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► **To cite this version:**

Sophie Cauvy-Fraunié, Olivier Dangles. A global synthesis of biodiversity responses to glacier retreat. Nature Ecology & Evolution, 2019, 3 (12), pp.1675-1685. 10.1038/s41559-019-1042-8 . hal-04898147

**HAL Id: hal-04898147**

**<https://cnrs.hal.science/hal-04898147v1>**

Submitted on 20 Jan 2025

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# A global synthesis of biodiversity responses to glacier retreat

Sophie Cauvy-Fraunié<sup>1\*</sup> and Olivier Dangles<sup>2</sup>

**Glaciers cover about 10% of the Earth's land area but they are retreating rapidly and many will disappear within decades. Glacier retreat is a worldwide phenomenon increasing the threat to water resources, biodiversity and associated ecosystem services for hundreds of millions of people, mostly in developing countries. Our understanding of the ecological consequences of glacier retreat has improved significantly in the past decade, but we still lack a comprehensive framework for predicting biodiversity responses to glacier retreat globally, across diverse habitats and taxa. By conducting a global meta-analysis of 234 published studies, including more than 2,100 biodiversity surveys covering marine, freshwater and terrestrial assemblages, we show here that taxon abundance and richness generally increase at lower levels of glacier influence, suggesting that diversity increases locally as glaciers retreat. However, significant response heterogeneity was observed between study sites and species: 6–11% of the studied populations, particularly in fjords, would lose out from glacier retreat. Most of the losers are specialist species, efficient dispersers, uniquely adapted to glacial conditions, whereas the winners are generalist taxa colonizing from downstream. Our global analyses also identify key geographic variables (glacier cover, isolation and melting rates, but not latitude or altitude) and species traits (body size and trophic position) likely to modulate taxon sensitivity to glacial retreat. Finally, we propose mechanistic diagrams for model development to predict biodiversity change following glacier retreat.**

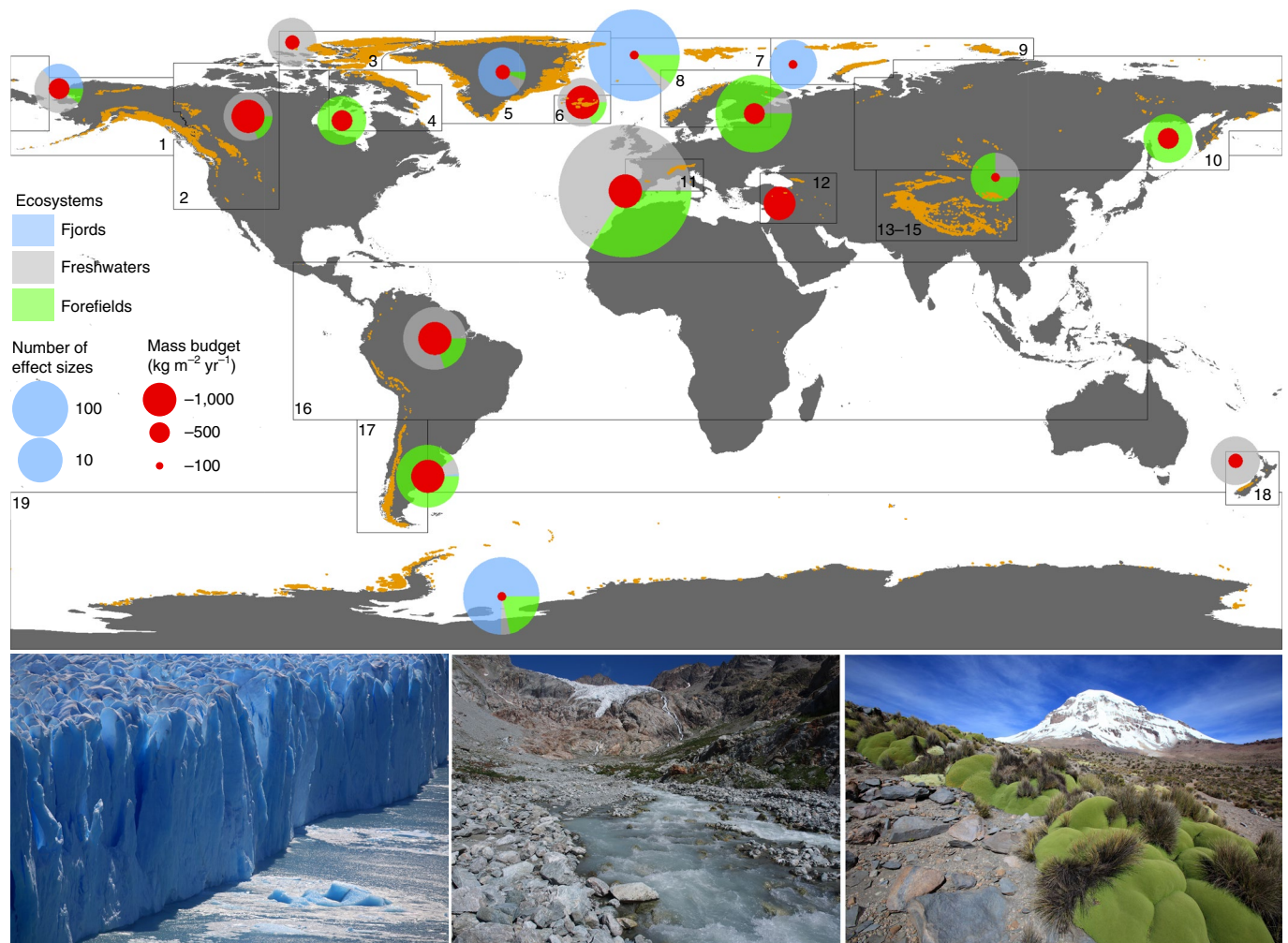
ying at the interface between the cryosphere, hydrosphere and pedosphere, glacier-influenced ecosystems are particularly sensitive to the impact of climate change<sup>1–4</sup>. Global warming has increased both the rate and extent of glacial melting in high-latitude and high-altitude environments<sup>5</sup>, foreshadowing global changes in biodiversity patterns and functions, and leaving these ecosystems critically endangered<sup>6</sup>. Most glaciers have been shrinking since the end of the Little Ice Age, about 150–250 years ago, but shrinkage rates have accelerated over the past five decades<sup>2,7</sup>, increasing threats to the environment and society<sup>3,8,9</sup>. These glacier-fed systems are generally considered to be hostile, harsh habitats characterized by high levels of disturbance (for example, substrate removal and sedimentation) and low nutrient availability, resulting in low levels of diversity (coldspots) and productivity<sup>4,10</sup>, in particular near the glacier snout. However, as glacial contributions to terrestrial, freshwater and marine systems affect key abiotic conditions such as moisture, temperature and salinity, weak glacier influences have been shown to have positive effects on biodiversity further from the glacier<sup>5,8,11</sup>. At the regional scale, glaciers—in particular meltwater influences—create a mosaic of environmental conditions that are crucial for a large number of plants and animals<sup>12</sup>, in turn supporting economically important farmlands and fisheries<sup>13</sup>.

Nevertheless, several critical gaps in our knowledge preclude accurate predictions of biodiversity responses to glacial retreat at the global level. First, although glaciers are generally assumed to have a net negative effect on biodiversity and productivity (abundance and biomass)<sup>14,15</sup>, positive effects of glaciers on the abundance of certain specialist taxa have been reported<sup>15–17</sup>. To clarify these inconsistencies, a global assessment of the proportion of ‘losers’ and ‘winners’ after glacier retreat across taxonomic groups (microorganisms, animals and plants) is therefore needed. Second, global syntheses covering a greater geographic range than local studies can test much broader latitudinal, altitudinal and climatic hypotheses

about biodiversity response to glacier retreat. For example, it has been suggested that Antarctic fjords may differ from their Arctic counterparts because they are at an earlier stage of glacier retreat<sup>11</sup>, and that tropical freshwater and terrestrial communities may respond differently from their temperate (and Arctic) counterparts to glacier retreat due to differences in the harshness and seasonality of the environment<sup>18</sup>. This is particularly true for sites at high altitudes, at which low atmospheric partial pressures and high levels of ultraviolet radiation hinder rapid colonization by living organisms<sup>4</sup>. Furthermore, biogeographical considerations, such as isolation at high altitude and on islands, may reveal significant drivers of the biodiversity response to glacier retreat. Third, most ecological studies on glacier-influenced biota have focused on a single system, and there has been no synthetic analysis addressing the biodiversity response to glacier retreat across marine, freshwater and terrestrial environments. Cross-system comparisons may shed light on general mechanisms and lead to the detection of specific (and/or) common biological traits accounting for the sensitivity of species to the influence of glaciers<sup>19</sup> and, therefore, their potential vulnerability to glacier retreat. Marine, freshwater and terrestrial habitats differ in terms of their geomorphology, circulation processes and inputs (including glacial ice, meltwater and sediments), and they may, therefore, display substantially different physical forcing<sup>10</sup>.

We addressed these gaps in knowledge by conducting a global meta-analysis of biodiversity change across spatial glacial influence gradients based on more than 2,100 relationships (effect sizes) from the three major glacier-influenced systems (tidewater glacier-fed fjords, glacier-fed freshwaters and glacier forefields), including regions with different rates of glacier retreat<sup>2</sup> (Fig. 1). These effect sizes covered more than 500 animal taxa, 50 fungal taxa, 50 vascular plant taxa and 70 algal taxa, among which ~265, 40, 35 and 30 identified at the species level, respectively. Effect sizes were defined as the population (taxon abundance) or community (richness)

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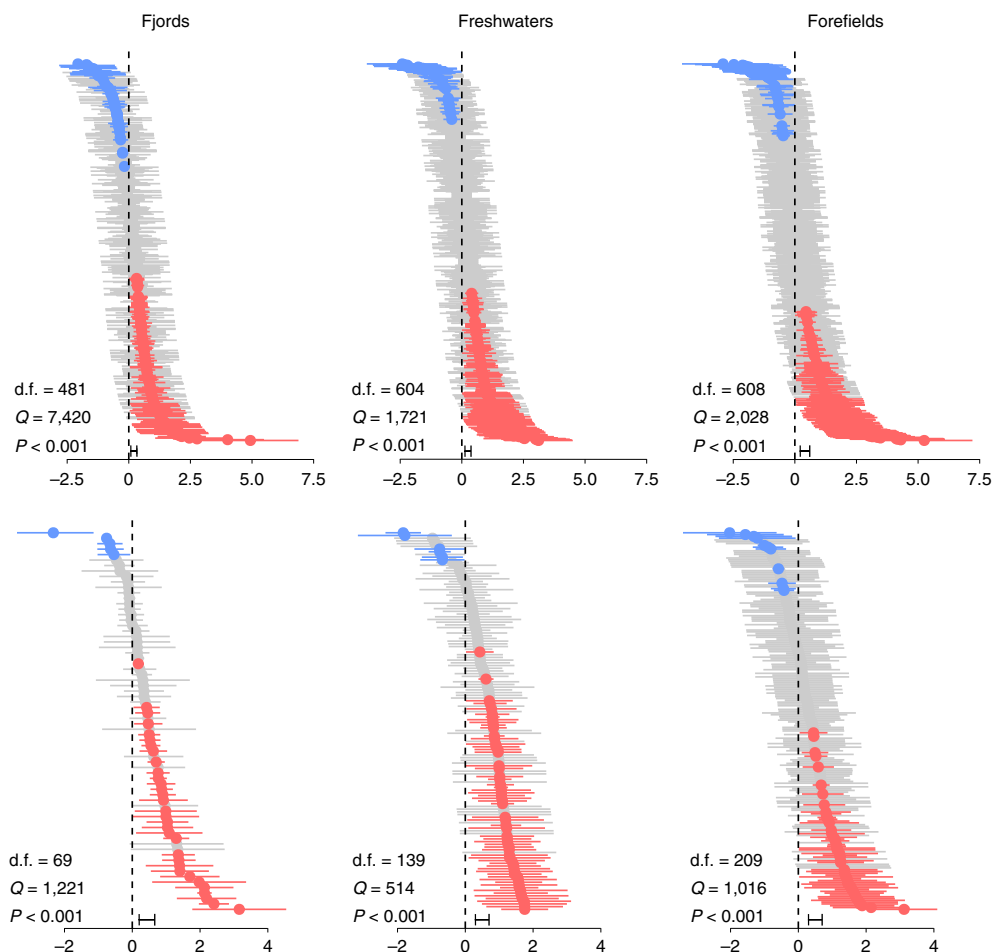
**Fig. 1 | Global distribution of the biodiversity surveys analysed in this study.** The map indicates the area of glaciers (orange), the rate of glacier retreat (red discs) and the number of effect sizes for abundance and richness (pie charts) for glacier-influenced fjord (blue), freshwater (grey) and forefield systems (green). Fjords are deep estuaries, carved by glaciers, that form important boundary zones between the cryosphere and the ocean. Freshwaters include streams and lakes influenced by periodic glacier melting. Glacier forefields are the leading edge of glaciers and moraines. We used the Randolph Glacier Inventory<sup>262,263</sup> which defines 17 regions with different ice mass budget ( $\text{kg m}^{-2} \text{yr}^{-1}$ )<sup>254</sup>. Photographs show (left to right) a fjord, freshwater, and forefield systems: O.D. and S.C.-F.

responses to glacial influence calculated as: (1) the Pearson's correlation coefficients ( $r$ ) for studies recording biotic observations along a gradient of glacial influence; and (2) the standardized mean difference ( $g$ ) for studies reporting means and variances between two zones (one close to and one further away from the glacier snout). A negative effect size designates a positive effect of the glacier on the population/community, indicating a high sensitivity to glacier retreat. Conversely, a positive effect size indicates a negative effect of the glacier and low sensitivity to glacier retreat. The heterogeneity of effect sizes was assessed with the  $Q$  statistic, with  $Q_m$  indicating the contribution of moderators to the heterogeneity, and  $Q_r$  the residual error variance.

## Results and discussion

The meta-analysis revealed that, overall, glaciers had a negative effect on natural populations and communities living in fjords, freshwaters and forefields (Fig. 2). This suggests that most sites are likely to display a gain in local species abundance and richness as glaciers retreat—a pattern frequently reported in previous studies<sup>6,14,15</sup>. However, the local responses of populations and communities varied considerably. Glaciers significantly affected biodiversity in about one-quarter to one-half of the 2,116 surveys (26–37% for

taxon abundance and 30–54% for taxon richness). For these significant responses, we classified the corresponding populations/species as 'winners' (red bars; positive effect sizes) or 'losers' (blue bars; negative effect sizes) with respect to ongoing glacier retreat. Overall, loser populations accounted for 6–11% of all responses, the highest proportion being reported for fjords (Fig. 2). We also identified significant positive effects of glaciers at the community level (4–7%; Fig. 2). Winner populations accounted for 19–26% of all responses in the three systems, whereas winner communities accounted for about 45% of responses in both fjords and freshwaters, and 25% of responses in glacier forefields (see the list of significant species losers and winners in Supplementary Table 1). Most losers were specialist species, adapted to the glacial environment/habitat, among which some were restricted to isolated glacier-influenced ecosystems (for example, the foraminifer *Cassidulina reniforme* in fjords, the arthropod *Diamesa davisi* in glacier-fed streams and the ground beetle *Nebria nivalis* in forefields). In contrast, the winners tended to be generalist/invasive taxa, generally colonizing from downstream<sup>12,15</sup>. The proportion of losers among taxa is probably underestimated because: (1) few studies have investigated organisms (for example, bacteria, algae and tardigrades) living at the surface of the glacier, and these populations will disappear completely with the loss of the



**Fig. 2 | Population and community responses to the effects of glaciers in fjords, freshwaters and forefields.** Effect sizes and 95% confidence intervals for taxon abundance (population; top graphs) and diversity (community; bottom graphs) responses to the influence of glaciers in fjord, freshwater and forefield systems. Colours indicate significantly negative (blue), positive (red) or non-significant (grey) effect sizes corresponding to positive (blue) and negative (red) effects of the glacier on biodiversity.

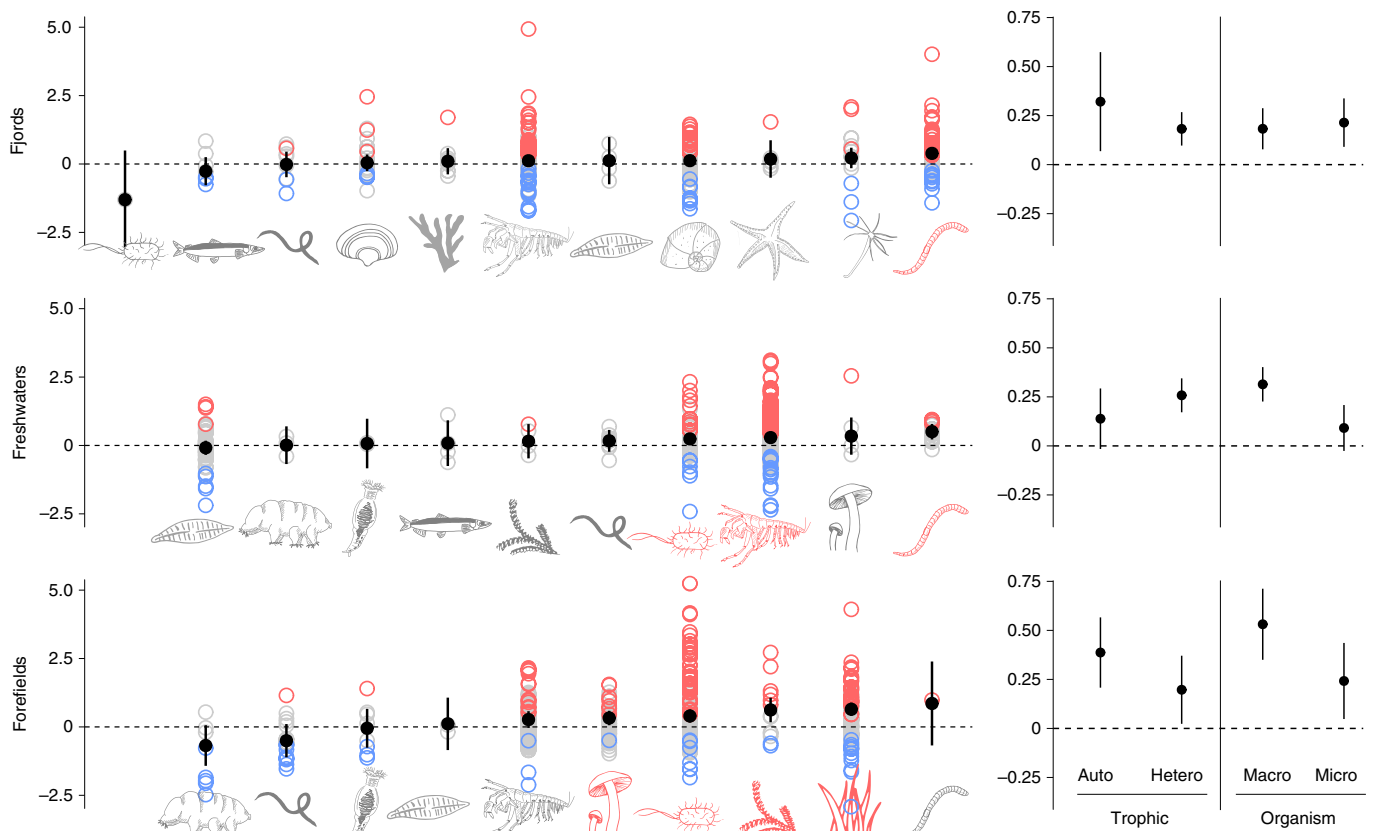
glacier<sup>20</sup>; and (2) populations with low occurrence, many of which are located close to the glacier, could not be included in the meta-analysis due to a lack of statistical power.

Our meta-analysis also showed that the biodiversity response to the influence of the glacier was independent of the latitude and altitude of the study site (Supplementary Table 2), suggesting that environmental filtering linked to glacial influence dominates over regional factors. However, regional glacier area, melting rate and site isolation were significant predictors of the biodiversity response to glacier influence, although their effects were not consistent between systems and metrics (richness versus abundance). Indeed, we found: (1) more winners in fjords (richness;  $Q_m = 5.5$ ; d.f. = 1;  $P = 0.019$ ) and glacier forefields (abundance;  $Q_m = 4.4$ ; d.f. = 1;  $P = 0.035$ ) in regions with high melting rates; (2) more losers in freshwaters (abundance;  $Q_m = 4.7$ ; d.f. = 1;  $P = 0.031$ ) in regions with extensive areas covered by glaciers; and (3) more winners (richness;  $Q_m = 4.5$ ; d.f. = 1;  $P = 0.034$ ) in continental fjords than on islands (Supplementary Table 2), supporting the importance of dispersal limitation for structuring the glacier-influenced communities.

In forefields, taxonomic group significantly explained the overall variability in population responses to glacier influence ( $Q_m = 21.9$ ; d.f. = 9;  $P = 0.009$ ; Supplementary Table 3). Nevertheless, the magnitude and direction of the mean effects of glacier influence on abundance were highly variable across taxonomic groups (Fig. 3). For example, in both fjords and freshwaters, glaciers had a significantly

negative mean effect on annelids ( $z = 4.6$  and  $P < 0.001$  for fjords; and  $z = 3.5$  and  $P = 0.005$  for freshwaters). Glaciers also had negative effects on cnidarians, echinoderms, foraminifers and arthropods in fjords. A low glacial influence had a significant positive mean effect on arthropods in freshwaters ( $z = 5.8$ ;  $P < 0.001$ ), on vascular plants ( $z = 5.2$ ;  $P < 0.001$ ), bryophytes ( $z = 2.7$ ;  $P = 0.007$ ) and fungi ( $z = 2.4$ ;  $P = 0.016$ ) in forefields, and on bacteria in both freshwaters ( $z = 2.2$ ;  $P = 0.026$ ) and forefields ( $z = 3.2$ ;  $P = 0.001$ ). These taxonomic groups would therefore be predicted to be overall winners in situations of glacier retreat, although they also include loser taxa. Glaciers also had positive effects on bacteria, chordates and nematodes in fjords, diatoms in freshwaters, and tardigrades, nematodes and rotifers in forefields. Body size and trophic levels were two traits significantly accounting for the observed patterns, with smaller taxa ( $Q_m = 9.8$ ; d.f. = 1;  $P = 0.002$  for freshwaters; and  $Q_m = 7.7$ ; d.f. = 1;  $P = 0.006$  for forefields) and heterotrophs (forefields:  $Q_m = 3.0$ ; d.f. = 1;  $P = 0.085$ ) more abundant under conditions of strong glacial influence.

Very few studies have experimentally tested the mechanisms underlying the biodiversity response to glacier retreat<sup>21</sup>, yet functional approaches identifying the physical and biological processes are crucial for ecological predictions. We therefore constructed mechanistic diagrams for each study system, based on information found in the 234 publications studied (Supplementary Table 4). By identifying pathways for the negative (red arrows) and positive



**Fig. 3 | Population responses to glacier influence in fjords, freshwaters and glacier forefields by taxonomic group, trophic level and organism size.**

Mean effect sizes and 95% confidence intervals are shown in black. Open dots correspond to the effect size for taxon abundance (see Fig. 2). Red icons indicate that glacial influence had a significant negative effect on the corresponding taxonomic groups, which were thus predicted to be winners in situations of glacier retreat. Taxonomic groups (icons; from left to right) include: bacteria, chordates, nematodes, molluscs, bryozoan, arthropods, diatoms, foraminifers, echinoderms, cnidarians, annelids in fjords; diatoms, tardigrades, rotifers, chordates, bryophytes, nematodes, bacteria, arthropods, fungi, annelids in freshwaters; tardigrades, nematodes, rotifers, diatoms, arthropods, fungi, bacteria, bryophytes, vascular plants and annelids in forefields (see Supplementary Table 3 for statistics). Auto, autotroph; hetero, heterotroph; macro, macroorganism; micro, microorganism.

(blue arrows) effects of glacier influence on biota, these diagrams reveal a number of mechanisms by which glaciers affect biodiversity in all systems (Fig. 4).

First, the harsh abiotic conditions generated by the glacier hinder the survival of many unadapted species living in terrestrial and aquatic environments. For example, low temperature selects for cryophilous species<sup>4,16,22</sup> and high concentrations of suspended sediments bury sessile organisms (for example, bryophytes and echinoderms), clog the filtering organs of filterers (for example, crustaceans and cnidarians) and enhance organism abrasion<sup>15,23</sup>. Moreover, substrate instability linked to glacier movement impedes the establishment of attached organisms, and both ice scouring and meltwater outflows dislodge and kill these organisms (for example, bryophytes, bryozoans and plants<sup>24</sup>) or their burrows (for example, for tube-dwelling polychaetes)<sup>15</sup>. Importantly, low temperatures in both terrestrial and aquatic systems, and the reduction of light by glacial flour, decrease primary production<sup>23</sup>. This indirectly favours heterotrophic organisms feeding on dead organisms unable to survive glacial conditions (for example, marine snow plankton killed by turbid freshwater<sup>25</sup> and attached organisms scoured by ice) or allochthonous matter (for example, wind-blown fallout of organisms and organic debris<sup>16</sup>), part of it being accumulated on the glacier and further dispersed downstream through meltwater<sup>26</sup>.

Second, glaciers create habitable areas for many range-restricted species dependent on the unique thermal and hydrological conditions found in glacier-influenced fjords, freshwaters and forefields

(for example, refuges for cold-adapted species<sup>22</sup>). At more local scales, organic or inorganic sinks on and below glaciers provide nutrients and microorganisms<sup>27</sup>, and dropstones in fjords may be important habitats for several taxa<sup>11</sup>. Moreover, in aquatic systems, glacial flour absorbs ultraviolet radiation<sup>23</sup>, which is particularly strong in high mountains, and acts as a habitat for bacteria<sup>28</sup>. The expansion of the ice-free area releases substantial quantities of new potential habitats for species<sup>5,29</sup>, but the decrease in meltwater levels decreases water availability for both superficial and aquifer recharge (for example, freshwater fish habitat<sup>4</sup>) and increases the risk of desiccation in glacier forefields<sup>29</sup>.

Third, the earliest stages of succession below glaciers help to reduce interspecific competition. The taxa benefiting from empty niches are mostly strong dispersers that are able to colonize isolated ecosystems (for example, small organisms passively transported by wind or water currents<sup>15,16,30</sup>) and are resilient to disturbance (for example, rapid recolonization of small mobile organisms from the hyporheic zone<sup>31</sup>). With glacier retreat, changes in the abiotic conditions and increases in between-habitat connectivity linked to the loss of glaciers and glacier-fed outflows acting as dispersal barriers within and between systems<sup>12,15</sup> would be expected to favour the spread of competitive taxa (for example, aquatic and terrestrial lowland and marine invasive species<sup>32</sup>) and pathogens<sup>33</sup>, leading to species extinction and biotic homogenization at the regional scale<sup>6,12</sup>.

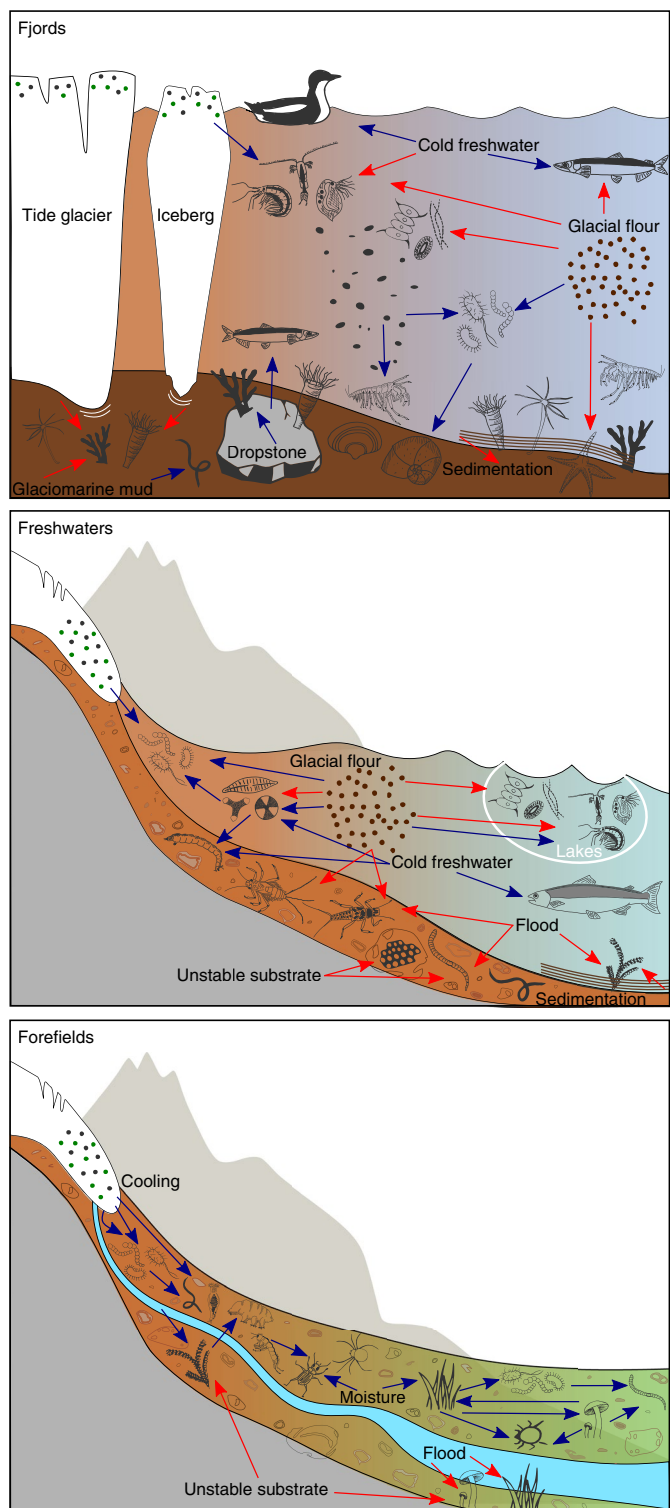
Our study reveals that climate change will cause extensive changes to glacier-fed biota across marine, freshwater and terrestrial

**Fig. 4 | Physical forcing of biological processes in the three glacier-influenced ecosystems.** The negative and positive effects of glaciers on biota are represented by red and blue arrows, respectively (see Supplementary Table 4 for corresponding references). In fjords, supraglacial organic and inorganic deposits provide nutrients and microorganisms. Ice scours the substrate, organic matter and sessile taxa. Unstable glaciomarine mud prevents the establishment of attached taxa but favours certain burrowing taxa. The dropstone provides habitats for attached taxa and fish eggs. Glacial flour clogs the filtering apparatus, limits visual predation, reduces light availability and primary production, dilutes organic matter and provides habitats for bacteria (potential foraminifer food). Sedimentation buries organic matter, sessile taxa and fish eggs, and impedes substrate irrigation, thereby reducing oxygenation. Freshwater provokes an osmotic shock in marine taxa. Cold water provides a refuge for cold-adapted taxa. Detritus from ice scouring and marine snow feed detritivores. In freshwaters, supraglacial organic and inorganic deposits provide nutrients and microorganisms. Glacial flour clogs the filtering apparatus (mostly in lakes), reduces light availability and primary production, protects against ultraviolet radiation and can serve as a source of bioavailable phosphorus. Sedimentation buries sessile taxa. Unstable substrates impede the establishment of attached taxa. Cold water provides a refuge for cold-adapted taxa. The supply of meltwater provides a habitat for aquatic taxa. Floods dislodge organic matter, substrate and taxa. Flowing glacial flour scours the periphyton and taxa (abrasion). In forefields, supra- and subglacial organic and inorganic matter provide nutrients and microorganisms. Meltwater provides moisture, prevents desiccation and disperses nutrients, organisms and seeds. The cooling effect of the glacier favours cold-adapted taxa. The unstable substrate impedes the establishment of attached taxa. Floods erode protozoans and dislodge organic matter and organisms. Wind-blown fallout feeds predators and detritivores. Far from the glacier, soil development and trophic interactions are maximized.

systems. The differences in mean sensitivity between communities result from the tremendous diversity of individual species responses, suggesting that the sensitivity of each species depends on multiple internal species traits (for example, dispersal capacity and feeding habit) and external drivers of change. In the next few decades, as anthropogenic climate change signals become more pronounced and glaciers disappear completely, more substantial changes in the biodiversity of glacier-fed systems will occur, with unclear consequences for ecosystem function and services to human populations.

## Methods

**Literature survey and data requirements.** Studies on the three glacier-influenced ecosystems—fjords, freshwaters and forefields—were identified through a comprehensive search of the Web of Science last updated in January 2018, based on the following search string: (biodivers\* OR biological diversity OR species richness OR species diversity OR taxonom\* OR phylogen\* OR animal diversity OR mammal diversity OR bird diversity OR fish diversity OR reptile diversity OR amphibian diversity OR frog diversity OR insect\* diversity OR plant diversity OR weed diversity OR microbial diversity OR bacteria\* diversity OR fung\* diversity OR virus diversity OR ecosystem diversity OR habitat diversity OR landscape diversity OR biological conservation OR species conservation OR habitat conservation OR genetic resource\* OR functional diversity OR functional trait\* OR invasive species OR biological invasion\* OR functional type OR functional group) AND (glac\* OR deglac\*) NOT (postglacia\* OR post-glacia\* OR last glacia\* OR interglacial period\* OR penultimate glacial period\* OR glacial period\* OR glaciatio\* OR late-glacia\* OR late glacia\* OR glaci\* cycles OR past glacia\* OR glacial relic\* OR glacial refuge\* OR glacial till OR palae\* OR paleo\* OR glacial history OR Pleistocene OR Quaternary OR Miocene OR Holocene OR Wisconsin\* OR Toarcian OR Pliocene OR Hirnantian OR Cryogenian OR Precambrian OR Marinoan) NOT (sea ice OR ice floe\* OR ice field\* OR cream OR polyglactin OR glaciei OR glacialis OR glacialia OR glacial acetic OR glaciallepis OR glacontryphan OR glaciecola). This search provided 1,396 records. We then removed all irrelevant publications (that is, those not assessing biodiversity change across a spatial gradient of glacial influence based on contemporary observations) and obtained 626 articles. We then carefully screened the reference lists of all of these articles to ensure that no studies were missed.



To be included in the meta-analysis, all of the publications had to meet the following criteria: (1) quantitative primary data reported in a usable form; (2) study including various study sites/zones at different known distances from the glacier snout; (3) study based on measurements/observations in the field (no experiments); and (4) the response variable had to be a measurement of biodiversity at the community level, characterizing taxonomic diversity (for example, taxon richness and Shannon diversity) and/or at the population level, characterizing taxon abundance (for example, density, biomass and abundance). Datasets analysed several times in different publications were included only once in our final database. After this selection process, we obtained a total of 234 studies<sup>11,12,14,15,17,22–250</sup>. For fjords, we excluded study sites in the open sea. The primary explanatory variable of glacial influence in the meta-analysis was the

distance of the study sites from the glacier snout. For both freshwaters and glacier forefields, we also used a glaciality index and age since deglaciation, respectively, when no information about distance was provided.

**Effect sizes.** Effect sizes were defined as the population (taxon abundance) or community (taxonomic diversity) responses to glacial influence. For studies reporting biotic observations at various distances from the glacier snout, effect sizes were determined as Pearson's correlation coefficients ( $r$ ) between the population or community response and glacial influence (explanatory variable). These coefficients were either: (1) directly extracted from the study; (2) converted from Spearman's rank correlation coefficients<sup>251</sup>; or (3) calculated from raw data or data extracted from figures with GetData Graph Digitizer 2.25. For studies reporting means, variances and sample sizes of biotic observations in two study zones (one close to and one further away from the glacier snout), effect sizes were first calculated as the standardized mean difference ( $g$ )<sup>252</sup>, and then converted to  $r$ <sup>253</sup>. Finally, we transformed all correlation coefficients ( $r$ ) to Fisher's scale ( $ES_Z$ ) as previously described<sup>253</sup>. Negative effect sizes imply a positive effect of the glacier on a population or community. For single studies reporting results for more than one taxon, we entered the effect size of each taxon as an independent estimate. For each study, only taxa occurring in more than 60% of sites were included in the analyses. We also recorded the latitude and altitude of each of the glacier-influenced systems studied, assigning a corresponding estimated regional total glacier area ( $\text{km}^2$ ) and mass budget (calculated in  $\text{kg m}^{-2} \text{yr}^{-1}$  and  $\text{Gt yr}^{-1}$  for 2003–2009), as previously described<sup>254</sup>, and clustering the systems according to their isolation (island or continent).

**Meta-analysis models.** For each analysis, and separately for the three glacier-influenced systems, we used multilevel meta-analysis models with random effects to account for differences between studies (for example, variation in sampling strategy), assuming they do not share a common (true) effect size but that there is random variation between studies, in addition to within-study sampling variation<sup>253,255</sup>. A publication-level random effect as a nesting factor was included to handle the potential lack of independence of our data as multiple effect sizes were obtained from the same study<sup>256,257</sup>. We first used two separate random-effects models to assess the overall responses (mean effect) of both populations (taxon abundance) and communities (diversity) to glacial influence. We then used separate mixed-effects models, including altitude, absolute latitude, regional glacier area and mass budget (continuous variables), as well as isolation (island versus continent) as fixed factors (moderators) for both the population and community levels. For populations, we performed the same analyses with taxonomic group (about ten groups; see Supplementary Table 3), species (see Supplementary Table 1), trophic level (autotroph versus heterotroph) and organism size (microorganisms  $\leq 2 \text{ mm}$  with high passive dispersal capacity versus macroorganisms  $> 2 \text{ mm}$ )<sup>258</sup> as fixed factors. Mixed-effects models were used to determine whether moderators explained the heterogeneity of effect sizes, to compare the mean effect for different groups (for categorical moderators) and to assess the relationship between continuous moderators and effect sizes. We discarded the taxonomic groups occurring in only one system and for which fewer than seven effect sizes were available.

Effect sizes were considered to be significantly different from zero if their 95% confidence intervals did not include zero<sup>252</sup>. We assessed the heterogeneity of effect sizes with the  $Q$  statistic, calculated as the weighted sum of squares, comparing the results obtained with a chi-squared distribution<sup>253</sup> to determine whether the proportion of the variance of observed effect sizes accounted for by the model was greater than that expected by chance. A significant  $Q$  statistic indicates heterogeneity in effect sizes. For mixed-effects models, total heterogeneity can be partitioned into the variance explained by the moderators in the model ( $Q_m$ ) and the residual error variance ( $Q$ ). A significant  $Q_m$  statistic indicates that moderators contribute to the heterogeneity in effect sizes. Models were fitted by restricted maximum-likelihood estimation. All analyses were performed in R with the metafor and esc packages<sup>259</sup> (R Core Development Team, 2015, version 3.6.1).

**Sensitivity analysis.** We explored the possibility of publication bias, defined as a greater likelihood of publication for studies reporting statistically significant effects than for those reporting non-significant effects, graphically (by plotting contour-enhanced funnel plots<sup>260</sup>) and statistically (with Egger's regression<sup>261</sup> test adapted to multilevel meta-analysis; see ref. <sup>256</sup> for details). We also compared random-effects models with (multilevel models) and without modelling non-independence (simple models), and assessed the impact of potential publication bias on simple models by the trim and fill method<sup>255</sup>. We checked that the nature of explanatory and response variables had no significant effect on our results by comparing, for studies providing various metrics, the summary effect size obtained with: (1) the glaciality index and distance to glacier front for freshwaters; (2) the time since deglaciation and distance to glacier front for forefields; and (3) the Shannon diversity and taxa richness for the three systems. We also tested whether spatial scale affected effect sizes using mixed-effects models with the maximum distance from glacier snout as a fixed factor (see Supplementary Table 5 and Supplementary Fig. 1).

**Review.** To deepen the interpretation of our results, we recorded all physical and biological processes mentioned in the 234 studies, and combined them into a mechanistic diagram for each glacier-influenced ecosystem.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## Data availability

Data are available at <https://doi.org/10.7910/DVN/ZAREWT>.

## Code availability

Code from this study is available at <https://doi.org/10.7910/DVN/ZAREWT>.

Received: 23 May 2019; Accepted: 15 October 2019;

Published online: 18 November 2019

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### Acknowledgements

We thank C. Randimbivololona and P. Bonneviot for drawing most of the icons in Figs. 3 and 4.

### Author contributions

S.C.-F. and O.D. conceived the study, acquired the data and wrote the manuscript. S.C.-F. performed the analyses and constructed the figures.

### Competing interests

The authors declare no competing interests.

### Additional information

**Supplementary information** is available for this paper at <https://doi.org/10.1038/s41559-019-1042-8>.

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- Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

Data collection

Data analysis

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

### Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

### Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences       Behavioural & social sciences       Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://nature.com/documents/nr-reporting-summary-flat.pdf)

## Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	This study is a meta-analysis including more than 200 published studies.
Data exclusions	We selected all publications assessing biodiversity change across a spatial gradient of glacial influence based on contemporary observations. To be included in the meta-analysis, all the publications had to meet the following criteria: (i) quantitative primary data reported in a usable form; (ii) study including various study sites/zones at different known distances from the glacier snout, (iii) study based on measurements/ observations in the field (no experiments), (iv) the response variable had to be a measurement of biodiversity at community level, characterising taxonomic diversity (e.g., taxon richness, Shannon diversity) and/or at population level, characterising taxon abundance (e.g., density, biomass, abundance). Datasets analysed several times in different publications were included only once in our final database. After this selection process, we obtained a total of 234 studies.
Replication	Given that this study was a meta-analysis of previous records, no replication was attempted.
Randomization	Effect-sizes were grouped according to taxonomic group, species, trophic level and organisms size.
Blinding	For each analysis, we used multilevel meta-analysis models with random effects to account for differences between studies (e.g. variation in sampling strategy), assuming they do not share a common (true) effect size but that there is random variation between studies, in addition to within-study sampling variation. A publication-level random effect as a nesting factor was included to handle the potential lack of independence of our data as multiple effect sizes were obtained from the same study.

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

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n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

### Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging