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Local climate modulates the development of soil nematode communities after glacier retreat

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Abstract

The worldwide retreat of glaciers is causing a faster than ever increase in ice-free areas that are leading to the emergence of new ecosystems. Understanding the dynamics of these environments is critical to predicting the consequences of climate change on mountains and at high latitudes. Climatic differences between regions of the world could modulate the emergence of biodiversity and functionality after glacier retreat, yet global tests of this hypothesis are lacking. Nematodes are the most abundant soil animals, with keystone roles in ecosystem functioning, but the lack of global-scale studies limits our understanding of how the taxonomic and functional diversity of nematodes changes during the colonization of proglacial landscapes. We used environmental DNA metabarcoding to characterize nematode communities of 48 glacier forelands from five continents. We assessed how different facets of biodiversity change with the age of deglaciated terrains and tested the hypothesis that colonization patterns are different across forelands with different climatic conditions.

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Nematodes colonized ice-free areas almost immediately. Both taxonomic and functional richness quickly increased over time, but the increase in nematode diversity was modulated by climate, so that colonization started earlier in forelands with mild summer temperatures. Colder forelands initially hosted poor communities, but the colonization rate then accelerated, eventually leveling biodiversity differences between climatic regimes in the long term. Immediately after glacier retreat, communities were dominated by colonizer taxa with short generation time and r-ecological strategy but community composition shifted through time, with increased frequency of more persister taxa with K-ecological strategy. These changes mostly occurred through the addition of new traits instead of their replacement during succession. The effects of local climate on nematode colonization led to heterogeneous but predictable patterns around the world that likely affect soil communities and overall ecosystem development.

KEYWORDS
climate change, colonization rates, eDNA metabarcoding, functional diversity, global scale, succession

1 | INTRODUCTION

Mountain glaciers are losing mass at an unprecedented rate due to ongoing climate change, and the pace of glacier recession is accelerating (Hugonnet et al., 2021; Rounce et al., 2023). This dramatic shrinkage will have major impacts on both the biotic and abiotic components of nearby ecosystems and the services they provide (Intergovernmental Panel on Climate Change, 2021; Pothula & Adams, 2022). Deglaciated areas undergo rapid geomorphological changes and are quickly colonized by multiple life-forms, which in turn determine the dynamics and the functioning of these emerging ecosystems (Ficetola, Marta, et al., 2021; Pothula & Adams, 2022; Sytsma et al., 2023). The loss of mountain glaciers is likely an irreversible process (Intergovernmental Panel on Climate Change, 2021); thus, we urgently need standardized, global-scale studies on how local to regional differences (e.g., differences in climate) determine the development of different biodiversity components under a changing climate (Crowther et al., 2019; Ficetola, Marta, et al., 2021). Such studies are required to identify general patterns of biotic colonization and to understand key drivers of successions in order to predict the future dynamics of these ecosystems (Cauvy-Frauniê & Dangles, 2019).

Biotic colonization after glacier retreat is generally characterized by an increase in diversity over time, at rates that differ among taxonomic groups (Guerrieri et al., 2023; Pothula & Adams, 2022; Rosero et al., 2021). Nonetheless, it has been proposed that the colonization dynamics of deglaciated areas are modulated by local climatic conditions (Ficetola, Marta, et al., 2021), given that the impacts of climate change on biodiversity are uneven at the global scale (Freeman et al., 2021). Climatic differences in temperature and, to a lesser extent, precipitation and solar radiation can influence the evolution of ecosystems after glacier retreat (Anthelme et al., 2022; Franco

et al., 2022; Kaufmann, 2002; Khedim et al., 2021). For instance, the accumulation through time of soil organic matter can be faster in proglacial forelands that experience relatively warm conditions (Kaufmann, 2002; Khedim et al., 2021). Thus, we expect that glacier forelands subjected to different climates will show differences in the development of communities, with earlier ecosystem formation and colonization in relatively warm areas (Ficetola, Marta, et al., 2021; Fridley & Wright, 2018; Vater & Matthews, 2015). However, broad-scale studies analyzing multiple proglacial landscapes located in different climates using the same approach are scarce, hampering tests of this hypothesis.

To better understand colonization dynamics due to global change, we must compare taxonomic and functional trajectories of biotic communities after glacier retreat. These biodiversity facets are complementary and influence ecosystem processes in different ways (Le Bagousse-Pinguet et al., 2019). Functional diversity encompasses the range of morphological, ecological, behavioral, and physiological traits among species within a given community. Given that species' traits are more directly connected with ecosystem processes than taxonomic diversity (Cadotte et al., 2011; Loreau et al., 2001; Naeem et al., 2012), changes in functional diversity should inform us about how changes in ecological processes might impact ecosystem functions. Analyzing functional diversity thus provides key information on the processes underlying the evolution of communities under global change, such as the relative importance of environmental filtering and competition (Kuczynski & Grenouillet, 2018).

Nematodes are the most abundant animals in soils and are excellent indicators of soil biological activity (Neher, 2001). Operating at all trophic levels, they play a crucial role in the development of ecosystems, as their diversity affects numerous ecosystem functions, including productivity, nutrient cycling, and decomposition of organic matter (Crowther et al., 2019; Delgado-Baquerizo et al., 2020;

Fontaneto, 2019; van den Hoogen et al., 2019; Zawierucha et al., 2021). Nematodes are particularly important components of soil communities in the first decades after glacier retreat (Devetter et al., 2021; Doblas-Miranda et al., 2008; Rosero et al., 2021), probably due to their small size and resistant propagules that facilitate dispersal and colonization (Fontaneto, 2019; Ptatscheck et al., 2018). Previous studies on nematode colonization after glacier retreat reported a range of successional patterns, with variation among trophic groups (Pothula & Adams, 2022) and study areas. For instance, in Lei et al. (2015), most of richness increase occurred during the first 50 years, while colonization required much longer time in Devetter et al. (2021). Furthermore, some studies showed linear increases in diversity over time (Devetter et al., 2021), while others suggested intermediate peaks followed by plateaus or even richness declines (Doblas-Miranda et al., 2008; Lei et al., 2015; van Leeuwen et al., 2018). Nonetheless, those studies were conducted in distinct regions of the world and covered different temporal ranges, making comparisons and generalizations difficult. We thus need a global assessment using a standardized protocol to examine the successional patterns of nematode diversity and its trophic groups. This will help to define how climate modulates nematode succession.

Here, we analyzed the development of taxonomic and functional diversity of nematode communities emerging since the retreat of glaciers in five continents (Figure 1). Molecular approaches, such as environmental DNA (eDNA) metabarcoding (Taberlet et al., 2018), enable rapid, cost-effective, and consistent estimates of soil biodiversity (Delgado-Baquerizo et al., 2020; Geisen et al., 2018) even over broad spatial scales (White et al., 2020), which would otherwise be prohibitive. We used a standardized eDNA-based approach to sample soil nematode communities along the proglacial chronosequences (Walker et al., 2010) of 48 receding glaciers that experience different climatic conditions (Figure 1). First, we tested the hypothesis that local climatic conditions (i.e., meso-climate) influence the rate at which communities develop after the retreat of glaciers. Under this hypothesis, we expected that communities would develop more quickly in mild climates compared to the cold ones. We tested this hypothesis by measuring how different facets of biodiversity (i.e., taxonomic and functional diversity, as well as the richness of trophic groups) changed over time and across forelands with different climates. Second, we tested whether nematode communities show functional changes along the colonization. The colonization of deglaciated terrains is often led by colonizer species with r-ecological strategy, that may be replaced over time by more competitive species with K-ecological strategy (Erschbamer & Caccianiga, 2016; Ficetola, Marta, et al., 2021). We thus predicted a shift from r-strategy to K-strategy species. Third, we sought to unravel the coexistence mechanisms that predominantly affected the functional assembly of communities (Gotelli & Graves, 1996). Under environmental filtering, communities are expected to be more functionally homogeneous, with taxa harboring traits that allow them to tolerate specific conditions. This coexistence mechanism would lead to a functional diversity that is lower than expected based on observed taxonomic diversity. Conversely, under a limiting similarity assembly process, colonization should be primarily underlined by a few groups

that are functionally different (e.g., that use different resources) (Götzenberger et al., 2012; Weiher & Keddy, 1999). We predicted stronger environmental filtering in harsh conditions (very cold climates and/or soon after glacier retreat), whereas limiting similarity could be more important under mild conditions and/or in more developed communities, where competitive interactions are stronger (Purschke et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Field activities

From 2014 to 2020, we collected 1197 soil samples in 48 glacier forelands, covering five continents from the Equator to polar regions (Figure 1). For these forelands, information on the dates of glacier retreat since the maximum extent of the Little Ice Age was available from the literature, remote sensing images and field surveys (Marta et al., 2021). For each foreland, we selected two to nine sites (mean = 5.2, SD = 1.5, Table S1) along the chronosequences of glacier retreat (that is the chronological sequence of specific geomorphological features, such as moraines or inter-moraine flat areas, along deglaciated terrains for which the date of glacier retreat is known; Figure S1). A site generally corresponded to the line representing the position of the glacier's front on a given date. We excluded sites impacted by recent surface instability and erosion. The number of sites per chronosequence depended on the number of known positions of the glacier available from the literature (Marta et al., 2021). At each site, we established an average of five regularly spaced plots (SD = 0.6) for more repeatable biodiversity estimates (Dickie et al., 2018), and, if possible, at distances of 20 m (Figure S1). Due to logistic constraints, in 9% of the sites, we sampled a slightly different number of plots. The average number of plots per site was similar between forelands in different climatic regimes and between sites with different ages since glacier retreat (linear models testing relationships between the number of plots and age or climate, both $p \geq .8$). At each plot, we collected five soil subsamples within 1 m (Figure S1), at a depth of 0–20 cm and pooled them together to form a composite sample of ~200 g per plot. We did not include soil litter and avoided roots, leaves and other large plant organs, as we focused on soil nematodes. While the analysis of litter nematodes can provide interesting patterns (Doblas-Miranda et al., 2008), many sites completely lacked leaf litter, particularly at early successional stages, thus hampering a standardized comparison. Composite samples were homogenized; from each composite sample, we took 15 g of soil and desiccated it immediately in sterile boxes with 40 g of silica gel (Guerrieri et al., 2021). Desiccation is a cost-effective approach allowing long-term preservation of eDNA for biodiversity assessments (Guerrieri et al., 2021). Before the collection of each sample, all the sampling equipment underwent strict decontamination protocols (burned at >1000°C with a portable blow torch). Using the same approach, we also collected 150 g of soil for chemical analyses at each plot in a subset of forelands. Sampling was always
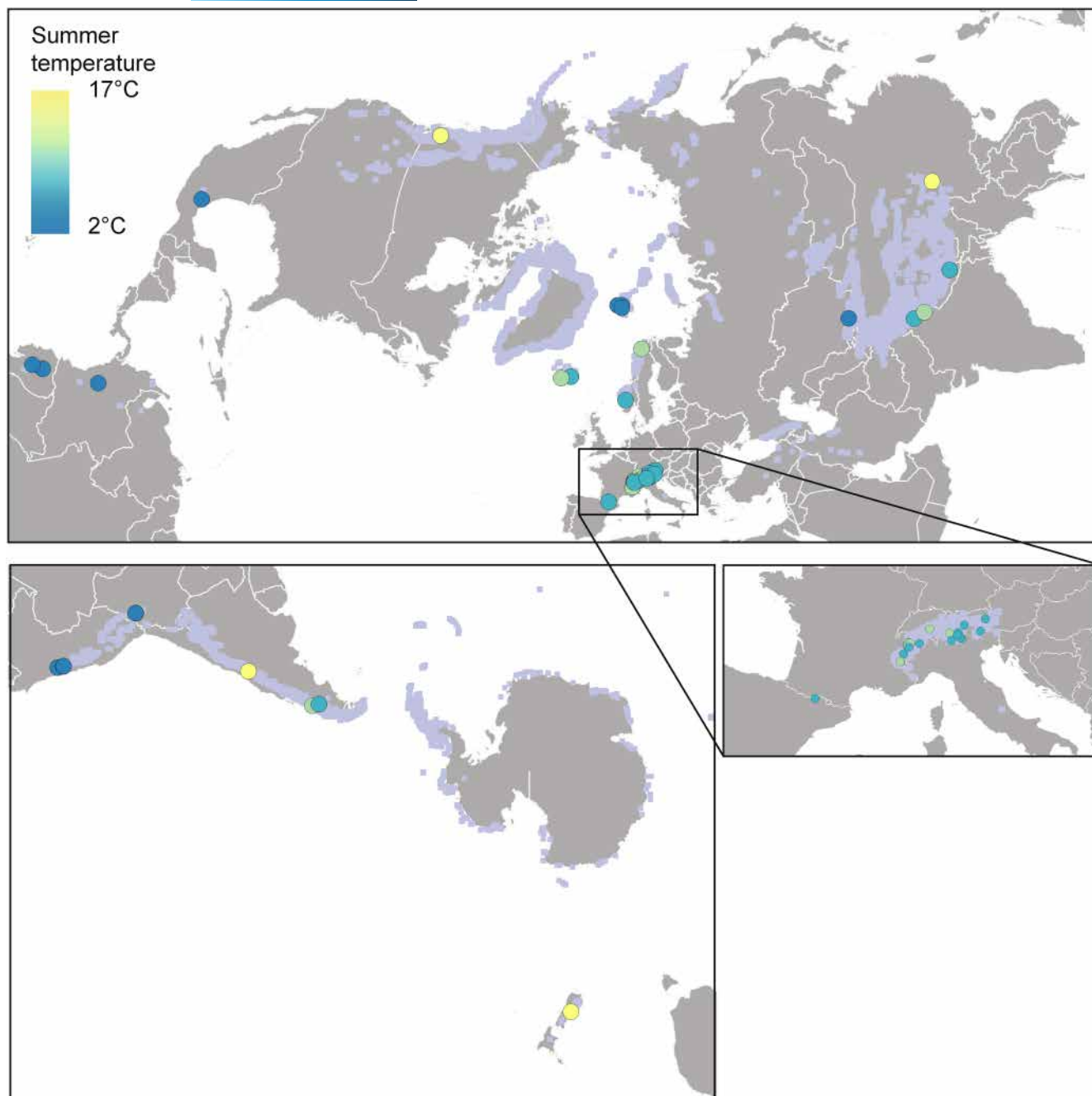
FIGURE 1 Global distribution of the 48 studied glacier forelands. The color of the dots represents the average temperature of forelands during the warmest quarter (ranging from 2 to 17°C). The background blue dots represent the distribution of glaciers according to the GLIMS database (www.glims.org). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

performed during the warmest season (i.e., for temperate areas from late July till early September in the Northern Hemisphere and in February–March in the Southern Hemisphere; Table S1).

2.2 | Molecular analyses and bioinformatics treatment

Environmental DNA from the 1197 15-g soil samples was extracted in a dedicated room using the NucleoSpin Soil Mini Kit

(Macherey-Nagel). Because we collected ~five soil samples per site, the total amount of soil used for extraction was on average 75 g per site, which is close to the values proposed for robust assessments of nematode communities (Wiesel et al., 2015). Before extraction, we added a preliminary step where the soil was mixed with 20 mL of phosphate buffer for 15 min (Taberlet et al., 2012). Elution was performed in 150 μL of elution buffer. To monitor contamination in the extraction room, we also included one extraction control every ~10 samples (total: 101 extraction controls; Zinger et al., 2019). DNA amplifications were performed using the universal Euka02

primer (Guardiola et al., 2015; Taberlet et al., 2018), which amplifies an ~120 bp fragment of the V7 region of the 18S rDNA gene. The short fragment length is well suited for eDNA analyses (Ficetola, Boyer, et al., 2021; Guardiola et al., 2015; Taberlet et al., 2018). Bioinformatics analyses showed that Euka02 is among the markers amplifying the highest proportion of nematode species and has good taxonomic resolution, particularly at the genus level (Ficetola et al., 2023). Reverse and forward primers included 8-nucleotide-long tags on the 5′ end. Each tag had at least five nucleotide differences from the others, thus allowing bioinformatic discrimination of PCR replicates after sequencing (Taberlet et al., 2018). DNA extracts were randomized in 96-well plates together with extraction controls, bioinformatic blanks, PCR negative and positive controls (total across all plates: 291 blanks, 90 negative and 53 positive controls). Positive controls consisted of 10 times diluted genomic DNA of eight bacterial and two fungal strains (ZymoBIOMICS Microbial Community DNA Standard II; Zymo Research) and were used to monitor potential cross-contamination of samples, as well as amplification and sequencing performances (Zinger et al., 2019). PCR-negative controls were used to monitor contaminations during PCR reactions and blanks allowed the identification of tag-jump issues. We used quantitative PCR (qPCR) to determine the optimal number of PCR cycles, following Guerrieri et al. (2023).

PCR amplifications of 1:10 diluted DNA samples were performed in 384-well plates and consisted of an initial step of 10 min at 95°C, followed by 45 cycles of 30 s denaturation at 95°C, 30 s annealing at 45°C, 60 s elongation at 72°C, and 7 min final elongation at 72°C. All samples and controls underwent four PCR replicates (Ficetola et al., 2015). The purified amplicons were sent to Fasteris (Switzerland) for library preparation using the MetaFast protocol (Taberlet et al., 2018) and sequencing with the Illumina HiSeq 2500 platform (paired-end approach, 2 × 150 bp; about 0.5% of PhiX added in each sequencing lane). See Guerrieri et al. (2023) for additional details on molecular analyses.

We performed the bioinformatic treatment of sequence data using the OBITools software suite version 1.2.9 (Boyer et al., 2016), following the steps described in Guerrieri et al. (2023), and then clustered sequences at a threshold of 96% sequence similarity using the suma-clust program (https://git.metabarcoding.org/obitools/sumaclust/wikis/home). The 96% threshold minimizes the risk that sequences belonging to the same species are clustered in different molecular operational taxonomic units (MOTUs) (Bonin et al., 2023). Finally, we performed a taxonomic assignment of cluster heads based on the EMBL reference database (version 140). The reference database was curated by carrying out an in silico PCR with the ecopcr program (Ficetola et al., 2010). We used the same primers as in the experiment, allowing three mismatches per primer and kept sequences assigned at least at the family level. Next, we assigned the detected sequences to MOTUs using the ecotag program, following the procedure described in Boyer et al. (2016). ecotag matches each sequence in the dataset against the reference database and then uses the lowest common ancestor algorithm to identify the taxonomic level of the assignation (e.g., genus, family, order) (Boyer et al., 2016). We then performed

an additional filtering in R (version 4.0) to remove contaminants and tag-jump errors based on sequences detected in controls and blanks (Guerrieri et al., 2023; Zinger et al., 2019). Specifically, we discarded MOTUs with best identity <80%, detected less than 10 times in the overall dataset and in at least one extraction or PCR negative control, as they are possible contaminants (Ficetola et al., 2015; Zinger et al., 2019), and MOTUs detected in only one sample, as they represent singletons. Alternative approaches for filtering contaminants compare the prevalence of each MOTU in "true" samples to their prevalence in negative controls, and identify the contaminants based on a threshold of occurrence on the negative controls (Davis et al., 2018). When we repeated the MOTU filtering using this approach with thresholds of 0.1 and 0.5, we removed 4 and 19 MOTUs, respectively. Estimates of taxonomic richness obtained with this filtering strategy were highly correlated (for both thresholds: $r > .86$, $p < .0001$) with the estimates obtained with our approach (22 contaminant MOTUs) and yielded models with nearly identical results (Figure S2).

2.3 | Assessing taxonomic and functional diversity

Due to the difficulty of relating the number of reads to the relative abundance of species in metabarcoding studies, we first measured the taxonomic diversity of PCR replicates as the total number of taxonomic units detected. Taxonomic data obtained from eDNA can be combined with available databases on functional traits to obtain estimates of functional diversity (Aglieri et al., 2020; White et al., 2020). We extracted functional traits from the NEMAPLEX database (http://nemaplex.ucdavis.edu/). We considered one life-history index (colonizer–persister index, hereafter "CP value") and eight consumption traits (parasites of animals, parasites of plants, bacterivores, fungivores, detritivores, omnivores, predators and feeding on unicellular eukaryotes). CP values ranged from 1 to 5, with low values representing colonizer species with short generation time and r-reproductive strategy (i.e., fast reproduction rate and release of numerous small eggs) and high values representing persister species with long generation time and K-strategy (Bongers, 1990; Ferris, 2010; Ferris et al., 2001). The NEMAPLEX database reports functional traits at genus-level resolution. Thus, we directly assigned CP values and consumption traits only for MOTUs identified at the genus level, whereas for MOTUs identified at the family level, CP values were calculated as the average of the genera within the family; consumption traits are conserved within family. The dataset resulted in 76 taxa that had sufficient taxonomic resolution (family level or better) to assign traits (Table S2). Taxa identified at coarser levels were excluded.

The number of detected taxa generally underestimates the actual diversity of a given site because some taxa often remain undetected. Therefore, several approaches have been developed to estimate the actual number of taxa based on the replicated sampling of a given site (Colwell & Coddington, 1994; Gotelli & Colwell, 2011). At each site, we estimated taxonomic richness with the first-order jackknife estimator for incidence data, which is among the best-performing approaches for evaluating

the completeness of biodiversity inventories. Analyses of datasets of completely surveyed areas and simulations suggest that this approach can provide robust estimates of the actual species richness, if a sufficiently large number of replicated samples are analyzed (Chazdon et al., 1998; Colwell & Coddington, 1994; Gotelli & Colwell, 2011). To extrapolate biodiversity values at each site, we considered the different plots and the four PCRs for each plot as replicated samples. On average, we had 20 replicates per site (~5 plots with four PCR replicates each); this replication level is appropriate for biodiversity estimation in environments with moderate diversity levels (Gotelli & Colwell, 2011). The use of estimated biodiversity allowed us to obtain diversity estimates that are comparable between sites with a different number of sampled plots. We estimated site-level taxonomic diversity using the *alpha. accum* function of the BAT R package (Cardoso et al., 2015).

Hill numbers are an alternative approach to biodiversity measurement and are particularly useful in metabarcoding studies, as they avoid issues related to the excessive weighting of rare MOTUs and are extremely robust to different filtering strategies. Hill numbers >0 take into account differences in read abundance that might be related to differences in biomass (Taberlet et al., 2018). We, therefore, repeated the analyses of taxonomic diversity using Hill numbers ($q = 0$ and $q = 1$, equivalent to richness and Shannon entropy, respectively) to estimate taxonomic diversity; increasing q values indicates a higher weight for the MOTUs with proportionally more reads. We could not perform this analysis with Hill numbers >1 because at several sites, we detected zero nematode MOTUs. The relationships between taxonomic diversity estimated using Hill numbers, time since glacier retreat, and climatic variables (see below for details about model structure) were identical to those observed for taxonomic diversity estimated with the first-order jackknife estimators (Figure S3).

Functional diversity describes the variation of ecological traits in a community and how traits are supported by the co-occurring taxa (Mouillot et al., 2013). The assessment of functional diversity requires the analysis of multiple metrics because the functional attributes can impact differently ecosystem dynamics (Grenié et al., 2017; Le Bagousse-Pinguet et al., 2019). We assessed functional diversity using functional richness and Rao's functional diversity (Mason et al., 2005; Petchey & Gaston, 2006), which provide complementary information. We did not use approaches based on measures of the multidimensional trait space (e.g., *N*-dimensional hypervolumes), as they cannot be applied to communities with less than three functionally diverse taxa, and we detected <3 functionally diverse MOTUs at 61% of sites. Functional richness represents the range of traits supported by species in a community (Mason et al., 2005; Petchey & Gaston, 2002) and was assessed using the adaptation of Faith's phylogenetic diversity developed in Petchey and Gaston (2002). We first estimated pairwise trait dissimilarities with Gower distances, with equal weights for each trait (Laliberté & Legendre, 2010; Petchey & Gaston, 2002). We then built an UPGMA dendrogram using functional distances between pairs of functionally characterized taxa. Functional richness was estimated using the first-order jackknife estimator with the *alpha.accum* function (Cardoso et al., 2015) in the same way as taxonomic richness.

Rao's functional diversity (i.e., Rao's index of quadratic entropy) integrates trait dissimilarity between taxa and the functional evenness of communities by considering the relative abundance of organisms (Mouchet et al., 2010; Petchey & Gaston, 2006). Rao's functional diversity was assessed based on the relative abundance of taxa in sites (proportion of reads) and trait dissimilarities between taxa, following de Bello et al. (2009). Using the proportion of reads can yield diversity measures that are less sensitive to parameters that are used for data filtering (Calderón-Sanou et al., 2019; Mächler et al., 2021). In a preliminary analysis, we also assessed phylogenetic diversity (see Supporting Information). However, estimates of phylogenetic diversity showed an almost perfect correlation with taxonomic richness ($r = .97$). The relationships between phylogenetic diversity, time since glacier retreat, and climatic variables were identical to that observed for taxonomic richness (Figure S4).

2.4 | Drivers of changes in taxonomic diversity and traits

To assess whether colonization patterns are different between forelands in different climatic regimes, we defined the meso-climate of each foreland as the average conditions of the sites within the foreland during the warmest quarter of the year. We calculated mean temperature and precipitation for the period 1979–2013 based on ChelsaClim dataset at the 1-km spatial scale (Karger et al., 2017). ChelsaClim is among the datasets that best describe climatic conditions in mountainous areas (Karger et al., 2017) and provided estimates of temperature that were strongly related to field records (correlation with temperature recorded with data-loggers in the soil of 26 glacier forelands: Pearson's $r = .82$, $p < .0001$) (Marta et al., 2023). Temperatures ranged from 2 to 17°C (average 7.8°C). We used climatic conditions of the warmest quarter (hereafter: summer) because, during winter, snow cover causes a strong decoupling between air temperature and soil temperature (see e.g., Lembrechts et al., 2022; Marta et al., 2023). Therefore, during winter, meso-climate does not represent conditions experienced by soil organisms whereas, in summer, it provides an excellent estimate of soil conditions (Marta et al., 2023). In fact, previous analyses showed that summer temperature is the strongest climatic driver of soil development in proglacial environments, probably because most biological activity occurs in this season (Khedim et al., 2021).

For a subset of sites ($N = 160$), we also collected additional soil samples to measure pH and total organic carbon (TOC). pH was measured with a pH-meter after having dispersed 4 g of soil into 10 mL of bi-distilled water (Gibbard, 1993). TOC was measured on bulk samples after drying, using an OEA Flash200 ThermoFisher elemental analyzer (see Khedim et al., 2021). We calculated average organic carbon and pH for each site. Sites with and without chemical features had similar ages since glacier retreat and mean temperatures (linear models; both $p > .3$).

We first used univariate Bayesian generalized linear mixed models (GLMMs) to assess how time since glacier retreat and meso-climatic conditions determine nematode diversity. We ran GLMMs with the

different site-level biodiversity metrics as dependent variables (taxonomic and functional richness, Rao's functional diversity and the mean CP value of each community, calculated by averaging the CP values of all the detected MOTU in each site). As independent variables, we considered time since glacier retreat (log-transformed), and mean temperature and total precipitation (log-transformed) during the warmest season. Mixed models also included the interactions between climatic variables and time since glacier retreat. These interactions were intended to test the hypothesis that the colonization rate is different between forelands experiencing different climatic conditions. We used the widely applicable information criterion to compare models with and without interactions (Gelman et al., 2014). We included the identity of glacier forelands as a random factor. Time and climatic variables were scaled (mean=0, SD=1) to allow a comparison of their estimated effects. Models were run with three MCMC chains using 10,000 iterations and a burn-in of 5000 in the *brms* R package (Bürkner, 2017). For taxonomic and functional richness, we used square root transformed data and a normal error distribution to better meet the normality assumption of models. Rao's functional diversity was rescaled following Smithson and Verkuilen (2006) to avoid zeros and ones, and the model was run using Beta distribution. For all models, c-hat was <1.01, indicating convergence; if the 95% credible intervals of an independent variable did not overlap zero, we assumed strong evidence of a relationship between the predictor and the response variable of the model. For taxonomic and functional richness, we included all the communities (N=240), while for Rao's functional diversity and the mean CP value, we excluded communities with observed richness=0 and thus analyzed 177 communities. To confirm that the observed relationships were not affected by unaccounted biogeographical processes, we assessed the relationship between the residuals of models and latitude (Bahram et al., 2018). Furthermore, we used Moran's *I* to confirm that the residuals of our models did not show patterns of spatial autocorrelation (Figure S5). Finally, several soil characteristics, such as nutrient content, can change along chronosequences and influence soil organisms (Ficetola, Marta, et al., 2021). To confirm that our conclusions were not biased by differences in soil features, we repeated the analyses for the subset of sites for which organic carbon and pH were available (N=160).

Threshold dynamics have been suggested to underline succession of glacier forelands, with a fast increase in community richness during the first years, followed by a plateau when high richness determines strong biotic interactions (Hanusch et al., 2022). We thus used segmented regressions to check the occurrence of thresholds in the relationships between taxonomic richness and time since glacier retreat (Ficetola & Denoël, 2009; Muggeo, 2003). We used maximum likelihood to build linear mixed models with one breakpoint (*segmented* package in R; Muggeo, 2003). We then compared models with the breakpoint with linear mixed models based on the Bayesian information criterion. As we hypothesized that climate modulates the relationships between time since glacier retreat and diversity, we analyzed separately glaciers with summer temperature above and below the mean (7.8°C being the mean summer temperature across all the study forelands).

We next built a multivariate GLMM to assess the impact of time and climatic variables on the richness of MOTUs belonging to the different trophic groups, defined on the basis of MOTU consumption traits. Multivariate GLMMs account for the multivariate collinearity between variables while providing a better statistical power than univariate tests. For each trophic group, the MOTU richness at the site level was used in the model as a dependent variable; we used a negative binomial distribution and considered all communities with at least one detected MOTU (N=177). We used the same independent variables and random effects of univariate GLMMs.

To further summarize the variation of all the considered functional traits tested by our models, we visualized trait and community locations in the functional space (the functional identity of communities; Mouillot et al., 2013). We built a multivariate functional space by ordinating taxa based on Gower trait distances using principal coordinates analysis (PCoA) and illustrated the global functional space of nematode communities with the first two axes of the PCoA (Borcard et al., 2011; Oksanen et al., 2013). This allowed us to ordinate communities according to their functional structure, by calculating the weighted mean of the PCoA scores of all the taxa detected in each community. We then used the *envifit* function from the vegan package to fit traits, time, and climatic variables onto the PCoA. The determination coefficient (R^2) was used to assess the strength of the correlations between the variables and the axes, and its significance was determined by comparing observed values with R^2 values obtained from 999 random permutations.

In order to evaluate the relative importance of environmental filtering (which predicts functionally homogeneous communities) versus competition (which predicts functionally different groups within the same community) (Götzenberger et al., 2012; Weiher & Keddy, 1999), we compared the observed values of Rao's functional diversity to those obtained from random community assemblies (Gotelli & Graves, 1996). We used null models to exclude the effects of taxonomic richness on functional diversity (Aros-Mualin et al., 2021) for all sites with at least two taxa and Rao's functional diversity >0 (N=142). We compared observed values of Rao's diversity to those obtained by randomizing the matrix of the 76 functionally characterized taxa 999 times, while keeping the number of detected taxa per community fixed. We then calculated standardized effect size (SES) values as the difference between the estimated values and the mean of randomly generated values of Rao's functional diversity, divided by the standard deviation of the 999 null values. Negative values of SES indicate that functional diversity is lower than expected by chance given the observed taxonomic richness, whereas positive values indicate that functional diversity is higher than expected under random assembly (Gotelli & McCabe, 2002). We then used Bayesian GLMMs to test whether SES values are related to time since glacier retreat and climatic conditions.

Finally, to characterize the processes underlying functional changes, we determined if functional dissimilarity between communities is caused by the addition of new traits or by the replacement of existing traits. We partitioned the functional β-diversity between sites within the same glacier foreland using the *beta* function in the package BAT (Cardoso et al., 2015). This function partitions total

functional β-diversity (β-Total) into the functional dissimilarity explained only by the replacement of traits (β-Replacement) and the dissimilarity explained by the loss/gain of new traits (β-Richness). We calculated functional beta diversity based on an UPGMA dendrogram built by clustering Gower functional distances between functionally characterized taxa. We only compared sites having at least one taxon (N = 177) and the comparisons were performed only between sites belonging to the same chronosequence (321 comparisons). All statistical analyses were performed in the R environment (version 4.0; www.r-project-org).

3 | RESULTS

After data filtering and clustering, DNA metabarcoding yielded a total of 3969 MOTUs of eukaryotes, 171 of which were identified as nematodes (Table S3; see Table S4 for the number of sequences kept at each step in the analyses). The number of nematode MOTUs detected per site ranged from 0 to 22 and was unrelated to the total number of DNA reads (Spearman's correlation: $r_s = .08$, $p > .05$), suggesting that nematode richness was not affected by sequencing performance.

Comparisons between observed taxonomic diversity (number of MOTUs) and biodiversity estimated using the first-order jackknife estimator (after excluding sites with zero detections) suggested that detected MOTUs represented on average 71% of the actual taxonomic richness (range of coverage: 56%–100%). The coverage was also high for functional richness (on average, 83% of actual diversity values were detected). For both taxonomic and functional richness, detected and estimated diversity values were strongly correlated (in all cases, Pearson's $r \geq .91$; Figure S6). Functional richness and Rao's functional diversity were positively correlated and correlated also with taxonomic and phylogenetic diversity (all $r \geq .4$ and $p < .01$; Table S5).

3.1 | Patterns of biotic colonization under different climates

The taxonomic richness of nematodes strongly increased with time since glacier retreat and was significantly higher in forelands with mild summers (i.e., with above-the-average summer temperature: >7.8°C; Figure 2a,b; Table S6). Furthermore, we detected a strong interaction between time and temperature. In mild forelands, nematodes were able to colonize the terrains in a very short time, being already present 4 years after glacier retreat. Conversely, in forelands with cold summers (temperature ≤7.8°C), taxonomic richness was close to zero at all sites aged less than 15 years (Figure 2a). Afterward, taxonomic richness increased over time, but the increase was relatively fast in cold forelands, so that the diversity became similar across all forelands ~150 years after glacier retreat. Segmented regressions did not indicate thresholds in the increase in taxonomic richness either in warm or cold summer environments (Table S7). All results were robust to the inclusion of soil features (pH and TOC) in the models (Table S8) or the use of Shannon diversity instead of taxonomic richness (Figure S3).

Among the 76 functionally characterized taxa, 57% occurred in both early (≤65 years) and late (>65 years) communities, whereas 26 taxa were exclusively observed in late communities, and seven taxa were only found in early communities (Figure S7). Among those pioneer taxa, five were only detected in mild forelands (Hemicycliophora_01755, Neotylenchidae_02938, Oostenbrinkia_01833, Rhyssocolpus_03988, and Tobrilidae_03778), one in both mild and cold forelands (Mononchus_02143), and one (Mesodorylaimus_04367) was exclusively detected in cold forelands. Overall, most taxa (61%) were found in both cold and mild forelands, although more taxa were exclusive to mild forelands (21) than to cold forelands (9; Figure S8). Similarly, 58% of the taxa was detected in both rainy and dry forelands, with a similar number of taxa exclusively found in rainy (17) or dry (15) forelands (Figure S9).

Both functional richness and Rao's functional diversity increased over time (Figure 2c,d; Table S6). Again, the functional richness of soils exposed for <150 years was consistently higher in mild forelands. A strong interaction between time and summer temperature indicated that the effect of climate on functional richness is particularly strong immediately after glacier retreat, similar to what is observed for taxonomic richness. In contrast, this interaction was not significant for Rao's functional diversity (Table S6). All measures of taxonomic and functional diversity were unrelated to precipitation differences across forelands (Table S6).

We also evaluated whether taxonomic richness consistently increases within the different functional groups of nematodes, defined based on their consumption traits. Most consumption traits were already present soon after glacier retreat (i.e., <15 years; Figure 3). The richness of most of them (bacterivores, fungivores, omnivores, predators, detritivores, and parasites of plants) increased through time (Figure 3; Table S9). Bacterivores and detritivores showed higher richness in forelands with mild summers, and the richness of predators decreased with precipitation (Table S9). In this case, we did not find strong support for an interaction between climatic features and time since glacier retreat (Table S9).

3.2 | Changes in functional traits

Communities changed their mean CP values across deglaciated terrains of different ages (Figure 2e; Table S6). Soon after glacier retreat, communities were dominated by colonizer taxa with r-ecological strategy and short generation time (i.e., low CP values). At later stages, communities were dominated by more persister taxa with K-strategy and long generation times. For this trait, we found neither relationships with climate nor an interaction between climate and time (Table S6). Fitting communities in the functional space using PCoA (Figure 4) confirmed that, immediately after glacier retreat, communities were dominated by colonizer taxa, mostly feeding on bacteria and fungi or plant parasites. In later stages, communities were dominated by persister taxa and hosted a greater diversity of trophic groups, with more omnivores and predators and, to a lesser extent, detritivores and animal parasites (Figure 4; Table S10).
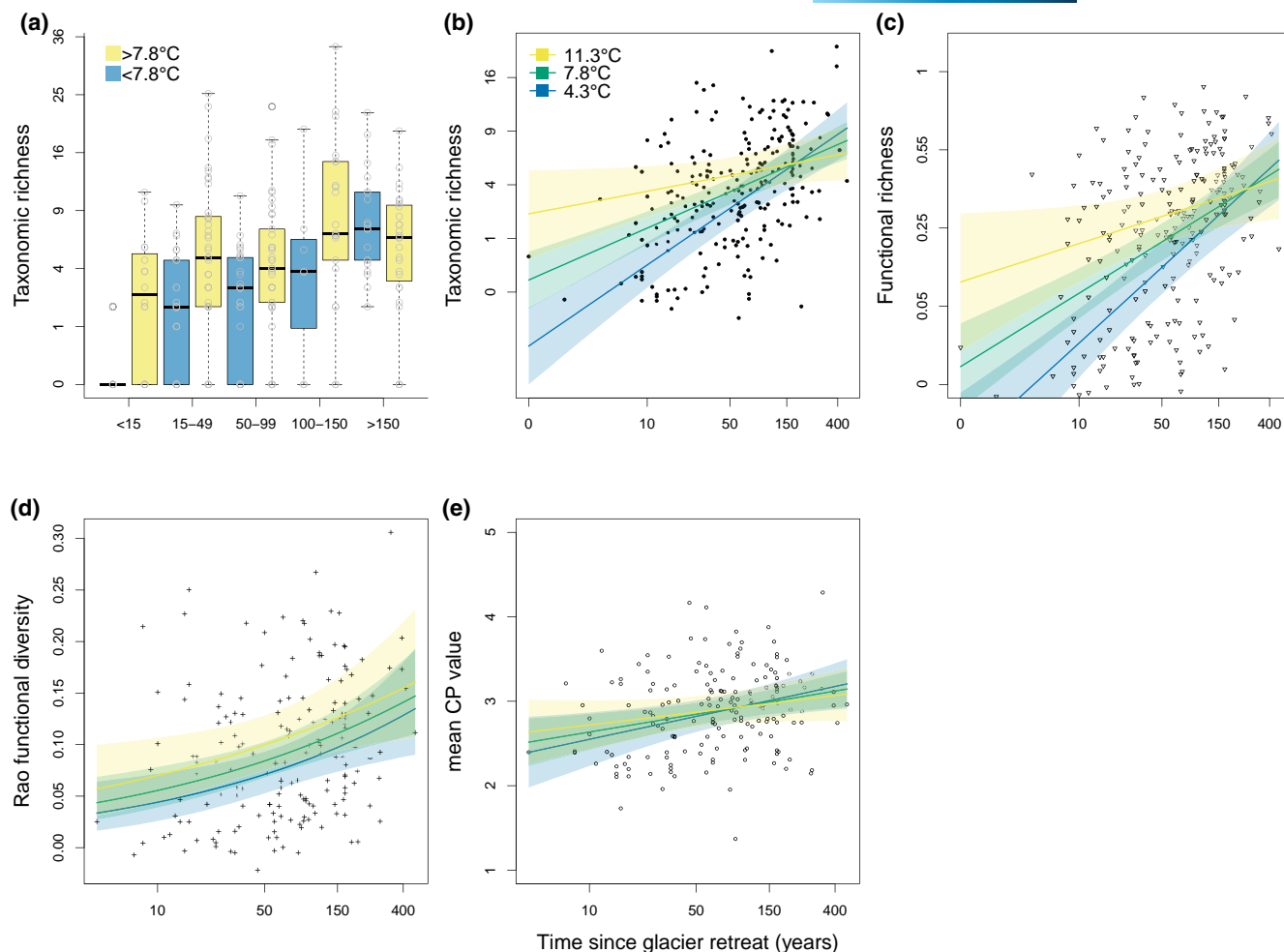
FIGURE 2 Changes in taxonomic and functional diversity of nematodes with age of deglaciated terrains. (a) Taxonomic richness (first-order jackknife estimator). Blue boxes: forelands with mean temperature during the warmest quarter (summer temperature) below the average (7.8°C); yellow boxes: forelands with summer temperature above the average. (b–e) Relationships between different measures of taxonomic and functional diversity and time since glacier retreat in forelands with different summer temperature conditions: 4.3 and 11.3°C are the average±SD. (b) Taxonomic richness. (c) Faith's functional richness. (d) Rao's functional diversity. (e) Mean colonizer–persister (CP) value of the communities, ranging from 1 (colonizer taxon with r-strategy) to 5 (persister taxon with K-strategy). (b–e) Represent conditional plots of Bayesian mixed models; partial residuals were calculated using fixed effects only; shaded areas are 95% credible intervals for forelands with different summer temperatures. For models in (b–e), conditional R^2: .52, .48, .36, .30; marginal R^2: .23, .22, .14, .07. In panels (a–c), $N = 240$ communities. In (d, e), $N = 177$ communities with observed richness >0.

## 3.3 | Processes underlying community assembly and functional changes

At 60% of sites, the observed functional diversity was similar to what we would expect based on taxonomic diversity (non-significant Rao's SES values; |SES| < 1.75), suggesting that the accumulation of traits over time was mostly caused by the addition of new taxa. Nevertheless, SES values were negatively related to precipitation (Figure 5; Table S6), with consistently positive SES in forelands with less precipitation during summer (on average, below 292.9 mm). This suggests that, in these forelands, communities were more functionally diverse than in more humid forelands. Additionally, SES values tended to increase over time (but this effect was weak with credible intervals slightly overlapping zero), with the oldest communities having more positive SES values regardless of climate (Table S6;

Figure 5). This indicates that early communities tended to be more functionally homogeneous than late communities.

Partitioning functional dissimilarity between communities from the same foreland showed that functional changes are characterized by both the addition of new traits and the replacement of traits (functional β-Replacement=46.5% and functional β-Richness=53.5%), although the contribution of the addition of traits was significantly higher than trait replacement (Figure S10, Wilcox paired test: $V = 20,019$, $p = .012$).

4 | DISCUSSION

Understanding how biodiversity components develop under different climates and assessing the variation of functional groups in response
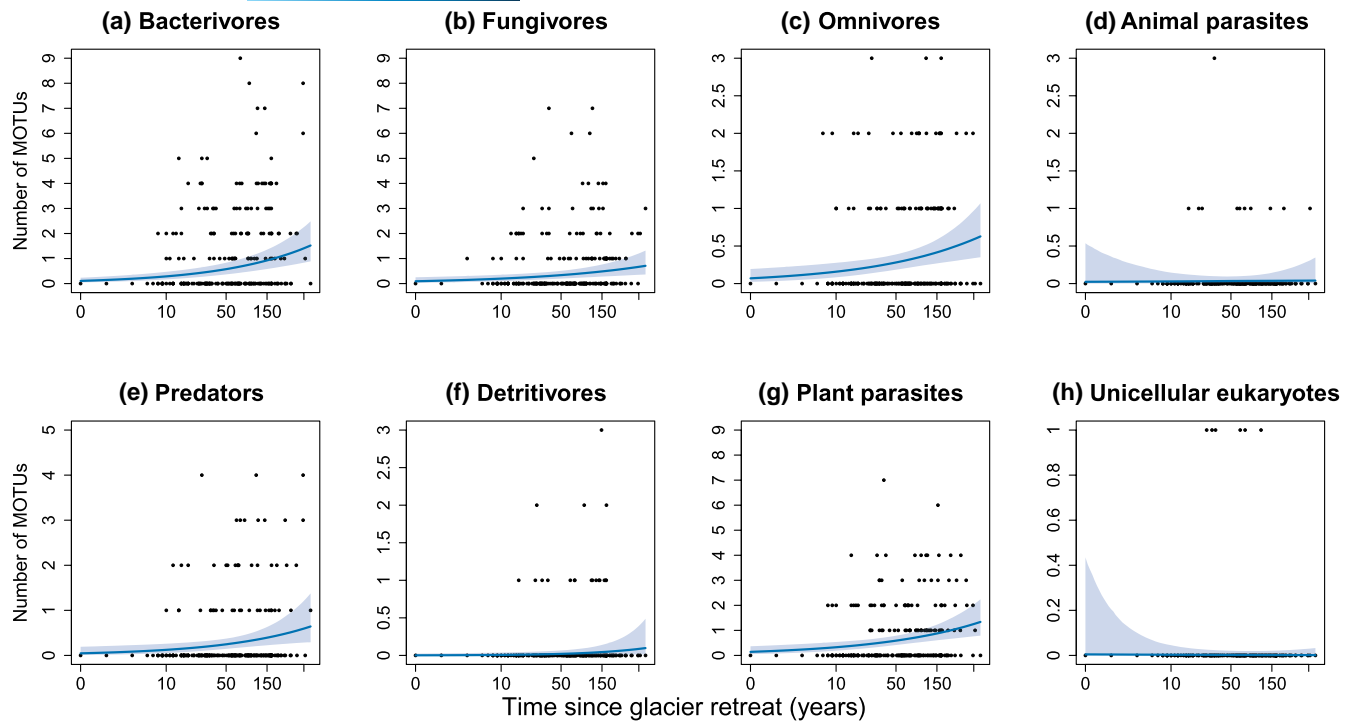
FIGURE 3 Changes in the richness (number of MOTUs) of trophic groups of nematodes over time in deglaciated terrains. The blue line represents the fitted values of a negative-binomial Bayesian mixed multivariate model; shaded areas are 95% credible intervals; $N = 240$ communities. In (a–h), conditional R^2: .5, .4, .2, .1, .2, .3, .2, .2; marginal R^2: .1, .04, .06, .02, .1, .1, .05, .01. MOTU, molecular operational taxonomic unit.
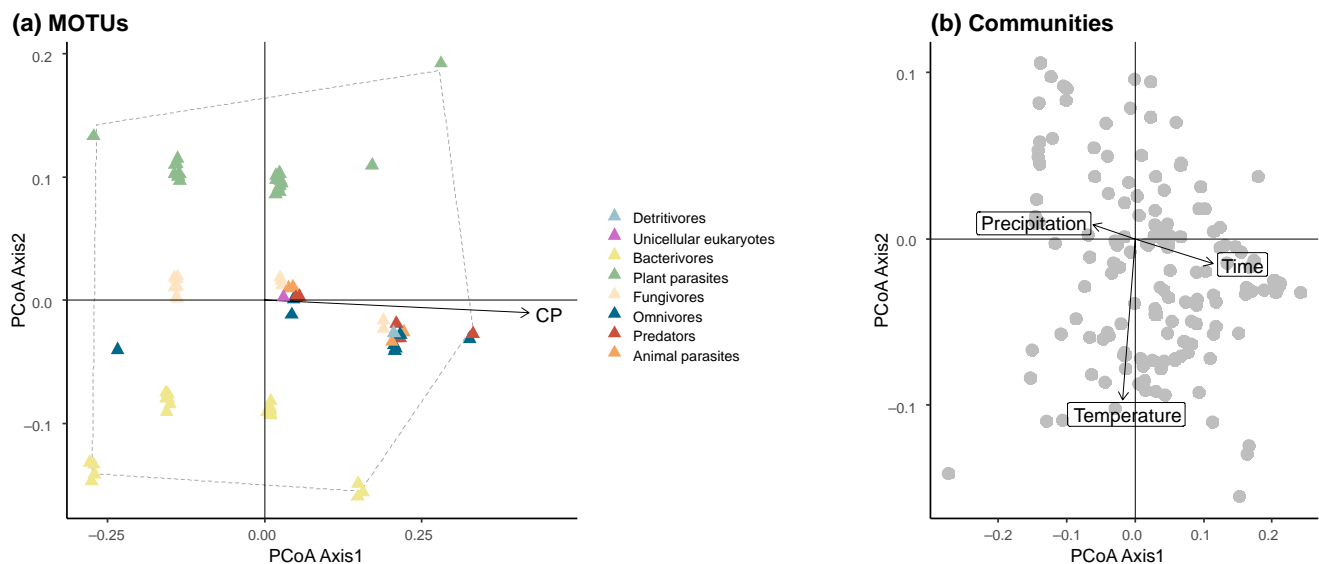

FIGURE 4 Results of the principal coordinate analysis (PCoA) showing changes in functional traits of nematode communities with nematode colonization. (a) Representation of detected taxa displayed according to their consumption traits within the global functional space (explained variance: 68% and 20% for axes 1 and 2, respectively). (b) Representation of communities and their trait composition based on the same PCoA. In (a, b), $N = 177$ communities with observed richness >0. MOTU, molecular operational taxonomic unit.

to glacier retreat is pivotal for predicting the future of these emerging ecosystems. After glacier retreat, soil colonization by keystone animals, such as nematodes, was affected by temperature differences among forelands (Figure 2), supporting the hypothesis that the retreat of glaciers impacts soil biodiversity in different ways depending on regional climates (Kaufmann, 2002; Khedim et al., 2021).

FIGURE 5 Relationship between standard effect sizes of Rao's functional diversity and time since glacier retreat in forelands with different precipitation conditions: 292.9 mm is the average summer precipitation across all the forelands (gray); 539.2 (purple) and 159.2 mm (orange) are the average ± SD. The SES sign indicates if the functional diversity is lower (SES < 0) or higher (SES > 0) than expected by chance, given the observed taxonomic diversity. The dashed line indicates SES = 0. Conditional R^2: .22; marginal R^2: .08. $N = 142$ communities with Rao's functional diversity > 0. SES, standardized effect size.
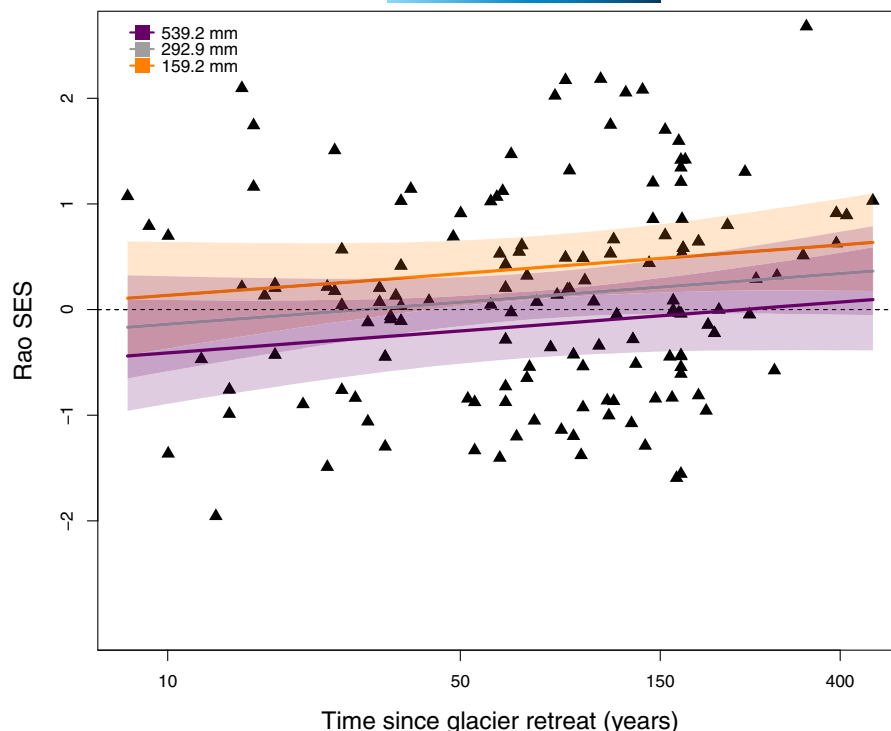
4.1 | Mesoclimate affects the development of nematode communities

Nematodes were able to colonize deglaciated terrains very soon (in 4–15 years; see also Lei et al., 2015). As nematodes are generally absent from supra-glacial environments (Zawierucha et al., 2021), their rapid colonization might be related to their excellent dispersal abilities (Fontaneto, 2019). Colonization started earlier in forelands with mild temperatures, where we found nematodes already 4 years after deglaciation. Under colder temperatures, 10–15 years were required for nematode communities to establish (Figure 2a), possibly because soil ecosystems were not developed enough. Despite these differences at the early stages, the successional trajectories observed in different climatic regimes converged and, after approximately 150 years, the coldest forelands achieved diversity values comparable to the warmest ones (Figure 2). Temporal patterns of nematode colonization in proglacial environments vary among studies: while some reported rapid colonization (within 3 years of glacier retreat; Lei et al., 2015), others suggested that nematode establishment may take one to several decades (Devetter et al., 2021; van Leeuwen et al., 2018). These studies analyzed different areas of the world; slow colonization was observed in subarctic regions (Devetter et al., 2021; van Leeuwen et al., 2018), whereas fast colonization was observed in a warmer region (Lei et al., 2015). Consistent with these findings, our results suggest that such disparities among studies can be attributed to key environmental features, such as climate.

The effect of climate was evident also on functional diversity, as temperature interacted with time to determine functional richness, and SES values were significantly related to precipitation. After accounting for taxa richness, functional diversity tended to be higher than expected under randomness (SES > 0) in late communities and

dry forelands. The effect of time on SES values was weak but followed the expected pattern (Purschke et al., 2013). Communities exhibiting high functional diversity often indicate limiting similarity due to niche differentiation (Macarthur & Levins, 1967). This can be underlined by competition for resource-rich conditions (Bertness & Callaway, 1994; Losapio et al., 2021; Pothula & Adams, 2022), as expected in late communities (Ficetola, Marta, et al., 2021). Moreover, the higher than expected functional diversity in forelands with low precipitation might arise because only a few taxa can colonize semi-arid environments, but these taxa included nematodes exhibiting diverse trophic specializations. The response of nematode communities to precipitation gradients is extremely complex and probably different across ecosystems, highlighting the importance of more studies relating nematode diversity and water availability (Franco et al., 2019; Ma et al., 2018; van den Hoogen et al., 2019). The lower than expected functional diversity obtained in early communities and rainy forelands may result from environmental filtering retaining taxa that share traits adapted to those specific conditions. However, competitive exclusion of taxa with traits associated with low competitive ability for the limiting resources can also explain those patterns (Münkemüller et al., 2020). We compared observed functional diversity to the one expected by assembling communities from a pool containing all the functionally characterized taxa detected across our sites. Therefore, we compared the functional diversity of a specific community to a global pool that included taxa capable of persisting but also those unable to persist in the conditions of the community. This makes our approach more sensitive to environmental filtering than to weaker competitor exclusion (de Bello et al., 2012), which operates among taxa able to persist given the specific abiotic constrains of a site.

Our global sampling design allowed us to identify the key role of climate, avoiding the confusion between temperature and biogeographical

context. Mild temperatures occurred in forelands across a broad range of latitudes (Figure 1) because temperature also depends on foreland elevation and solar radiation. Therefore, the observed patterns are not biased by differences between tropical, temperate, and boreal areas (Freeman et al., 2021) (Figure S11), suggesting that local climate is a better proxy of the factors driving biodiversity than latitude. Forelands under different climates have thus distinct trajectories, likely determined by the balance between dispersal, environmental filtering and competition (Lei et al., 2015; Losapio et al., 2021). The biomass and diversity of below-ground animals, including nematodes, are tightly linked to the accumulation of organic matter (Fan et al., 2023; Fierer et al., 2009; Lei et al., 2015; van den Hoogen et al., 2019), which can be particularly fast under a mild summer climate (Khedim et al., 2021). Nematode colonization immediately after glacier retreat was fostered by mild climates with a pattern very similar to the one observed for soil organic matter (Khedim et al., 2021), and this effect was evident even after accounting for the heterogeneity of soil features within forelands (i.e., TOC and pH; Table S8). Overall, our results highlight that the interplay between climate and time is a major driver for the development of a broad range of features (from biotic to abiotic ones), determining ecosystem-level responses to glacier retreat.

Some studies observed nonlinear patterns in the colonization of deglaciated terrains by nematodes (Doblas-Miranda et al., 2008; Lei et al., 2015; Pothula & Adams, 2022). For instance, Doblas-Miranda et al. (2008) suggested that nematode diversity increases through time, with a peak around 5000 years after glacier retreat, and then decreases. Regardless of the climatic conditions, we did not detect analogous thresholds (Table S7). This outcome probably resulted from our shorter timespan (<400 years), which is well suited to unravel the consequences of ongoing climate change but cannot detect nonlinear dynamics that often occur over long (millennial) timescales (Losapio et al., 2021).

4.2 | Functional changes during colonization

Nematodes from most of the trophic groups were present since the early successional stages (Figure 3; Figure S7). The dispersal ability of nematodes, particularly the ones with r-ecological strategy and short generation time (low CP values), may allow their propagules to quickly (<15 years) reach deglaciated terrains from already structured communities in nearby sites. Indeed, early communities were mostly composed of nematodes with a r-strategy (Figures 2e and 4) that probably have high dispersal abilities and/or better fitness in these environments: a pattern observed for several organisms during the colonization of proglacial landscapes (Cauvy-Frauni é & Dangles, 2019; Erschbamer & Caccianiga, 2016; Ferris et al., 2001; Hågvar et al., 2020; Hågvar & Gobbi, 2022). With time, the richness of many trophic groups grew (Figure 3), and the functional identity of communities shifted, with an increase of functional richness through the addition of persister taxa (Figure 4). We did not find evidence for distinct successional trajectories among trophic groups, although the rates of richness increase over time differed among them (Table S9), in

accordance with previous observations (Doblas-Miranda et al., 2008; Pothula & Adams, 2022; van Leeuwen et al., 2018).

The accumulation of traits and the increase in richness of trophic groups over time might enhance the redundancy within functional groups and improve the resilience and stability of late communities (Naeem, 1998; Pillar et al., 2013). Such a pattern suggests a growing number of available niches and a potentially weaker environmental filtering over time, as also suggested by the shallow growth of SES values over time (Figure 5). Late communities are probably more sensitive to resource availability than to environmental filtering hosting taxa having better fitness in well-developed soils, but can play a larger number of functions (Bongers, 1990; Mulder & Maas, 2017; Sechi et al., 2018).

4.3 | Study limitations

The global scale of our analysis imposed some limitations. First, we considered average climatic conditions in each foreland, due to data availability constraints. As forelands are heterogeneous landscapes, fine-scale studies evaluating soil features and microclimatic conditions (e.g., soil humidity and below-surface temperature) are required to better understand processes acting locally (Ficetola, Marta, et al., 2021; Marta et al., 2023). Nevertheless, the inclusion of key fine-scale features of soil (pH and organic carbon content) did not affect our conclusions (Table S8), suggesting that results are robust to processes occurring at a fine scale.

We assessed nematode diversity with eDNA metabarcoding and a generalist marker targeting all eukaryotes to obtain broad-scale data that would be challenging to assemble with traditional methods. The Euka02 marker has an excellent amplification rate and a good taxonomic resolution for nematodes (Ficetola et al., 2023). This marker amplifies short DNA fragments, being particularly well suited for eDNA-based studies, where DNA is extracted from difficult substrates and is often degraded, consisting of short sequences (Taberlet et al., 2018). Nevertheless, the eDNA approach does not provide estimates of absolute biomass and often does not allow for species-level identification. This methodological limitation prevented the use of traits representing body size, as those traits can change across life stages, show phenotypic plasticity, and are imprecise when applied at the genus level (Mulder & Vonk, 2011). Primers amplifying longer fragments could provide a more accurate taxonomic identification and enable better differentiation of closely related species (Ficetola et al., 2023; Gattoni et al., 2023). However, long markers are suited for the analysis of DNA extracted directly from specimens and are not appropriate for DNA extracted from soil. We highlight that the functional database used in this study provides traits assigned at the genus or family level; thus, coarse taxonomic assignments should not strongly impact functional diversity analyses.

The number of detected taxonomic units was generally lower than what was observed using traditional approaches in glacier forefields (Doblas-Miranda et al., 2008; Lei et al., 2015). Such differences may occur due to the imperfect primer resolution, because multiple taxa are merged into the same molecular taxonomic unit or because some taxa

(e.g., the rare ones) remain undetected. To limit issues related to under-detection, we used statistical approaches that consider the possibility of missing rare taxa (Chazdon et al., 1998; Colwell & Coddington, 1994; Gotelli & Colwell, 2011) and verified that our results remained consistent when using metrics that account or do not account for the relative abundance of taxa (Figure S3). Despite these limitations, soil eDNA provides biodiversity estimates and patterns highly consistent with those obtained with traditional approaches (Cantera et al., 2023; Treonis et al., 2018), and the observed changes in nematode communities are generally consistent with the patterns observed by both local-scale and meta-analytic studies (Calderón-Sanou et al., 2019; Devetter et al., 2021; Ji et al., 2013; Lei et al., 2015; Meyer et al., 2021; Pothula & Adams, 2022). Furthermore, the large number of analyzed chronosequences, their global distribution, and the coverage of a broad range of conditions help to smooth the impact of these limitations and reveal emergent signals with high generality (Mestre et al., 2022).

4.4 | Conclusion

There is growing evidence that climate change has uneven consequences across the globe, with high mountain and artic environments being among the most sensitive and impacted ecosystems (Hock et al., 2019). In these areas, biotic responses can be heterogeneous, as climatic differences across regions of the world can influence the trajectories of ecosystem evolution. We showed, on a worldwide scale, that nematodes colonizing soil after glacier retreat have successional trajectories that vary in speed among forelands. Local climate is a key driver for predicting the rate and nature of successions, and this is especially true at early stages of succession. Ecosystem functions and stability depend on local taxa and the traits they exhibit (Cardinale et al., 2012; Naeem et al., 2012). Nematodes play a key role in soil functioning, and the observed changes in their biodiversity might impact the whole dynamics of the ecosystems emerging after glacier retreat, as they can influence soil formation and the communities that follow. A key next step will be the development of multi-trophic analyses evaluating the complex relationships between ecosystem evolution and different biodiversity components (e.g., bacteria, fungi, protists, plants, and other animals; Giachello et al., 2023; Potapov et al., 2022). This will allow a better understanding of how climate change modifies habitats and trophic links in alpine environments and drives the development of new ecosystems (Martinez-Almoyna et al., 2019). Due to ongoing climate change, newly deglaciated terrains are expected to be increasingly important ecosystems in this century (Intergovernmental Panel on Climate Change, 2021; Rounce et al., 2023). Recognizing the complexity of biodiversity responses across climates will enhance our understanding of how these environments evolve and our ability to predict cascading effects at both global and local scales.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Supplementary materials including Figures S1–S11 and Tables S1–S10 underlying the main results of the study are provided in the online version of the article. Raw sequencing data are deposited in Zenodo (https://zenodo.org/record/6620359). Sequences assigned to Eukaryotes after the bioinformatics pipeline are in the "Euka02_global_cluster_filt_tag.txt" file provided in Figshare (https://figshare.com/s/839b43ed65f9ffae809c), as well as scripts for reproducing (1) bioinformatic steps, (2) taxonomic assignation, (3) MOTU filtering, (4) the measurement of estimated biodiversity using first-order jackknife estimator, (5) functional variables analyses, and (6) model computation and visualization.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Local climate modulates the development of soil nematode communities after glacier retreat

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Supplementary material includes:

Supplementary Text

Supplementary Figures

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Supplementary Text

Analyses of phylogenetic diversity

DNA metabarcoding usually produces very short sequences that are often deemed insufficient for accurate estimates of phylogenetic diversity. In our study case, DNA metabarcoding produced sequences of <150 bp in length. Such sequences often matched the published ones with limited similarity, and some of them matched more than one genus, making it impossible to estimate the phylogenetic diversity from published phylogenies. We thus relied our phylogenetic analyses on the obtained sequences, by first evaluating if they provide phylogenetic reconstructions that are consistent with the known relationships between taxa. Nematode sequences were aligned using MAFFT v7 with Q-INS-i settings to account for the secondary structure of ribosomal markers (Katoh et al., 2019); we obtained a 151 bp alignment. The phylogenetic reconstruction was obtained from the alignment with Bayesian Inference using BEAST v2.5 (Bouckaert et al., 2019) through the CIPRES online portal (Miller et al., 2010). We obtained an ultrametric rooted tree, with terminals equidistant from the root and with edge lengths proportional to evolutionary rate and time, on a relative scale. Parameters in BEAST were set as default, except for GTR+I+G as evolutionary model, estimated random local clock, and 50,000,000 generations with a burnin of 20%. The obtained three was highly consistent with the known taxonomic relationships between identified taxa, the clades showed good support and the effective sample size of parameters was always >1,000, thus we assumed that the obtained tree provides an acceptable approximation of the relationships between these taxa (Alberdi & Gilbert, 2019). We then calculated Faith's phylogenetic diversity of each site as the total branch length of the phylogenetic tree linking all MOTUs represented in a community, using the alpha.accum function in BAT (Cardoso et al., 2015; Petchey & Gaston, 2002). The correlation obtained between phylogenetic and taxonomic diversity was extremely high ($r = 0.97$; Table S5). The relationship between phylogenetic diversity, time since glacier retreat and climatic variables was identical to that observed for taxonomic diversity (Figure S4). Those relationships were tested using the same model structure and parameters used for the univariate mixed models in the main text; Faith's phylogenetic diversity was square-root transformed.

Supplementary figures

Figure S1. Sampling design. For each receding glacier, we identified 2-9 sites, representing the past position of the glacier on known dates. For each site, we established ~5 plots, at regular intervals of 20 m. Within each plot, we collected 5 soil sub-samples within 1 m^2; the distribution of sub-samples is shown by the pink inset. The five sub-samples were then pooled to form one composite sample per plot.
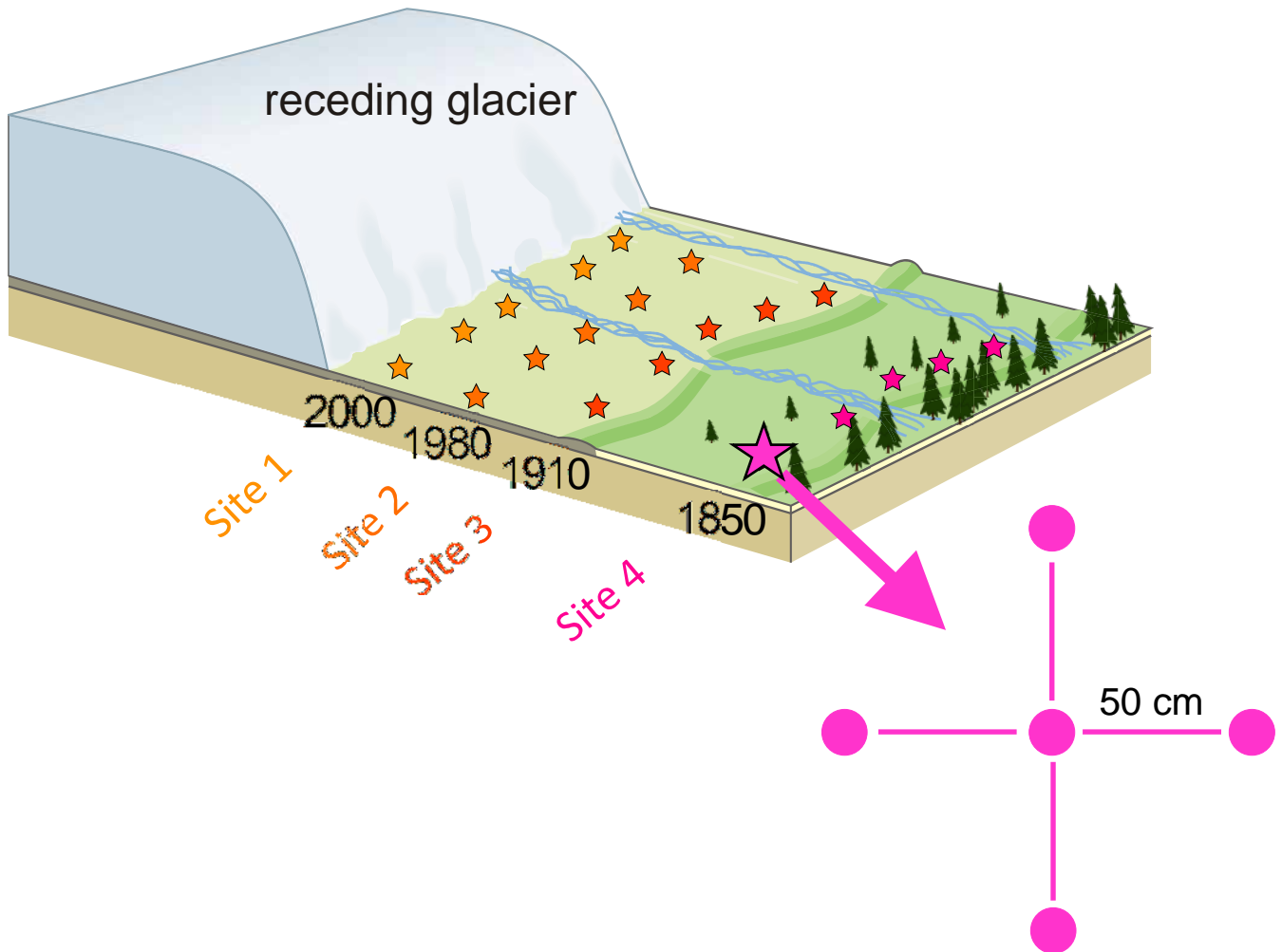
Figure S2. Changes in taxonomic diversity of nematodes in deglaciated terrains with different ages. Here, taxonomic diversity is estimated after filtering contaminants using the Davis et al. (2018)'s approach, with a threshold of a) 0.5 and b) 0.1. We show the conditional plots of Bayesian mixed model with associated conditional R^2 values. Shaded areas are 95% credible intervals for forelands with different summer temperatures; $N = 240$ communities. The model structure is the same as the one used for the univariate mixed models in the main text.
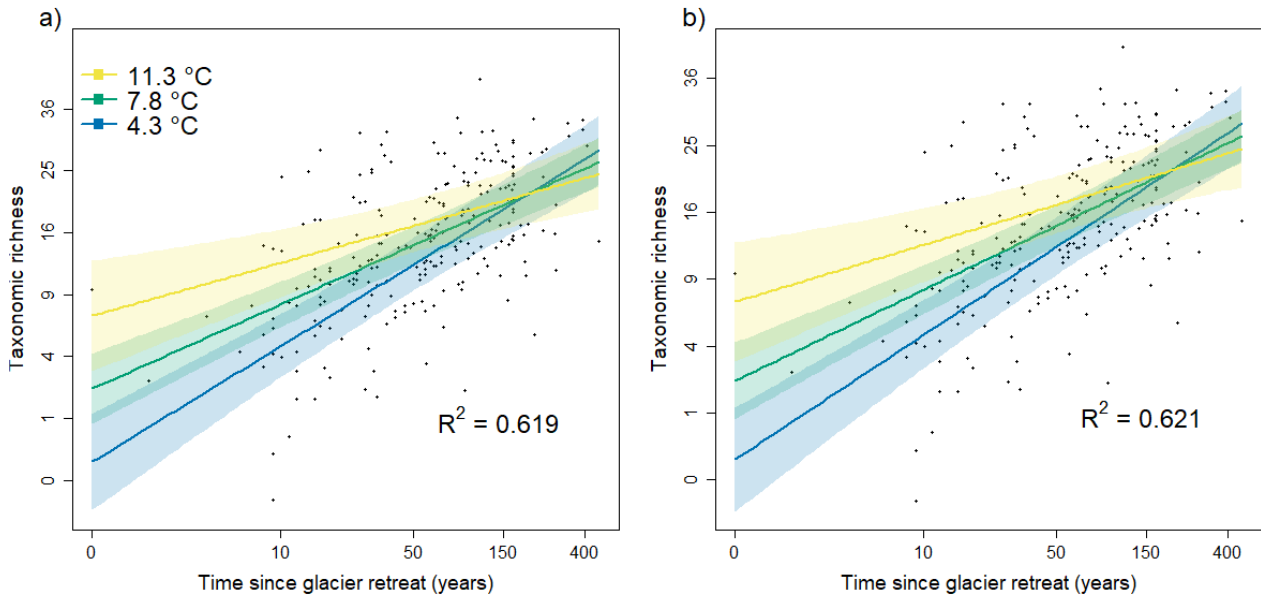

Figure S3. Changes in taxonomic diversity of nematodes in deglaciated terrains with different ages. Here, taxonomic diversity is estimated using different Hill's numbers (q = 0 and q = 1; diversity estimates are log-transformed to improve normality). We show the conditional plots of Bayesian mixed model with associated conditional R^2 values; shaded areas are 95% credible intervals for forelands with different summer temperatures; $N = 240$ communities. Note that Hill numbers > 1 cannot be computed because in several sites we detected zero nematode MOTUs. Model structure is the same as the one used for the univariate mixed models in the main text.
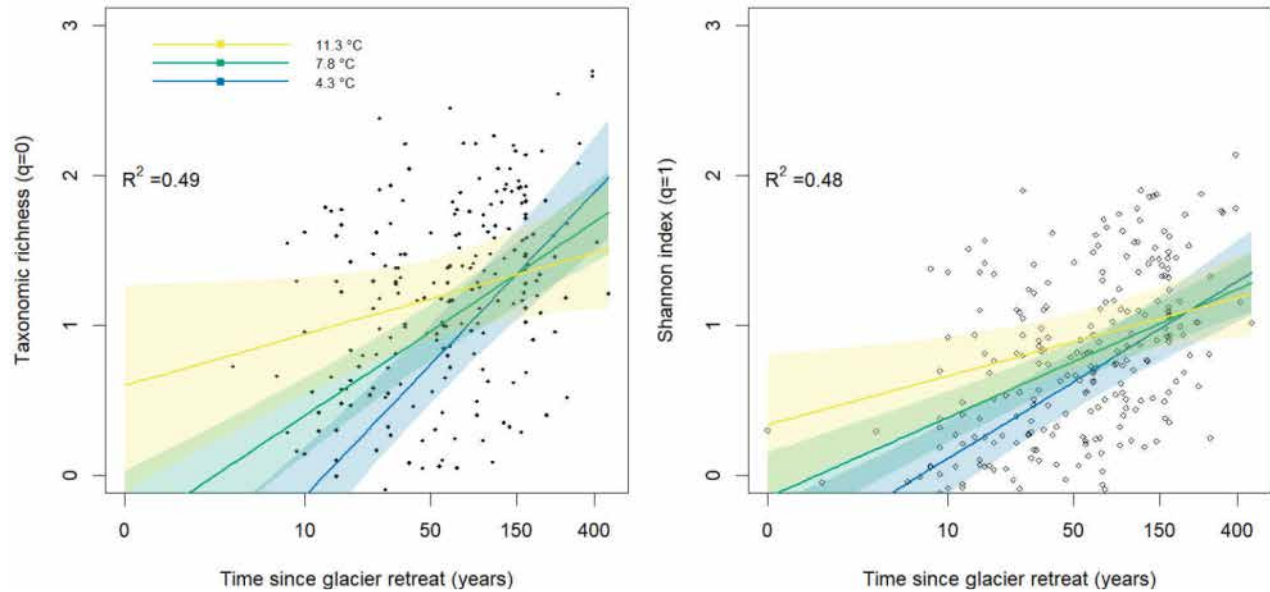

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Figure S4. Changes in phylogenetic diversity of nematodes in deglaciated terrains with different ages. Conditional plot of Bayesian mixed model with associated conditional R^2 values; shaded areas are 95% credible intervals for forelands with different summer temperatures; $N = 177$ communities with observed richness > 0. Model structure is the same as the one used for the univariate mixed models in the main text.
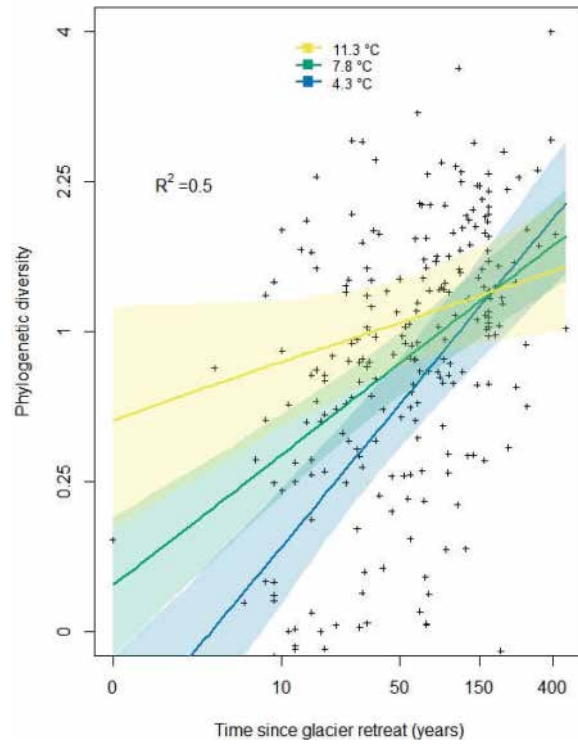
Figure S5. Spatial autocorrelation of the residuals of Bayesian models for taxonomic richness, functional richness and RAO functional diversity. Distance is measured in km; the shaded areas represent the 95% confidence interval of spatial autocorrelation (Moran's *I*).
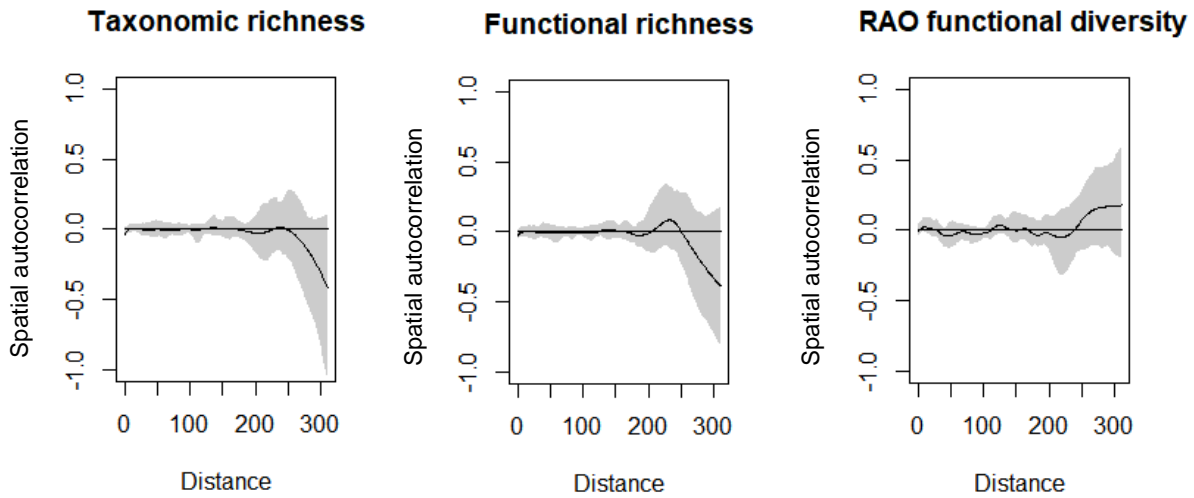

Figure S6. Pearson's product-moment correlations (*r*) between observed and estimated richness. a-b) All the communities (*N* = 240). c-d) Communities with observed richness > 0 (*N* = 177). Taxonomic and functional richness were estimated with the first-order jackknife estimators for incidence data (see methods).
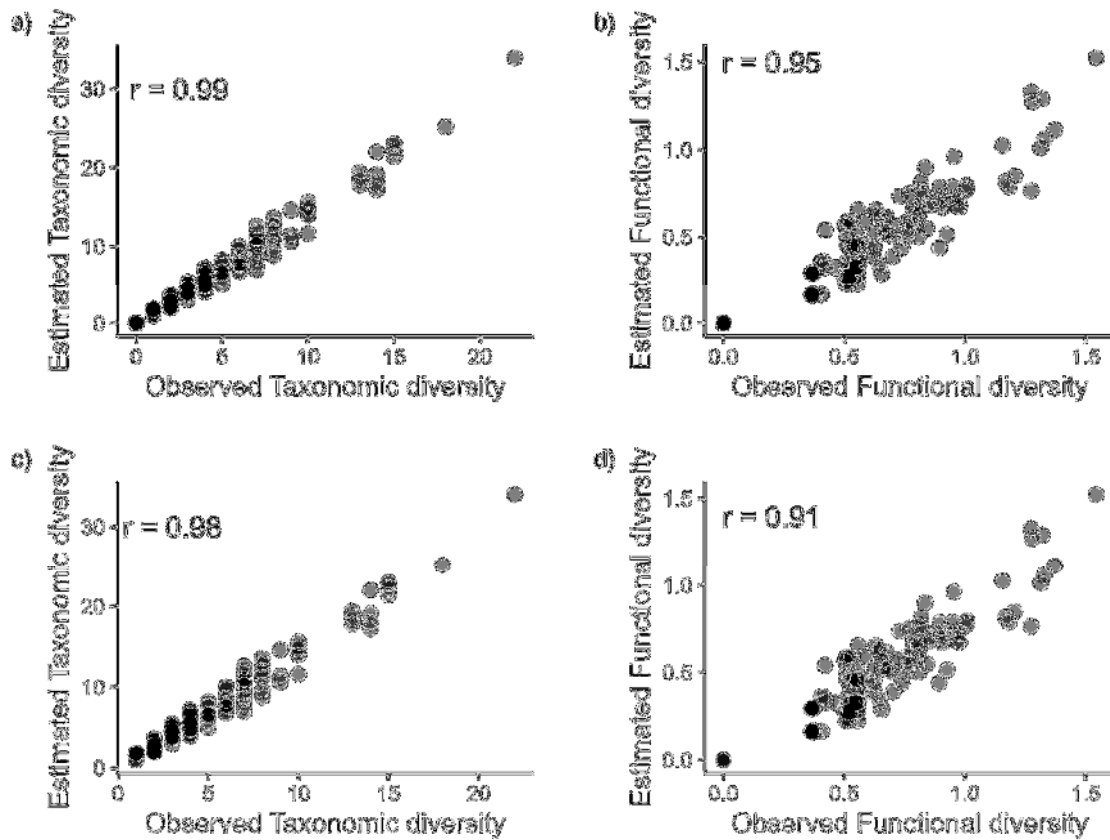
Figure S7. Proportion of occurrences of the 76 functionally characterized taxa across early (age ≤ 65 years) *versus* late communities (age > 65 years). The labels of taxa indicate their taxonomic assignation (genus or family name) and their trophic group. Fun: fungivorous; Pla: plant parasite; Pre: predator; Bac: bacterivorous; Ani: animal parasite; Omn: omnivorous; Det: detritivorous; Uni: feeding on unicellular eukaryotes.
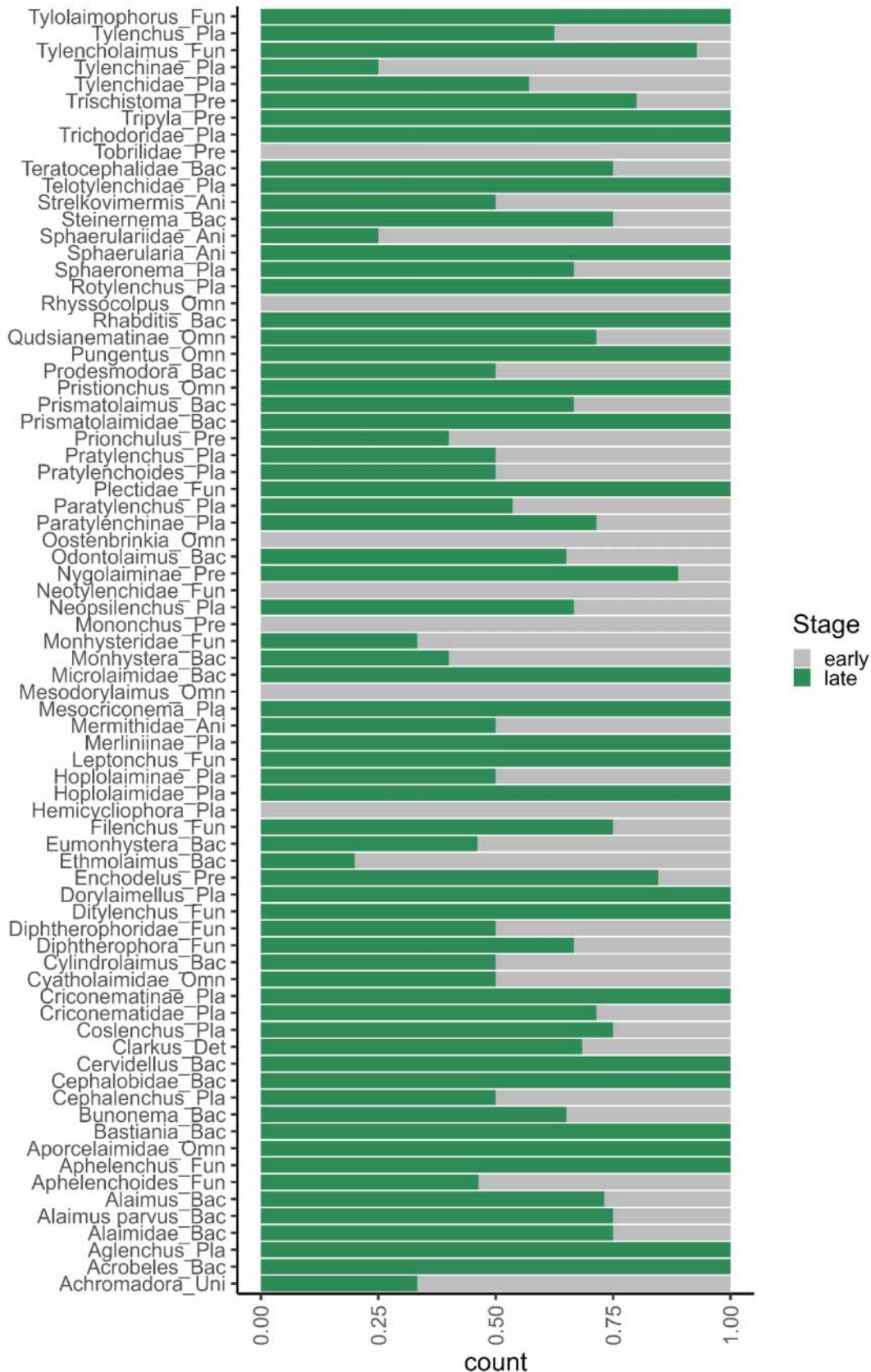
Figure S8. Proportion of occurrences of the 76 functionally characterized taxa across forelands with "mild" summers (*i.e.*, above-the-average summer temperature: > 7.8°C) *versus* forelands with "cold" summers (temperature ≤ 7.8°C). See Fig. S7 for taxa labels.
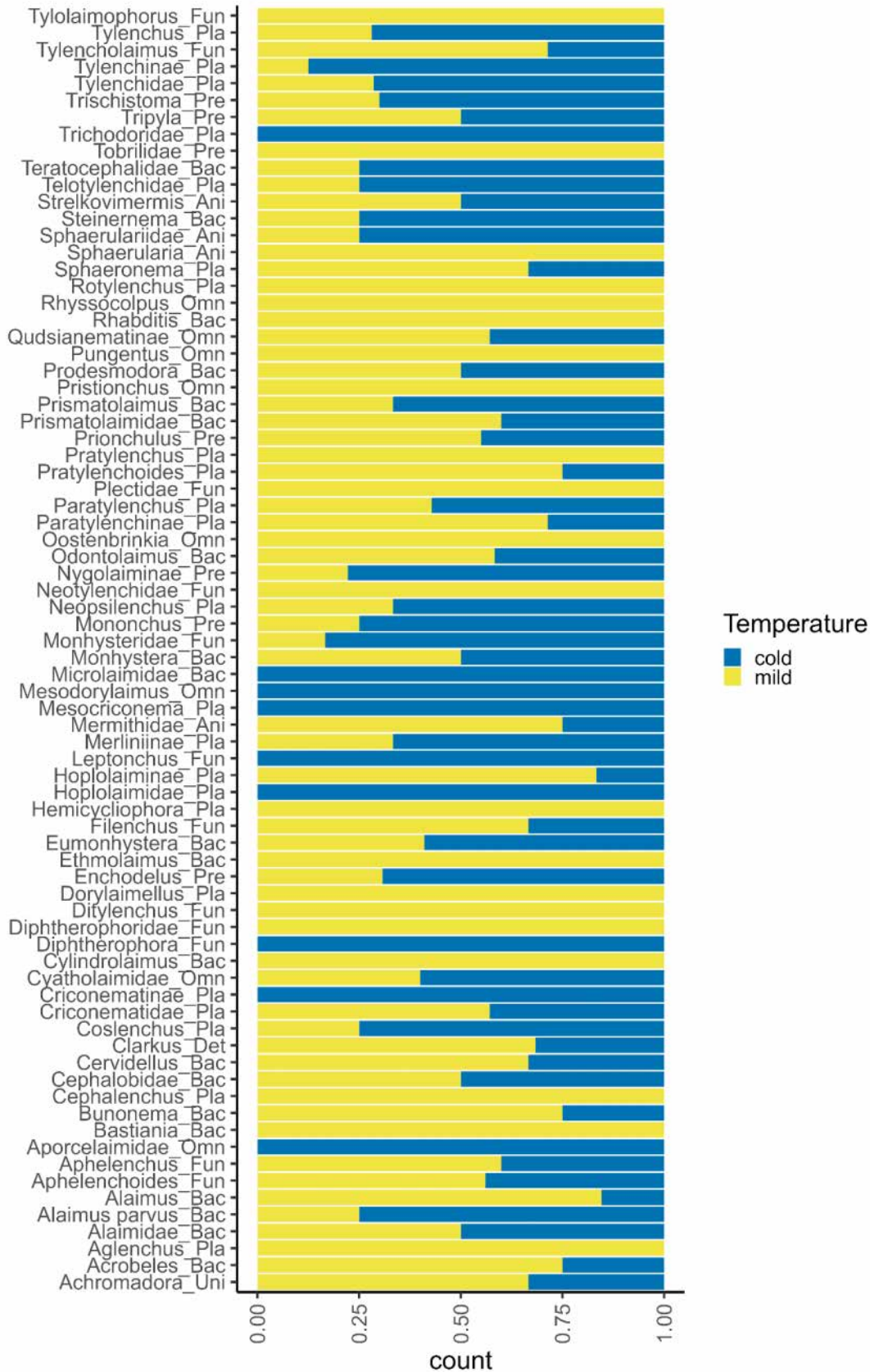
Figure S9. Proportion of occurrences of the 76 functionally characterized taxa across dry (*i.e.,* with less than average summer precipitation: ≤ 293 mm) *versus* rainy (> 293 mm) forelands. See Fig. S7 for taxa labels.
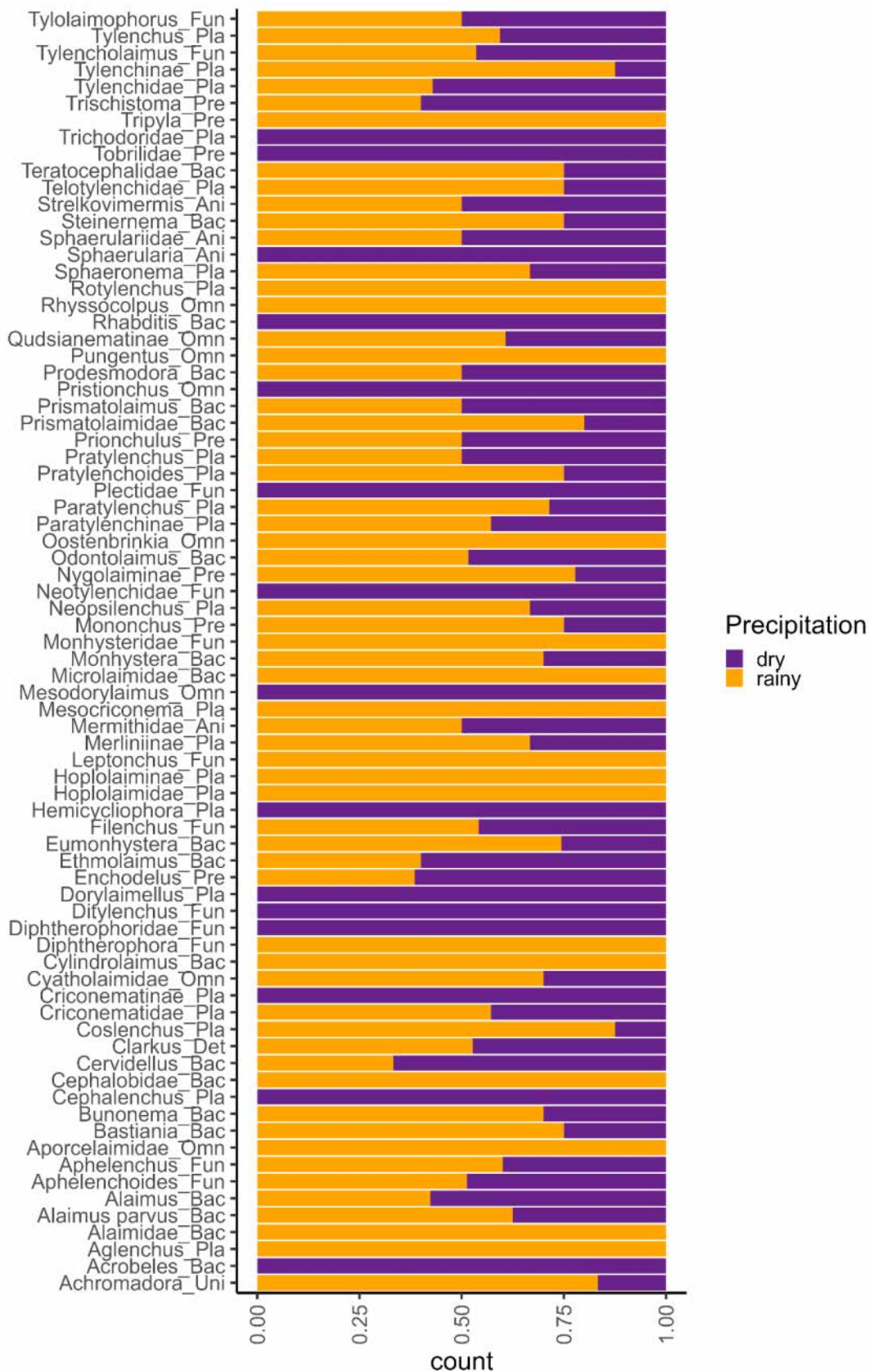
Figure S10. Partitioning functional β-diversity between sites within each glacier forelands. Total functional β-diversity (β-Total) is decomposed into the functional dissimilarity explained by the replacement of traits alone (β-Replacement) and the functional dissimilarity explained by the loss/gain of new traits alone (β-Richness). Differences between β-Replacement and β-Richness values are significant (Wilcoxon paired test: V = 20019, *P* = 0,012).
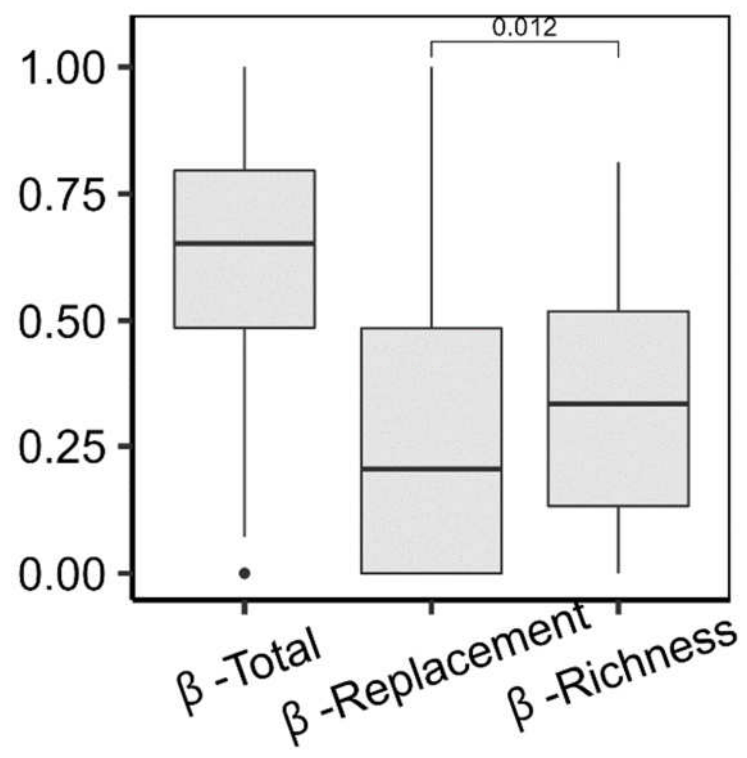
Figure S11. Relationship between latitude of sampled sites and the residuals of taxonomic richness, functional richness, Rao functional diversity and mean CP values.

Supplementary tables

Table S1: Site information of the sampled communities (*N*=240). Table containing information about sampling dates, geographical locations, time since glacier retreat, climatic variables (average temperature [°C] and precipitation [mm] of the sites within the foreland during the warmest quarter of the year for the time period 1979–2013; based on ChelsaClim dataset at the 1-km spatial scale), number of repl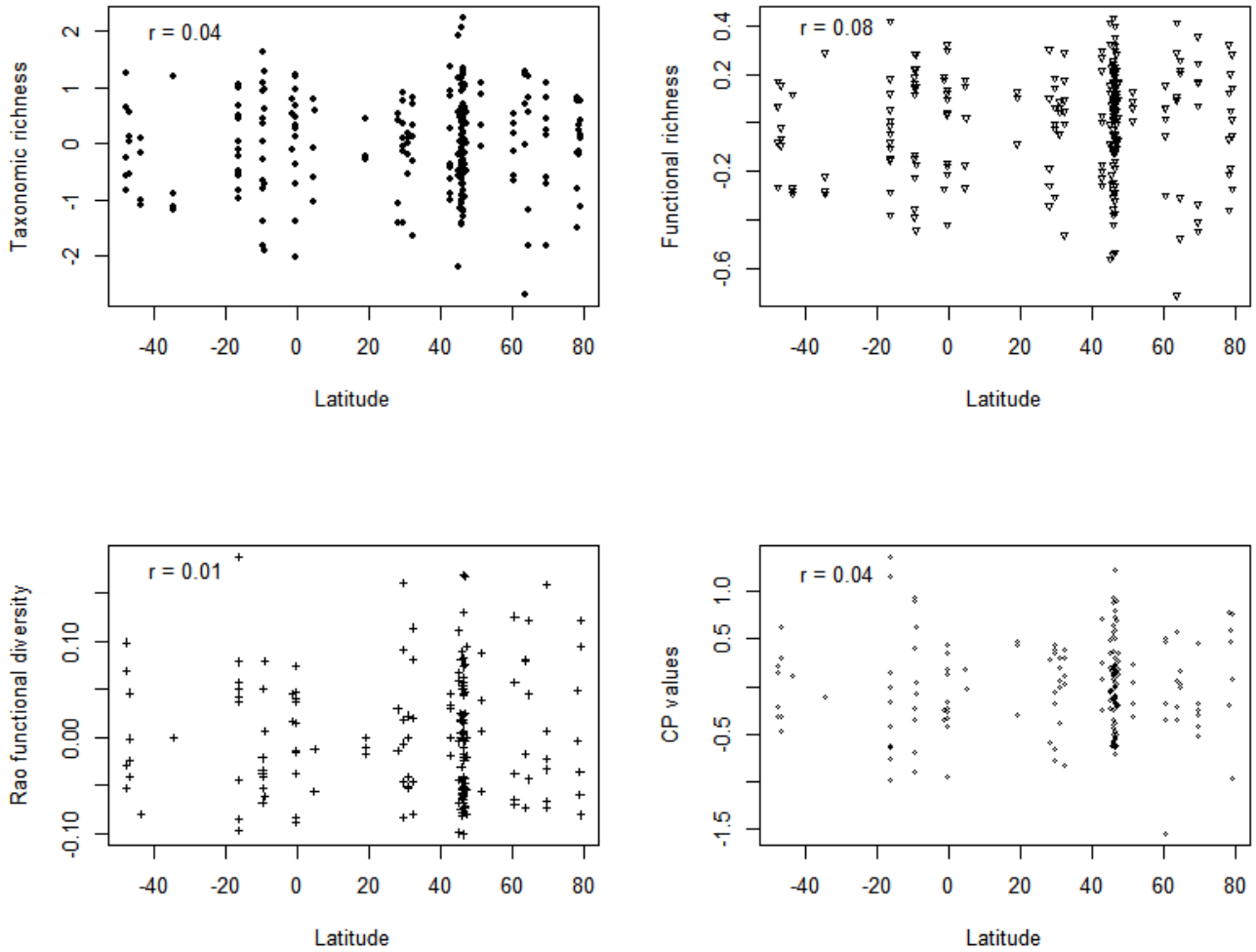icates per community, soil features (total organic carbon and pH), and biodiversity measures (see methods) at each site.

Table S2: Functional traits of the 76 taxa that had sufficient taxonomic resolution (family level or better) to assign traits using the Nemaplex database (http://nemaplex.ucdavis.edu/). Traits included one life-history index and 8 consumption traits (parasites of animals, parasites of plants, bacterivores, fungivores, detritivores, omnivores, predators, feeding on unicellular eukaryotes). The Nemaplex database reports functional traits at genus-level resolution. Thus, we directly assigned traits for MOTUs identified at the genus level; for MOTUs identified at the family level, CP values were calculated as the average of the genera within the family and consumption traits were conserved within the families.

Table S3: Detected MOTUs per site. The table provides information on the number of reads for each detected MOTU (*N* = 171) at each site (*N* = 240), along with associated taxonomic information, after bioinformatic steps, data filtering and cleaning. The table also specifies to which of the 76 functionally characterized taxa the MOTU belongs.

Table S4: Number of sequences retained at different steps of the bioinformatic treatment and data filtering.

	Number of reads	Number of different MOTUs
Raw sequences	169.700.440	
Kept after alignment	163.481.209	
Kept after ngsfilter	124.634.214	
Kept after filtering	97.845.376	72.437
Kept after clustering	97.845.376	16.033
Kept after removal of contaminants and sequences detected in just one sample	30.473.982	3.969
Assigned to Nematoda	1.550.956	171

Table S5: Pearson's product moment correlations (*r*) between all diversity metrics. Significant correlations (*P* < 0.05) are in bold. For correlations involving taxonomic diversity, phylogenetic diversity and functional richness: *N* = 240. For correlations involving Rao functional diversity: *N* = 177 (*i.e.*, all the communities with observed richness > 0). For correlations involving Rao SES: *N* = 142 (*i.e.*, all the communities with > 1 functionally characterized MOTUs).

	Phylogenetic Diversity	Functional Richness	Rao Functional Diversity	Rao SES
Taxonomic Diversity	**0.97**	**0.85**	**0.56**	0.1
Phylogenetic Diversity		**0.85**	**0.59**	0.12
Functional Richness			**0.44**	-0.1
Rao Functional Diversity				**0.75**

Table S6: Results of Bayesian univariate models assessing the relationship between nematode biodiversity [Taxonomic richness, Functional richness, Rao's Functional diversity, mean CP values and Rao's standard effect sizes (SES)] and time since glacier retreat, precipitation and temperature. Parameters with 95% confidence intervals non-overlapping zero indicate strong predictors of the response variable of the model and are highlighted in bold. Interactions were not included in the model for SES and mean CP values, as the models without interactions showed lower WAIC than the model with interactions (SES model without interaction: WAIC = 425 *versus* with interaction WAIC = 429; mean CP values model without interaction: WAIC = 301 v*ersus* with interaction WAIC= 304).

Dependent variable	Independent variables	*B*	Q2.5	Q5	Q95	Q97.5
Taxonomic richness	Time since glacier retreat	**0.44**	**0.30**	**0.32**	**0.57**	**0.58**
	Summer temperature	**0.28**	**0.01**	**0.04**	**0.52**	**0.56**
	Summer precipitation	0.07	-0.20	-0.17	0.3	0.34
	Time x Temperature	**-0.25**	**-0.40**	**-0.38**	**-0.12**	**-0.10**
	Time x Precipitation	-0.07	-0.22	-0.20	0.06	0.08
Functional richness	Time since glacier retreat	**0.11**	**0.07**	**0.08**	**0.14**	**0.15**
	Summer temperature	**0.08**	**0.01**	**0.02**	**0.14**	**0.15**
	Summer precipitation	0.03	-0.04	-0.03	0.09	0.10
	Time x Temperature	**-0.05**	**-0.09**	**-0.09**	**-0.02**	**-0.01**
	Time x Precipitation	-0.01	-0.05	-0.05	0.02	0.03
Rao functional diversity	Time since glacier retreat	**0.27**	**0.11**	**0.13**	**0.4**	**0.42**
	Summer temperature	0.18	-0.05	-0.02	0.37	0.39
	Summer precipitation	0.02	-0.19	-0.16	0.20	0.23
	Time x Temperature	-0.04	-0.19	-0.17	0.10	0.11
	Time x Precipitation	-0.12	-0.30	-0.27	0.03	0.05
Mean CP value	Time since glacier retreat	**0.12**	**0.03**	**0.04**	**0.21**	**0.22**
	Summer temperature	0.01	-0.13	-0.11	0.14	0.16
	Summer precipitation	-0.06	-0.19	-0.17	0.06	0.08
SES	Time since glacier retreat	0.12	-0.09	-0.07	0.31	0.34
	Summer temperature	0	-0.29	-0.24	0.23	0.27
	Summer precipitation	**-0.27**	**-0.53**	**-0.50**	**-0.04**	**-0.01**

Table S7. Comparison between segmented and linear mixed models, assessing relationships between time since glacier retreat and taxonomic richness. The models with breakpoint showed Bayesian Information Criterion (BIC) consistently higher than the respective models without the breakpoint, indicating weak support for the breakpoint.

	Forelands with T > 7.8°C	Forelands with T ≤ 7.8°C
Model with breakpoint (BIC)	445.5	296.2
Model without breakpoint (BIC)	438.3	293.3

Table S8. Results of Bayesian univariate models with the inclusion of soil features (total organic carbon and pH) assessing the variation of Taxonomic and Functional richness of nematode communities (conditional R^2 = 0.5 and 0.48, respectively). Parameters with 95% confidence intervals non-overlapping zero indicate strong predictors of the response variable of the model and are highlighted in bold.

Dependent variable	Independent variables	B	Q2.5	Q97.5
Taxonomic richness	Time since glacier retreat	**0.30**	**0.11**	**0.49**
	Summer temperature	0.09	-0.19	0.37
	Summer precipitation	0.19	-0.07	0.45
	Soil organic C	0.01	-0.24	0.28
	Soil pH	-0.18	-0.42	0.07
	Time x Temperature	**-0.28**	**-0.45**	**-0.11**
	Time x Precipitation	-0.04	-0.19	0.12
	Time x Soil organic C	-0.03	-0.16	0.10
	Time x pH	0.05	-0.11	0.21
Functional richness	Time since glacier retreat	**0.09**	**0.04**	**0.14**
	Summer temperature	0.02	-0.06	0.09
	Summer precipitation	0.07	**0**	**0.14**
	Soil organic C	-0.01	-0.07	0.05
	Soil pH	-0.05	-0.11	0.02
	Time x Temperature	**-0.07**	**-0.11**	**-0.02**
	Time x Precipitation	0	-0.04	0.04
	Time x Soil organic C	0	-0.03	0.04
	Time x pH	0.01	-0.04	0.05

Table S9. Results of the Bayesian multivariate model assessing richness (number of MOTUs) variation of consumption traits across nematode communities. Parameters with 95% confidence intervals non-overlapping zero indicate strong predictors of the response variable of the model and are highlighted in bold. Interactions were not included in the models as the model without interactions showed lower WAIC (2740 *versus* 2741).

Dependent variable	Independent variables	*B*	Q2.5	Q5	Q95	Q97.5
Bacterivores	Time since glacier retreat	**0.45**	**0.26**	**0.28**	**0.63**	**0.65**
	Summer temperature	**0.48**	**0.04**	**0.10**	**0.87**	**0.93**
	Summer precipitation	0.14	-0.30	-0.25	0.52	0.58
Fungivores	Time since glacier retreat	**0.35**	**0.09**	**0.12**	**0.58**	**0.62**
	Summer temperature	0.34	-0.11	-0.05	0.75	0.82
	Summer precipitation	0.06	-0.41	-0.35	0.51	0.58
Omnivores	Time since glacier retreat	**0.38**	**0.10**	**0.14**	**0.62**	**0.66**
	Summer temperature	0.31	-0.05	-0.01	0.65	0.70
	Summer precipitation	0.15	-0.22	-0.17	0.49	0.55
Parasites of animals	Time since glacier retreat	0.10	-0.84	-0.69	1.00	1.19
	Summer temperature	0.04	-0.94	-0.78	0.94	1.14
	Summer precipitation	-0.31	-1.69	-1.41	0.64	0.81
Predators	Time since glacier retreat	**0.45**	**0.07**	**0.12**	**0.79**	**0.85**
	Summer temperature	-0.22	-0.69	-0.63	0.15	0.20
	Summer precipitation	**-0.41**	**-0.87**	**-0.80**	**-0.05**	**-0.01**
Detritivores	Time since glacier retreat	**0.75**	**0.03**	**0.12**	**1.53**	**1.69**
	Summer temperature	**1.14**	**0.09**	**0.22**	**2.36**	**2.62**
	Summer precipitation	0.32	-0.78	-0.62	1.41	1.62
Parasites of plants	Time since glacier retreat	**0.39**	**0.12**	**0.15**	**0.62**	**0.66**
	Summer temperature	0.12	-0.21	-0.17	0.41	0.46
	Summer precipitation	0.07	-0.26	-0.22	0.38	0.43
Feeding on unicellular eukaryotes	Time since glacier retreat	-0.25	-1.77	-1.43	0.89	1.12
	Summer temperature	0.82	-1.43	-1.08	3.29	3.98
	Summer precipitation	0.96	-1.33	-1.01	3.74	4.43

Table S10. Results of the Principal Coordinates Analysis (PCoA) assessing the variation of traits in the functional space of nematodes communities. Fit between PCoA 1 and PCoA 2 axes with traits and environmental variables. The table shows the determination coefficient R^2 of the correlation between each trait or variable and the ordination, P-values based on random permutations of the data indicate if observed R^2 are higher than R^2 with randomly permuted data and the direction cosines of the continuous variables on the PCoA axes.

Variable	Axis 1	Axis 2	P	R^2
Consumption and life history traits				
Plant parasites	**-0.1**	**1**	**0.001**	**0.72**
Animal parasites	0.96	-0.27	0.23	0.04
Bacterivores	**-0.2**	**-0.98**	**0.001**	**0.68**
Fungivores	-0.93	0.35	0.56	0.02
Detritivores	0.92	-0.39	0.5	0.02
Unicellular Eukaryotes	0.83	0.55	0.96	0
Omnivores	**0.83**	**-0.56**	**0.03**	**0.09**
Predators	**0.96**	**-0.28**	**0.02**	**0.11**
CP value	**1**	**0**	**0.001**	**0.98**
Environnemental variables				
Glacier	**-**	**-**	**<0.001**	**0.45**
Time	**1**	**-0.04**	**0.004**	**0.06**
Temperature	-0.1	-1	0.07	0.03
Precipitation	-0.9	0.33	0.33	0.01

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