except that a different probabilistic species pool can be specified for each individual site, enhancing realistic representation of the metacommunity and increasing power to infer stochastic dispersal processes.

We assessed the mean similarity of null picks under the four different community assembly models to the observed community using Jaccard's index for presence-absence and the inverse of the Bray-Curtis index (i.e. Bray-Curtis similarity) for abundances. Because the results for both similarity indices were very similar, we focused subsequently on Bray-Curtis. To standardise the results, we calculated the residual similarity from a 1:1 line through results from the uniform model and each of the other three components (Supplementary

Figure 5). GAMMs (Gaussian family, identity link) were used to relate Bray-Curtis similarity residuals to glacier cover. Alaska was excluded from the community assembly analyses because all data came from one site, and Svalbard was excluded due to low regional taxonomic richness.

The apparent importance of dispersal limitation could have been related to spatial autocorrelation of environmental variables. Therefore, to assess the extent of any such autocorrelation, we generated spatial variables using Moran's Eigenvector Maps (MEM) using the PCNM function in the Vegan package [58]. Derived spatial Eigenfunctions associated significantly ($p<0.05$) with four environmental variables (water temperature, PI, Suspended sediment concentration [SSC], electrical conductivity) in a redundancy analysis were retained to assess relationships with residuals from the dispersal based null model of community assembly (Supplementary Figure 6). Turbidity data were provided by some studies, thus we used a generic regression model to estimate SSC from turbidity [59] to allow comparable analyses. Electrical conductivity data were measured in-situ during the primary research studies.

Data and code availability statement: Trait fuzzy codes, functional diversity metrics, contextual river physicochemical data and community assembly model code can be accessed from the Research Data Leeds repository at https://doi.org/10.5518/267. Macroinvertebrate species and abundance datasets are available directly from the authors of the original studies listed in Supplementary Table 1.

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Declaration of Financial Competing Interests

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Supplementary (online) material

Extended data summary figures and tables are available in the supplementary files.

Table 1. Regression model results for combinations of the four community assembly models (data plots are shown in Supplementary Figure 5). With an intercept significantly >0, a slope significantly >1 and an R^2 of 0.83, the dispersal component was a consistently a better fit to the observed community than the uniform model. It was the strongest performing of all model components.

x	***y***	***df***	**β_0 (±SE)**	**β_1 (±SE)**	**R^2**	***P***
Uniform	Dispersal	236	0.174 (0.012)	1.150 (0.034)	0.83	<0.0001
Uniform	Trait selection	236	0.127 (0.011)	0.619 (0.032)	0.61	<0.0001
Uniform	Mixed	236	0.277 (0.013)	0.554 (0.037)	0.49	<0.0001
Dispersal	Trait selection	236	0.099 (0.018)	0.421 (0.030)	0.45	<0.0001
Dispersal	Mixed	236	0.194 (0.015)	0.479 (0.026)	0.58	<0.0001
Trait selection	Mixed	236	0.184 (0.013)	0.834 (0.036)	0.69	<0.0001

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Figure captions

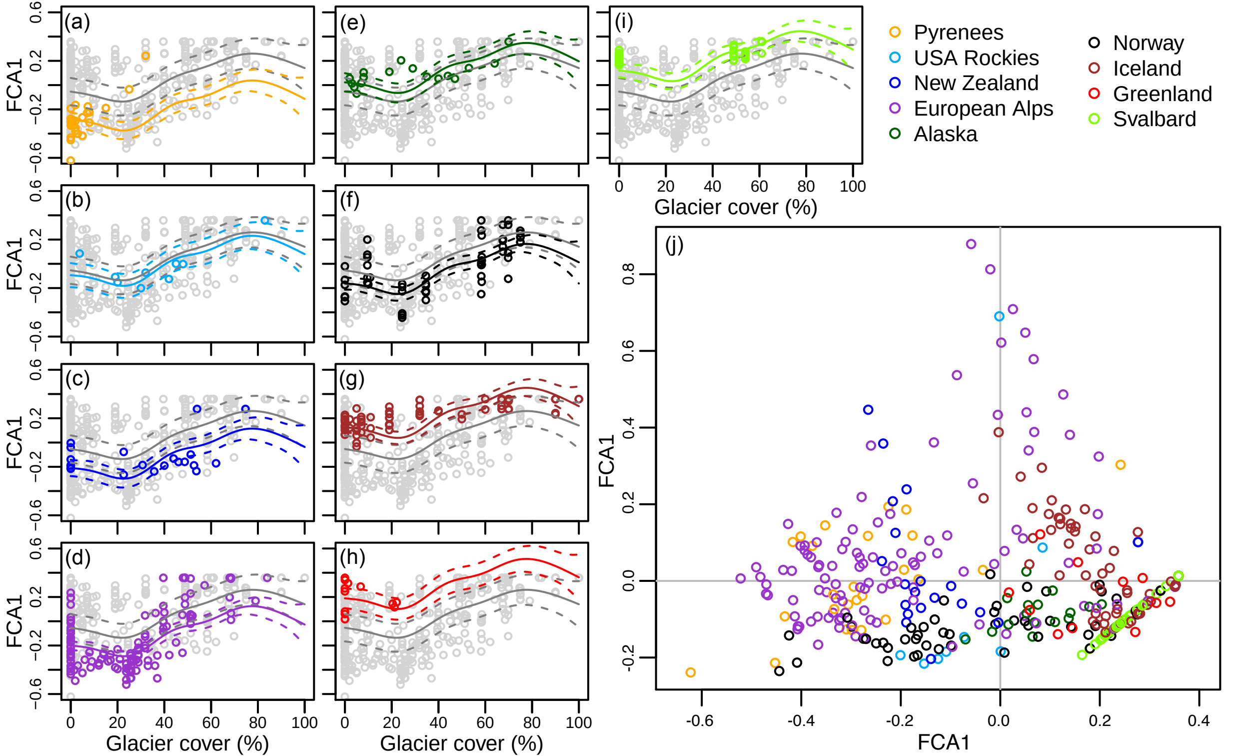
Figure 1. (a-i) General Additive Mixed Model (GAMM) results for Fuzzy Correspondence Analysis (FCA) axis 1 scores with region-level random effects structure. Mean global fit shown with solid grey line and 95% confidence intervals shown with dashed grey line. Coloured lines show mean fit (solid) and 95% confidence intervals (dashed) for each region. For summary statistics see Supplementary Material. (j) Site scores on FCA axes 1 and 2. [See Supplementary Table 3 for relationships between FCA axis scores and traits, and Supplementary Table 4 for model summary statistics; overall n=363]

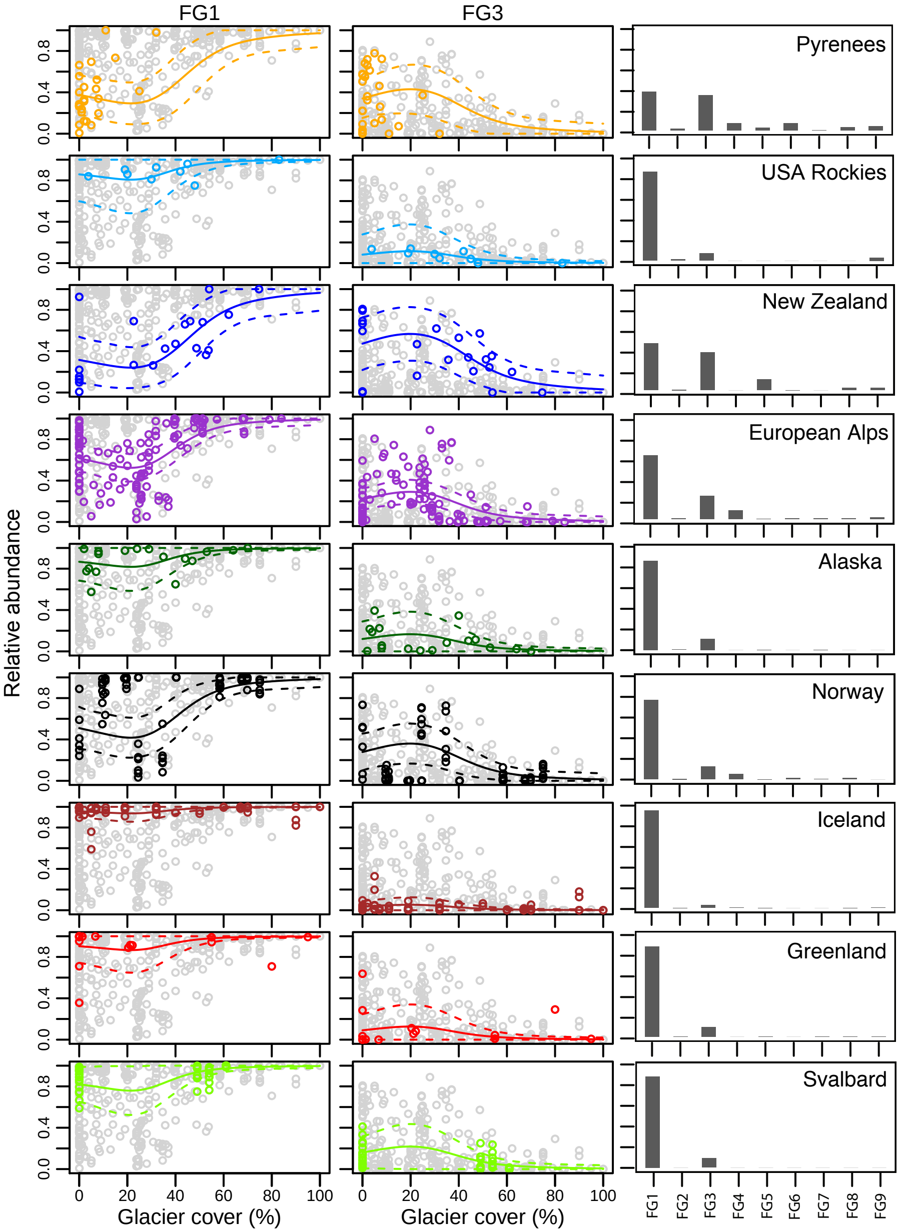
Figure 2. GAMM results for Functional Groups 1 (FG1) and 3 (FG3) with region-level random effects structure. Bar charts show relative abundance of all FGs per region. Coloured lines show mean fit (solid) and 95% confidence intervals (dashed) for each region. [See Supplementary Table 4 for model summary statistics, and Supplementary Table 5 for FG constituent taxa; overall n=363]

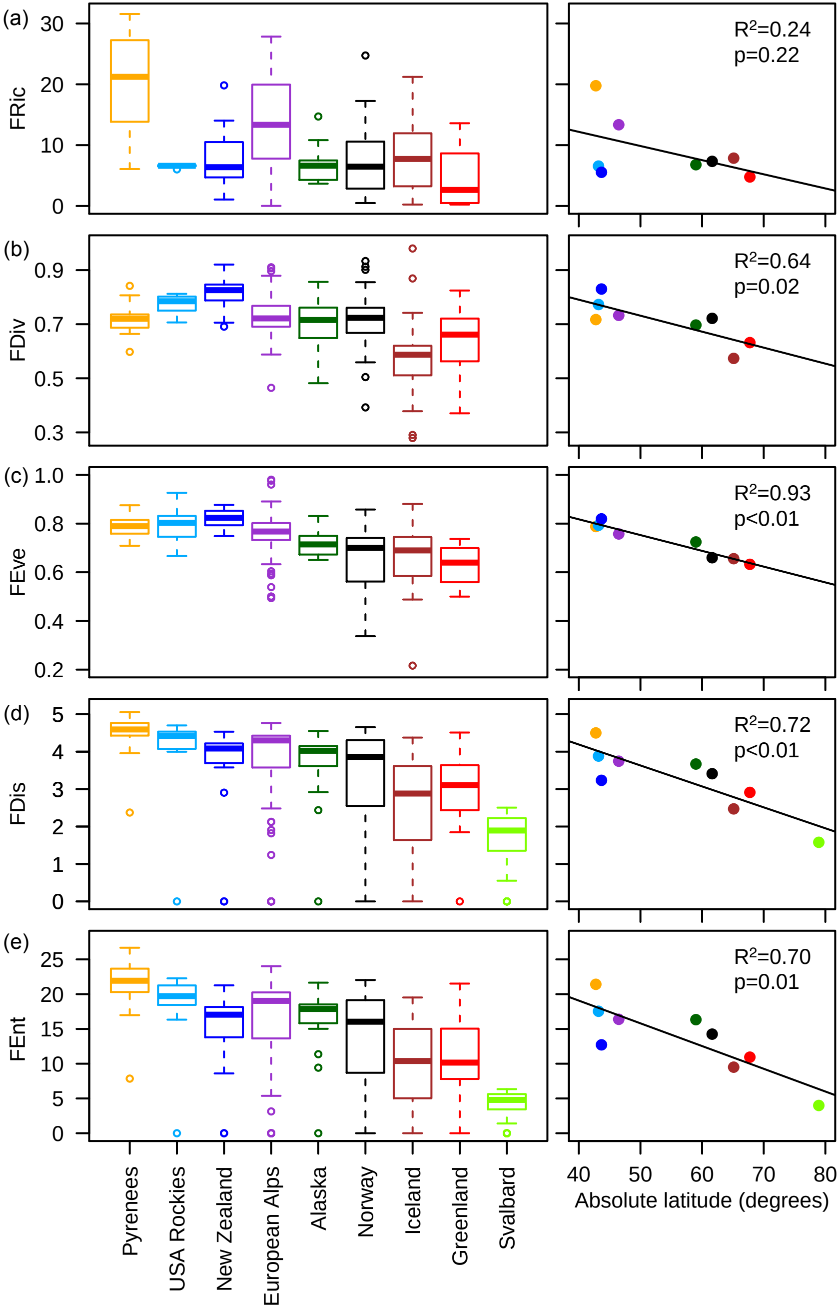
Figure 3. Boxplots of functional diversity indices, and results of general linear models based on regional functional diversity means versus absolute latitude, for (a) functional richness (FRic), (b) functional divergence (FDiv), (c) functional evenness (FEve), (d) functional dispersion (FDis) and (e) Rao’s quadratic entropy (FEnt). FRic, FDiv and FEve could not be calculated for Svalbard due to insufficient taxonomic richness. [See Supplementary Table 6 for model summary statistics; a-c overall n=271; d-f overall n=363]

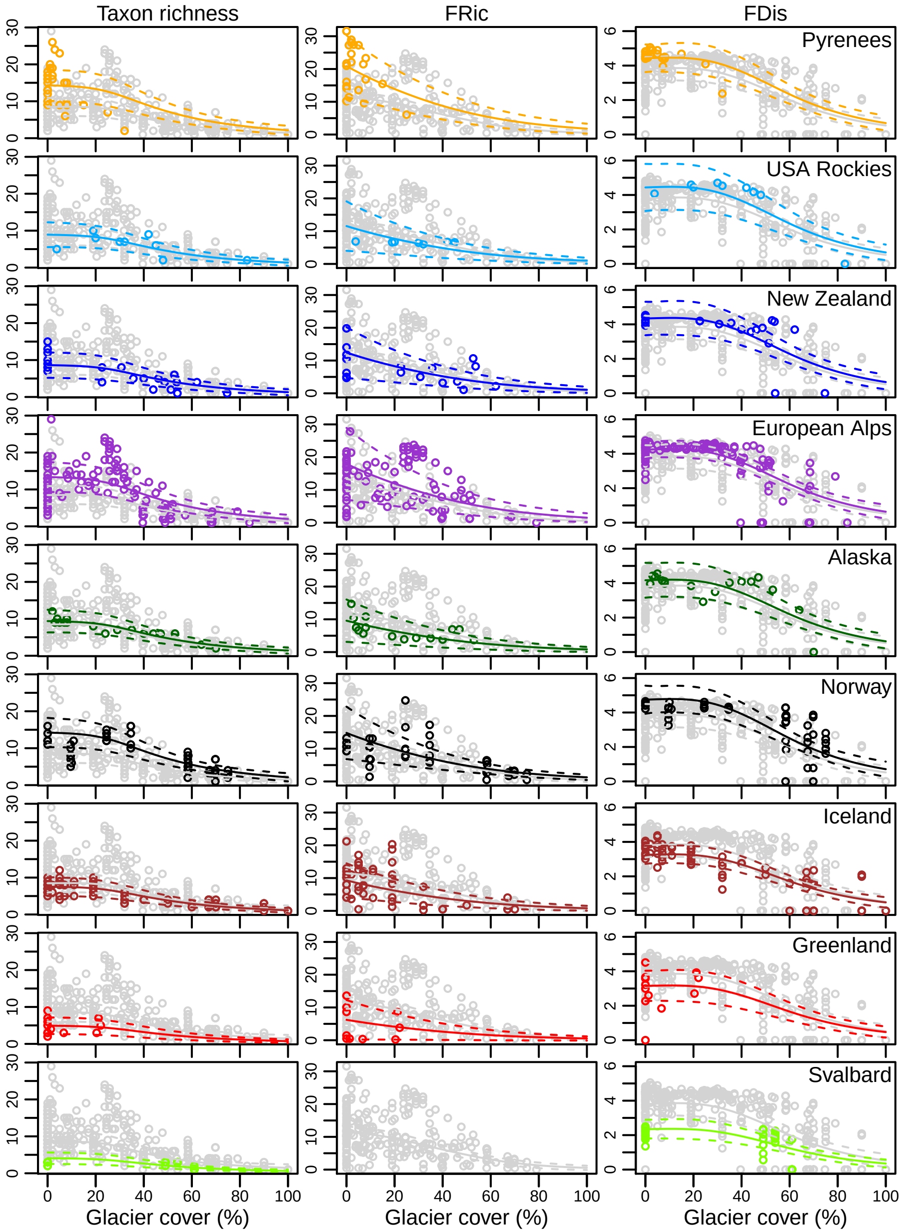
Figure 4. GAMM results for taxonomic richness and selected functional diversity indices (FRic and FDis) with region-level random effects structure. Mean global fit shown with solid grey line and 95% confidence intervals shown with dashed grey line. Coloured lines show mean fit (solid) and 95% confidence intervals (dashed) for each region. FRic could not be calculated for Svalbard due to insufficient taxonomic richness. [See Supplementary Figure 4 for all FD index plots, and Supplementary Table 4 for model summary statistics; n=363 except FRic n=271]

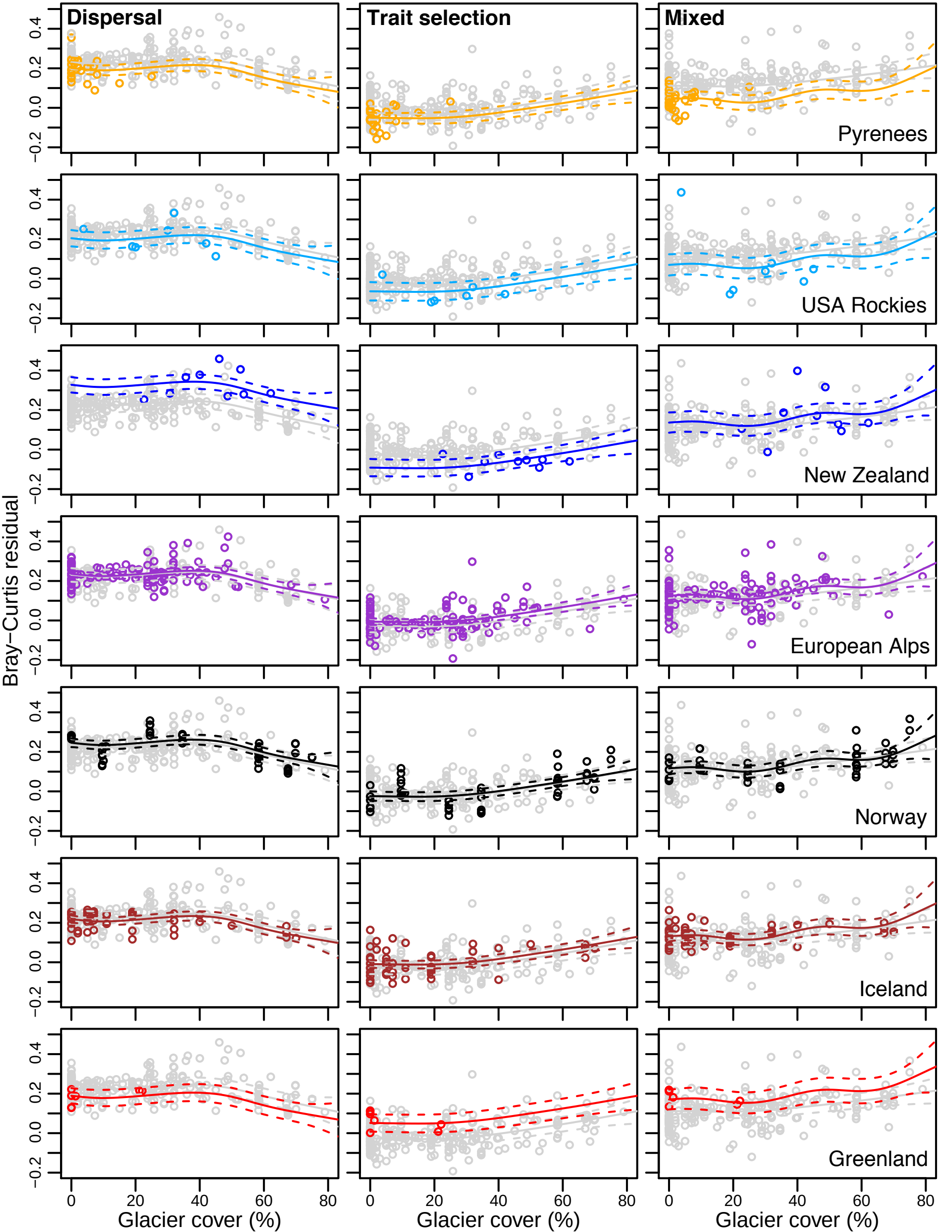
Figure 5. Generalized Additive Mixed Model (GAMM) results for residuals from BC dispersal, trait selection and mixed models, with region-level random effects structure. Mean global fit shown with solid grey line and 95% confidence intervals shown with dashed grey line. Coloured lines show mean fit (solid) and 95% confidence intervals (dashed) for each region. Alaska and Svalbard were excluded from this analysis. [See Supplementary Table 4 for summary statistics; n=238]


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
FCA1
0.6
0.2
−0.2
−0.6
Glacier cover (%)
0
20
40
60
80
100
Pyrenees
USA Rockies
New Zealand
European Alps
Alaska
Norway
Iceland
Greenland
Svalbard
0.8
0.6
0.4
0.2
0.0
-0.2
-0.6
-0.4
-0.2
0.0
0.2
0.4
FCA1


FG1
FG3
Pyrenees
USA Rockies
New Zealand
European Alps
Alaska
Norway
Iceland
Greenland
Svalbard
Relative abundance
0.0
0.4
0.8
0
20
40
60
80
100
Glacier cover (%)
Glacier cover (%)
FG1
FG2
FG3
FG4
FG5
FG6
FG7
FG8
FG9


(a)
FRic
0
10
20
30
R^2=0.24
p=0.22
(b)
FDiv
0.3
0.5
0.7
0.9
R^2=0.64
p=0.02
(c)
FEve
0.2
0.4
0.6
0.8
1.0
R^2=0.93
p<0.01
(d)
FDis
0
1
2
3
4
5
R^2=0.72
p<0.01
(e)
FEnt
0
5
10
15
20
25
R^2=0.70
p=0.01
Pyrenees
USA Rockies
New Zealand
European Alps
Alaska
Norway
Iceland
Greenland
Svalbard
40
50
60
70
80
Absolute latitude (degrees)


Taxon richness
FRic
FDis
Pyrenees
USA Rockies
New Zealand
European Alps
Alaska
Norway
Iceland
Greenland
Svalbard
0
10
20
30
0
2
4
6
0
20
40
60
80
100
Glacier cover (%)
Glacier cover (%)
Glacier cover (%)


Dispersal
Trait selection
Mixed
Pyrenees
USA Rockies
New Zealand
European Alps
Norway
Iceland
Greenland
Bray−Curtis residual
−0.2
0.0
0.2
0.4
0
20
40
60
80
Glacier cover (%)
Glacier cover (%)
Glacier cover (%)