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RESEARCH ARTICLE

Community assembly in the wake of glacial retreat: A meta-analysis

Satyendra K. Pothula[1] | Byron J. Adams[1,2,3]

[1]Department of Biology, Brigham Young University, Provo, Utah, USA

[2]Evolutionary Ecology Laboratories, Brigham Young University, Provo, Utah, USA

[3]Life Science Museum, Brigham Young University, Provo, Utah, USA

Correspondence
Satyendra K. Pothula, Department of Biology, Brigham Young University, Provo, UT 84602, USA.
Email: satyendra.pothula@gmail.com

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Abstract

Ecosystems shaped by retreating glaciers provide a unique opportunity to study the order and timing of biotic colonization, and how this influences the structure of successive ecological communities. In the last century glaciers across most of the cryosphere have receded at an unprecedented pace. Many studies have been published from different parts of the world testing hypotheses about how soil ecosystems are responding to rapid, contemporary deglaciation events. To better understand and draw general conclusions about how soil ecosystems respond to deglaciation, we conducted a global meta-analysis of 95 published articles focused on the succession of various organisms and soil physicochemical properties in glacier forefields along the chronosequence. Our global synthesis reveals that key soil properties and the abundance and richness of biota follow two conspicuous patterns: (1) some taxa demonstrate a persistent increase in abundance and richness over the entire chronosequence, (2) other taxa increase in abundance and richness during the first 50 years of succession, then gradually decline 50 years onward. The soil properties and soil organisms that are intimately tied to vegetation follow the first pattern, consistent with the idea that aboveground patterns of vegetation can drive patterns of belowground biodiversity. The second pattern may be due to an initial increase and subsequent decline in available nutrients and habitat suitability caused by increased biotic interactions, including resource competition among soil biota. A consensus view of the patterns of historical and contemporary soil ecosystem responses to deglaciation provides a better understanding of the processes that generate these patterns and informs predictions of ongoing and future responses to environmental changes.

KEYWORDS
climate change, community assembly, deglaciation chronosequence, ecological succession, glacial forefields, soil ecosystems

1 | INTRODUCTION

Ecological succession is an important continuous process by which the structure of an ecological community evolves over time (Drake, 1990; Glenn-Lewin et al., 1993; Hobbs et al., 2007; Måren et al., 2018; Pickett et al., 2009; Pickett & Cadenasso, 2005). Receding glaciers across the world is one of the hallmark effects of increasing temperatures (Hågvar, 2012). Glaciers across most of the cryosphere have receded at an unprecedented pace, particularly during the last century (IPCC, 2007; Oerlemans, 2005; Paul et al., 2004; Pepin et al., 2015). Retreating glaciers expose new terrestrial habitats, which become colonized by organisms dispersed through wind, rain, glacial meltwater, and in situ microorganisms (Bauer et al., 2002; Blaalid et al., 2012). The newly unveiled rocks

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and gravel are subjected to weathering and soil formation processes. Initially, young soils are colonized by microbes that can thrive under low-nutrient conditions. These microbes initiate biogeochemical cycling, accelerate weathering and release of nutrients, and facilitate subsequent colonization by complex organisms (Jones, 1998; Lazzaro et al., 2010; Tscherko et al., 2003). Glacier forefields serve as unique natural experiments for studying the order and timing of biotic colonization and how this influences the structure of successive soil communities (Matthews, 2008).

Globally, several studies have been conducted on the successional patterns of different biotic communities onto the newly exposed land surfaces and changes in their soil properties after deglaciation along the chronosequence (microbes: Fernández-Martínez et al., 2017; Kazemi et al., 2016; Kim et al., 2017; Schütte et al., 2010; Zumsteg et al., 2012; animals: van Leeuwen et al., 2018; Vater, 2012; Vater & Matthews, 2015; plants: Garibotti et al., 2011; Wietrzyk et al., 2018). Most of these studies dealt with the succession of these organisms onto glacier forefields that had been exposed for different periods of time (chronosequence). This inference is necessary because it is difficult to address ecological succession over decades to centuries by direct experimentation or observation (Foster & Tilman, 2000; Kaufmann & Raffl, 2019; Matthews, 1992). Although much research has been conducted on the succession of different organisms in glacial forefields across the world, several critical knowledge gaps remain. For example, most studies of this kind are restricted to one or few taxa—there is yet-to-be-completed a single study that comprehensively explores patterns of succession for all biota along a deglaciation chronosequence. Furthermore, most glacier forefield studies have been limited to local scales. Expanding the geographic range of these studies would enable us to better identify and predict universal patterns of succession at a global scale.

Meta-analysis is a statistical approach developed to produce summary effects by combining and analyzing results from all of the published literature (Arnqvist & Wooster, 1995). To better understand how soil ecosystems are responding to rapid, contemporary deglaciation, we conducted a global meta-analysis focused on identifying common patterns of community succession and soil properties in response to glacial recession. Accordingly, the relative abundance and richness of all measured biota and soil properties were considered as effect sizes. In total, we compared 186 effect sizes across different deglaciated soil chronosequences. We hypothesized that the richness and abundance of all soil biota would increase as a function of successional age.

2 | MATERIALS AND METHODS

2.1 | Data collection

Publications on glacier forefields were located through a systematic search of the Web of Science core database on July 22, 2020, using a search string (Supplementary information 2), which resulted in 1059 records. Inclusion and exclusion criteria were set up for the publications to be included in the meta-analysis. Our inclusion criteria encompassed: studies conducted in glacier forefields; studies reporting taxon richness or taxon abundance or soil property; studies reporting data across various study sites/zones along successional age; and samples collected and analyzed directly from glacier forefields without further manipulation. Criteria for excluding a publication from the analysis were: studies conducted with soil samples incubated at different temperatures; studies conducted in mesocosms or greenhouses; studies conducted in lakes or streams or marine environments, and studies with no successional age. The titles and abstracts of 1054 records were screened and 252 relevant publications that contained richness and/or abundance of biota or soil properties in glacier forefields were selected. Among the 252 publications, 95 publications (Supplementary information 1) were selected based on the inclusion criteria, and data were extracted. The Google Scholar database was also searched using the above search terms and the first 300 articles were examined, which did not yield any additional publications. The literature cited sections of the 95 publications were screened carefully to identify potentially missing studies. Information from each publication such as authors, title, year of publication, name of the glacier, location of the study, latitude, longitude, richness or abundance of biota or soil properties, site or zone, sample size, and succession age, etc. was extracted and pooled into a single datasheet. The richness of each group of biota was estimated by totaling the number of genera/families. The abundance of each group of biota was estimated by totaling the abundance of genera/families. In meta-analysis, multiple sites at different successional ages from one publication were considered as separate studies. For instance, Fernández-Martínez et al. (2017) examined the primary succession of soil microbes in 11 sites corresponding to different successional ages at two glacier forefields on the Cordillera Darwin (Tierra del Fuego, Chile), resulting in 11 studies from that publication. Based on this, 1561 studies were derived from 95 publications. Among the 1561 studies, 221 studies were conducted on bacteria and fungi, 60 studies were conducted on nematodes, 193 studies were conducted on arachnids, 273 studies were conducted on insects, 91 studies were conducted on other arthropods, 292 studies were conducted on plants, 41 studies were conducted on lichens and 390 studies reported soil properties (Figure 1). For data reported in figures, mean values were extracted using WebPlotDigitizer (Rogatgi, 2020).

2.2 | Effect size and moderator variables

In general, effect size usually denotes the association between two variables in the meta-analysis, however, the effect size can also be regarded as the estimate of a single group or value. Therefore, in our meta-analyses, richness or abundance of biota or soil properties of each study were considered as effect sizes (Borenstein et al., 2009; Pothula et al., 2019). The weighted mean of richness or abundance or soil properties of all studies in each successional age were considered as summary effect sizes. A total of 186 summary effect sizes including 86 from the richness, 86 from the abundance of all groups

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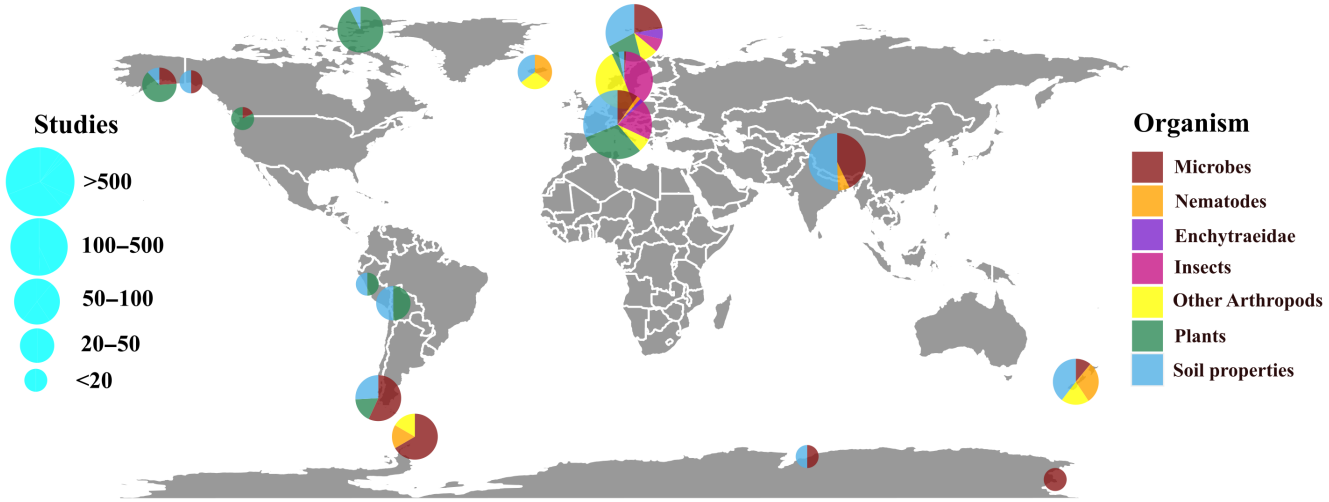

FIGURE 1 Geographic distribution of studies included in our analysis. Pie chart proportion represents the number of studies for each taxonomic group (by color). Circle size indicates the number of studies conducted in that location. The map indicates the number of studies conducted on microbes (221), nematodes (60), Enchytraeidae (20), insects (273), other arthropods (264), plants (333), and soil properties (390) by location. Map lines delineate study areas and do not necessarily depict accepted national boundaries. [Colour figure can be viewed at wileyonlinelibrary.com]

of biota and 14 from soil properties were tested in our analyses. The summary effect sizes of abundance and richness of several groups of biota and soil properties were compared across successive soil ages since glacial recession. Successional ages were categorized into six groups, 0–10, 11–30, 31–50, 51–100, 101–500, and 501–1000 years. These six groups of successional ages were considered as moderator levels. The successional age was selected as a moderator variable to determine how the richness and abundance of biota and soil properties change over time.

2.3 | Meta-analysis

Summary effect sizes of biota at each successional age were estimated using Comprehensive Meta-Analysis software (Version 3, Biostat; 2014) and 95% confidence intervals (CIs), p_{hetero} values, Q statistics, and I^2 values were generated. In our meta-analysis, a random-effects model, which includes both within-study variance and between-studies variance was used rather than fixed-effects models. Most of the studies did not furnish information such as standard errors or standard deviations required to calculate variance. Therefore, studies were weighted based only on sample size, that is, non-parametric variance (Supplementary information 2). Heterogeneity, sensitivity analysis, and publication bias were performed (Supplementary information 2).

2.4 | Mantel test

Correlations among biotic communities and between biotic communities (Bray–Curtis dissimilarity matrices) and soil properties (Euclidean-based distance matrices) were evaluated using Mantel tests based on Spearman's rank correlations (Mantel, 1967; Smouse et al., 1986). The significance of the results was evaluated through permutational analyses ($n = 9999$).

3 | RESULTS

3.1 | Meta-analysis

In our meta-analyses, we tested 186 summary effect sizes. Among the 186, 71 summary effect sizes were significantly different ($p_{hetero} < .05$), and 115 summary effect sizes were not significantly different. I^2 values were positive for all the summary effect sizes (Supplementary information 1). The results from the sensitivity analysis indicated that not a single study altered the summary effect sizes significantly (Supplementary information 1). Evidence for publication bias was not detected (Supplementary information 1).

3.2 | Soil properties

Total carbon (TC) and total organic carbon (TOC) gradually increased in soils that were exposed for 100 years since glacial recession but abruptly increased after 100 years ($p_{hetero} < .05$). Microbial carbon (MC) steadily increased along the chronosequence ($p_{hetero} < .05$). Total nitrogen (TN) increased with the increase in age of the soil after glacial retreat ($p_{hetero} < .05$). Ammonium and nitrate gradually increased in soils of 0–500 years since deglaciation but started to decline after 500 years ($p_{hetero} < .05$). Available phosphorus (AP) increased over successional time ($p_{hetero} < .05$). Total potassium (TK) steadily decreased in the soils that were exposed for 50 years since

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glacial retreat and increased after 50 years (p_{hetero} < .05). The moisture content decreased in soils of 0–50 years after the glacial recession and increased after 50 years (p_{hetero} < .05). Conductivity was highest in soils that had been deglaciated for 50 years followed by a significant decline (p_{hetero} < .05). Soil pH gradually declined along the chronosequence (p_{hetero} < .05) (Figure 2).

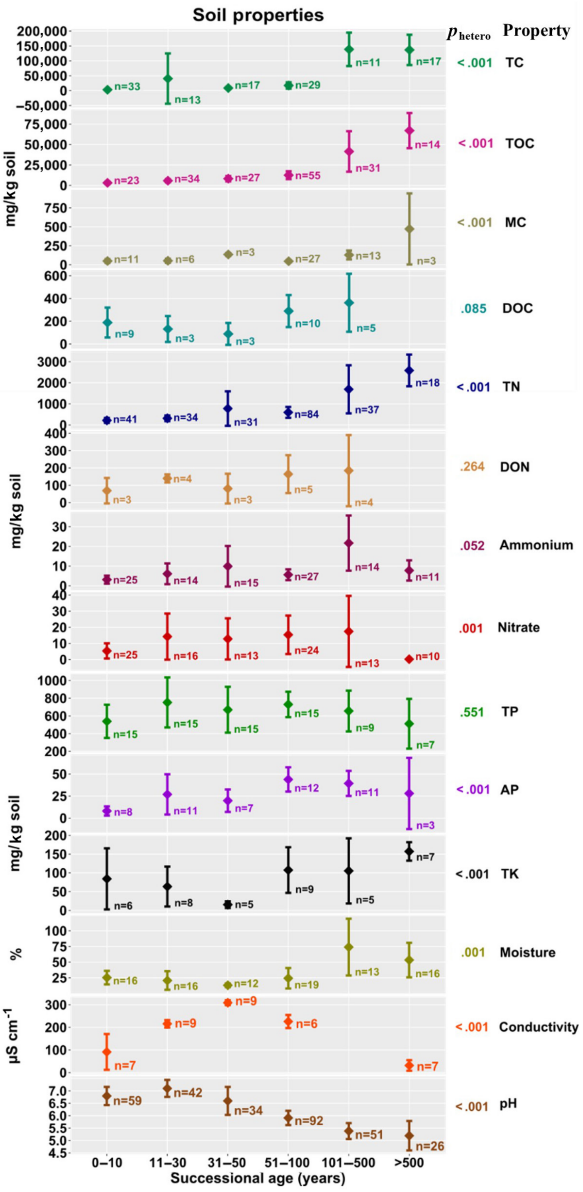

FIGURE 2 Successional patterns of soil properties along the chronosequence. Each panel represents different soil property. Mean values indicate summary effect sizes, error bars indicate standard errors, and *n* is the number of studies within each successional age. p_{hetero} < .05 indicates significant differences among successional age groups within each soil property. AP, available phosphorus; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; MC, microbial carbon; TK, total potassium; TN, total nitrogen; TOC, total carbon; TOC, total organic carbon; TP, total phosphorus [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Plant and lichen succession

The percentage of vegetation cover increased with the successional age of the soil (p_{hetero} < .05). The cover percentage of vascular plants, non-vascular plants, and lichens increased with time since deglaciation (p_{hetero} < .05) (Figure 3). The richness of vascular plants, non-vascular plants, and lichens increased along the chronosequence (p_{hetero} < .05) (Figure 3). The abundance of Magnoliopsida, Pinopsida, and Bryopsida increased with increasing soil age (p_{hetero} < .05) (Figure S1). Even though there were no statistically significant differences across the successional ages of the richness of Magnoliopsida, Pinopsida, and Bryopsida, patterns were apparent. The richness of all plant classes increased with the successional age of the soil (Figure S1).

3.4 | Microbial succession

The abundance and richness of communities along the chronosequence are expressed in relative abundance and number of operational taxonomic units (OTUs), respectively. Predominant taxa that embody >1% of bacterial community composition in at least one of the successional ages are reported. Among these taxa, Proteobacteria followed by Actinobacteria, Alphaproteobacteria and Acidobacteria were more abundant compared to other taxa throughout the chronosequence. The relative abundance of Acidobacteria, Chloroflexi, and Planctomycetes was significantly increased in soils of 0–50 years since deglaciation and gradually decreased after 50 years (p_{hetero} < .05). The relative abundance of Actinobacteria steadily declined in soils that were exposed for up to 50 years since glacial recession, gradually increased up to 500 years, and rapidly increased after 500 years (p_{hetero} < .05). The relative abundance of Bacteroidetes, Proteobacteria, and Betaproteobacteria significantly declined over successional time (p_{hetero} < .05). The relative abundance of Cyanobacteria was significantly reduced in soils that were exposed for 50 years after deglaciation after which they became stable (p_{hetero} < .05) (Figure 4). For bacterial communities, overall OTU richness increased along the chronosequence except at 31–50 years (p_{hetero} < .05). The richness of Acidobacteria significantly increased in soils in the first 50 years after deglaciation but decreased thereafter (p_{hetero} < .05). Betaproteobacteria richness abruptly declined in soils over the first 50 years of deglaciation following by a gradual increase (p_{hetero} < .05) (Figure 4).

Major taxa that represent >1% of fungal community composition in at least one of the successional ages were reported. Analysis of fungal communities revealed that Ascomycota and Basidiomycota are predominant throughout the chronosequence. The relative abundance and richness of most of the fungal taxa were not significantly heterogeneous among successional ages. Even though there were no statistically significant differences across the successional ages, trends were evident in a few of the fungal taxa. The relative abundance of Ascomycota and Basidiomycota increased in soils of 0–50 years after deglaciation and started to decline after 50 years. The relative abundance of Zygomycota increased over successional time (Figure 5). Fungal OTU richness increased in soils of 0–100 years since

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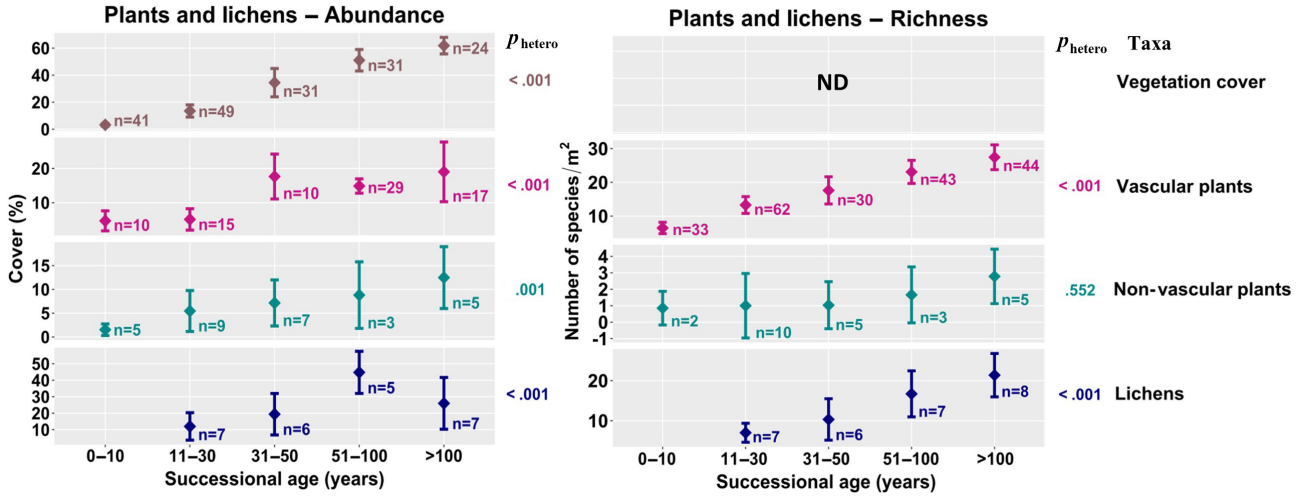

FIGURE 3 Successional patterns of cover percentage and richness of plants and lichens along the chronosequence. Each panel represents different taxa. Mean values indicate summary effect sizes, error bars indicate standard errors, and *n* is the number of studies within each successional age. $p_{hetero} < .05$ indicates significant differences among successional age groups within each taxon. ND, no data [Colour figure can be viewed at wileyonlinelibrary.com]

deglaciation and decreased after 100 years ($p_{hetero} < .05$). Zygomycota richness significantly increased with increasing soil age ($p_{hetero} < .05$). Ascomycota richness increased in soils that were exposed for 50 years after the glacial recession and then declined (Figure 5).

3.5 | Nematode succession

Among nematode trophic groups, the relative abundance of omnivores steadily increased along the deglaciation chronosequence ($p_{hetero} < .05$). Although the differences among the relative abundances of other nematode trophic groups were not statistically significant across the successional ages, patterns were observed. The relative abundance of plant feeders increased with the increasing age of the soil. The relative abundance of bacterial feeders and predators increased in soils that had been deglaciated for 50 years and gradually leveled off after 100 years. The relative abundance of fungal feeders decreased in the first 50 years after the glacial recession and increased after 50 years (Figure 6). The richness of bacterial feeders gradually increased with increasing soil age ($p_{hetero} < .05$). The richness of omnivores increased in soils that were exposed for 100 years since deglaciation but declined after 100 years, whereas the richness of plant feeders increased in soils that had been deglaciated for 500 years and decreased after 500 years ($p_{hetero} < .05$) (Figure 6).

3.6 | Arthropods and Enchytraeidae succession

The abundance of Collembola, mites, and Enchytraeidae significantly increased with time since glacial recession ($p_{hetero} < .05$) (Figure 7). The richness of collembola and mites also significantly increased over successional time ($p_{hetero} < .05$) (Figure 7). The succession of different families of Coleoptera shows that the abundance of Hypogastruridae increased in soils of 0–100 years, then declined ($p_{hetero} < .05$). The abundance of Isotomidae and Sminthuridae increased with the increase in the successional age of the soil ($p_{hetero} < .05$) (Figure S2). The richness of all subgroups of Collembola was not significantly heterogeneous among the successional ages except the richness of Isotomidae, which gradually increased with the increase in age of the soil since glacial recession ($p_{hetero} < .05$) (Figure S2). Among other arthropods, the abundance of Hymenoptera significantly increased with the increase in age of the soil since deglaciation ($p_{hetero} < .05$). The abundance of spiders increased rapidly in soils that were exposed for 50 years after the glacial retreat and decreased after 50 years ($p_{hetero} < .05$). Although the abundance of other arthropods was not significantly heterogeneous across the successional ages, trends were noticed. The abundance of Coleoptera increased in soils that had been deglaciated for 50 years but started to decline after 50 years (Figure 8). The richness of Coleoptera, Hymenoptera, and spiders increased along the chronosequence ($p_{hetero} < .05$), whereas the abundance and richness of Diptera followed a zigzag pattern over successional time ($p_{hetero} < .05$) (Figure 8). The succession of different families of Coleoptera, Diptera, and spiders along the deglaciation chronosequence was also analyzed. The families of Coleoptera were not significantly different across the successional ages and no significant trends were found except for the richness of Carabidae and Staphylinidae, which were significantly increased with increasing soil age ($p_{hetero} < .05$) (Figure S3). Among the families of Diptera, the abundance of Anthomyiidae gradually declined with the increase in age of the soil since deglaciation ($p_{hetero} < .05$) (Figure S4). The richness of Empididae and Muscidae increased with the successional age of the soil however, the abundance of Heleomyzidae increased in soils that were exposed for 100 years after glacial retreat but started to decline after 100 years ($p_{hetero} < .05$) (Figure S4). Within spiders, the abundance of Linyphiidae and Lycosidae increased in soils of 0–50 years after the glacial recession and decreased after 50 years ($p_{hetero} < .05$) and the abundance of Phalangiidae increased

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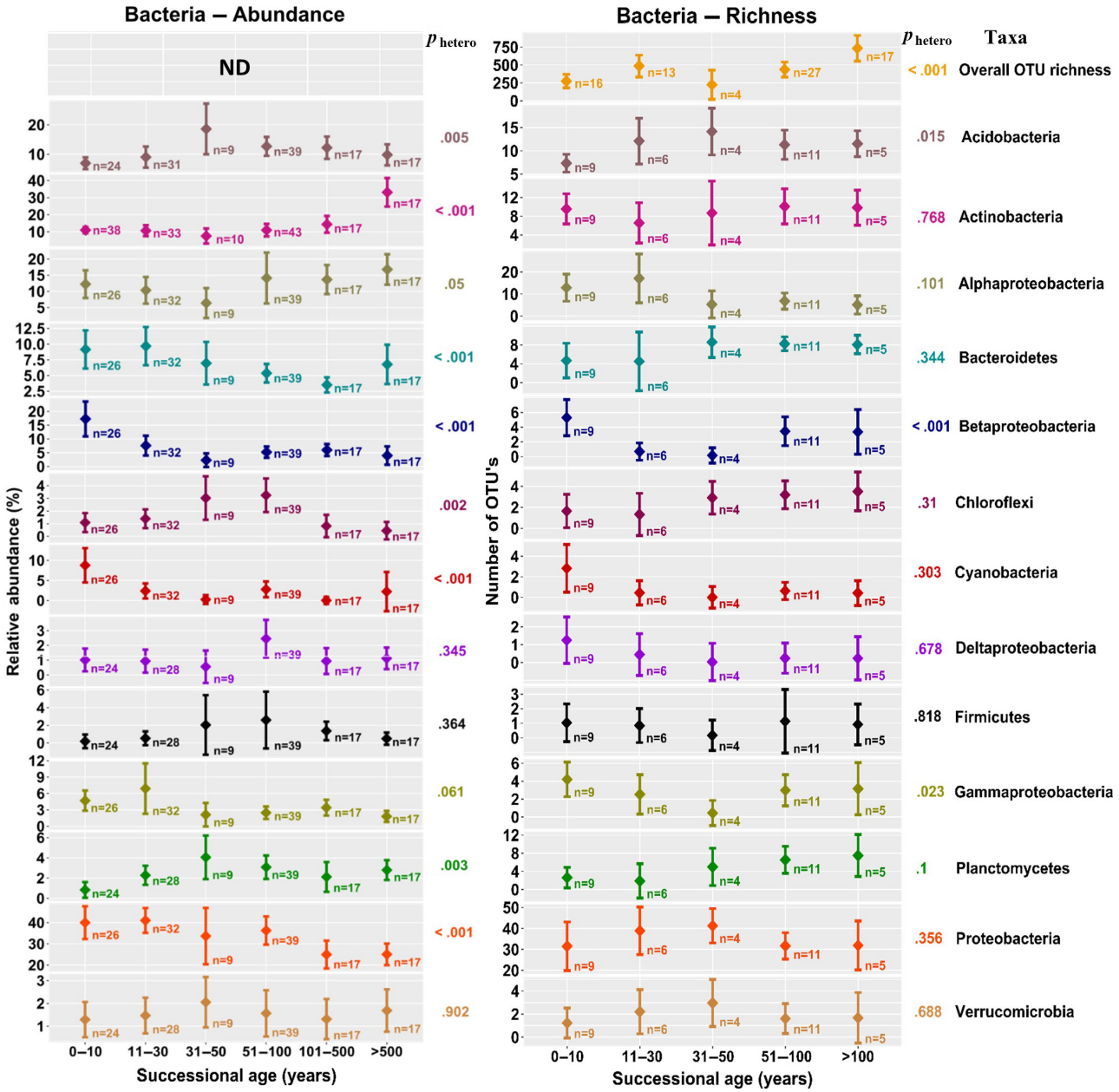

FIGURE 4 Successional patterns of abundance and richness of bacteria along the chronosequence. Each panel represents different bacterial taxa. Mean values indicate summary effect sizes, error bars indicate standard errors, and *n* is the number of studies within each successional age. $p_{hetero} < .05$ indicates significant differences among successional age groups within each taxon. ND, no data [Colour figure can be viewed at wileyonlinelibrary.com]

over successional time ($p_{hetero} < .05$) (Figure S5). The richness of Gnaphosidae, Linyphiidae, and Lycosidae increased along the chronosequence ($p_{hetero} < .05$) (Figure S5). The key trends of all the statistically significant taxonomic groups at a higher level of organization are summarized in Figure 9 (created with BioRender.com).

3.7 | Mantel test

Relationships among biotic communities and relationships between abundance and richness of communities and soil properties over successional time were tested using Mantel tests based on Spearman's rank correlations. Results were reported in supplementary information 1. Statistically significant results are presented in supplementary information 2.

4 | DISCUSSION

4.1 | Soil properties

Soil properties of glacier forefields correspond in predictable ways with increasing age (Liu et al., 2012). The increase in TC and TOC is likely due to increased organic matter inputs from the

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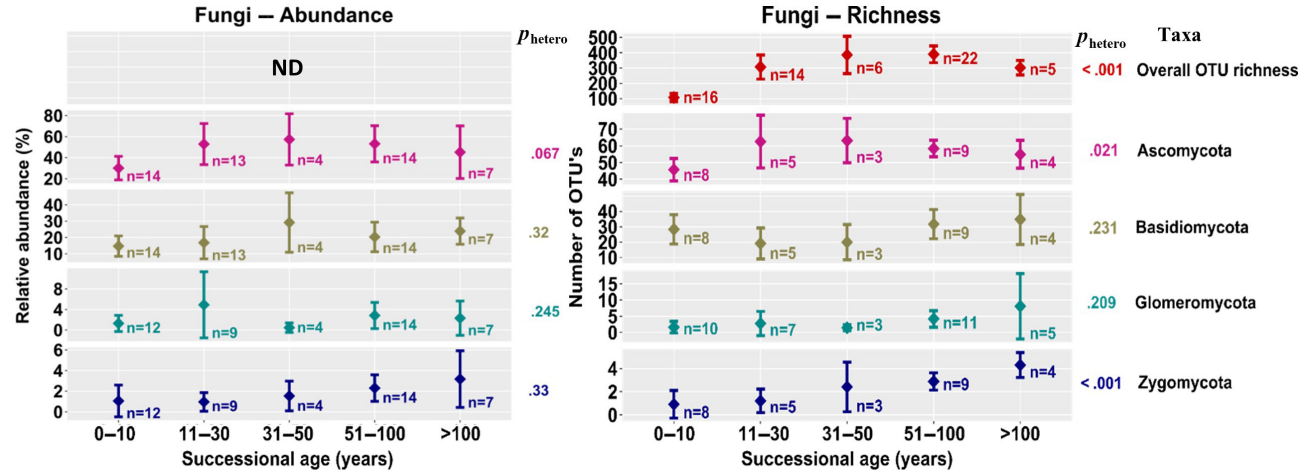

FIGURE 5 Successional patterns of abundance and richness of fungi along the chronosequence. Each panel represents different fungal taxa. Mean values indicate summary effect sizes, error bars indicate standard errors, and *n* is the number of studies within each successional age. $p_{hetero} < .05$ indicates significant differences among successional age groups within each taxon. ND, no data [Colour figure can be viewed at wileyonlinelibrary.com]

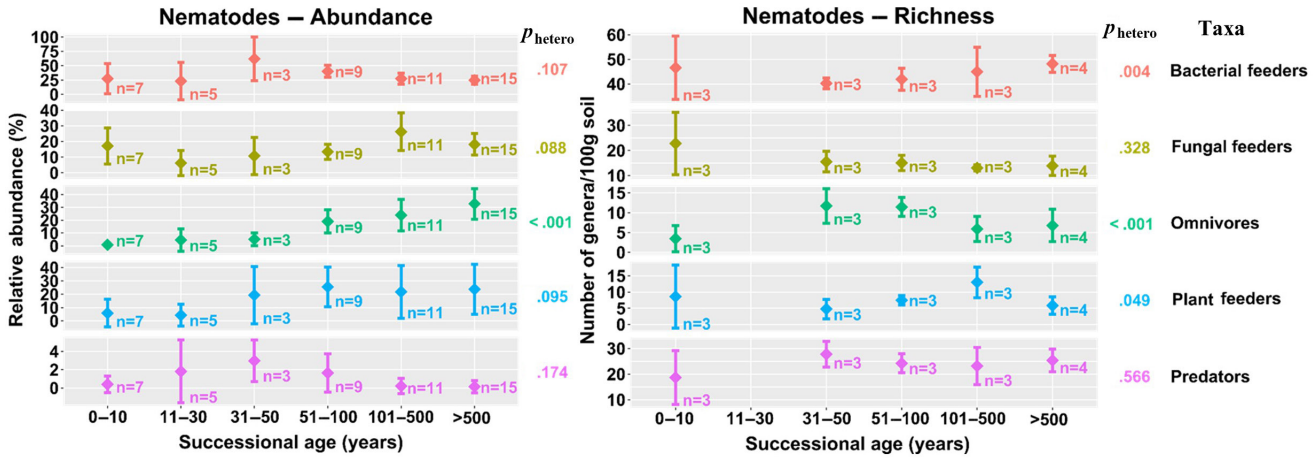

FIGURE 6 Successional patterns of abundance and richness of nematodes along the chronosequence. Each panel represents different trophic groups. Mean values indicate summary effect sizes, error bars indicate standard errors, and *n* is the number of studies within each successional age. $p_{hetero} < .05$ indicates significant differences among successional age groups within each taxon. No studies on nematode richness were conducted during the 11–30 time period. [Colour figure can be viewed at wileyonlinelibrary.com]

corresponding increase in plants and other soil biota over successional time (Bradley et al., 2014; Brown & Jumpponen, 2014; Duc et al., 2009; Hahn & Quideau, 2013; Kazemi et al., 2016; Miniaci et al., 2007; Tscherko et al., 2003). Our Mantel test results also supported the correlation between TOC and the richness of plant communities. The steady increase in MC along the chronosequence is probably due to the concomitant increase in microbial abundance (Brankatschk et al., 2011). Initial carbon levels in the newly deglaciated soils are likely the legacy of ancient carbon locked under the glacier (Bardgett et al., 2007), streams from glaciers, detritus transported by wind, microbial autotrophs, and animal droppings (Bradley et al., 2014; Schulz et al., 2013; Zumsteg et al., 2012). The availability of nitrogen during the initial stage of succession is mostly due to contemporary biological nitrogen fixation (Bokhorst et al., 2017). The increase in TN with the increase in soil age could be due to increased organic nitrogen turnover and increased vegetation (Göransson et al., 2016; Tscherko et al., 2003). In young and intermediate-aged soils, the nitrogen-fixing microbes and the carbon input from plants increase nitrogen fixation. However, increased vegetation densely covers soils in the late-successional stage, triggering nitrification and denitrification processes, which result in reduced levels of ammonium and nitrate in older soils (Brankatschk et al., 2011; Zeng et al., 2016). AP increased along the chronosequence, likely due to increased microbial activity and weathering processes (Bokhorst et al., 2017; Mapelli et al., 2018; Walker et al., 1981). The high concentration of TK in newly deglaciated soils may result from chemico-physical and microbial weathering processes (Mapelli et al., 2018). The decline of TK in

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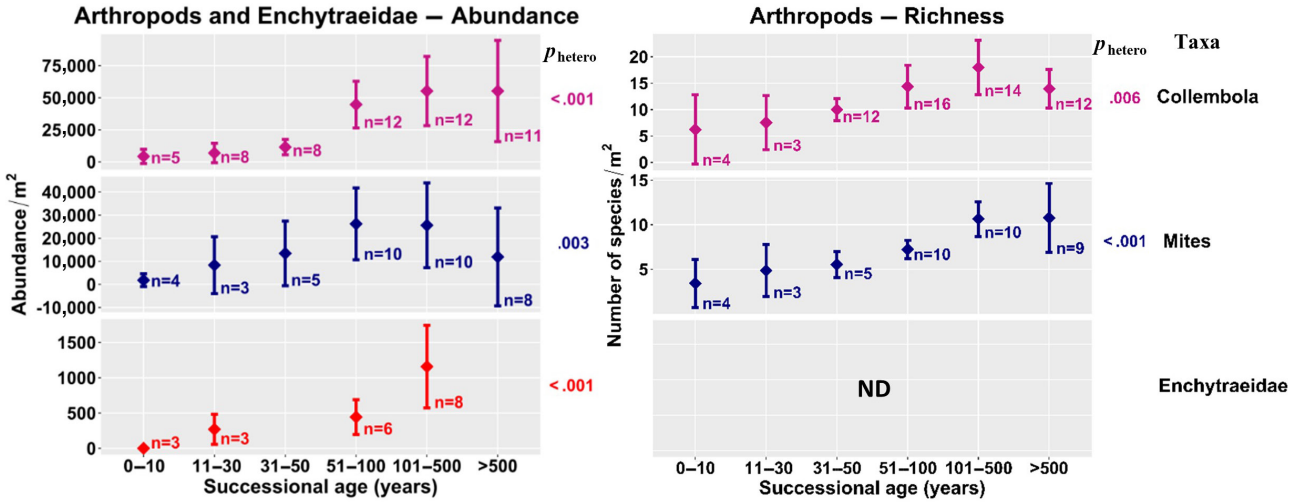

FIGURE 7 Successional patterns of abundance and richness of collembola, mites, and Enchytraeidae along the chronosequence. Each panel represents a different organism. Mean values indicate summary effect sizes, error bars indicate standard errors, and *n* is the number of studies within each successional age. $p_{hetero} < .05$ indicates significant differences among successional age groups within each taxon. ND, no data [Colour figure can be viewed at wileyonlinelibrary.com]

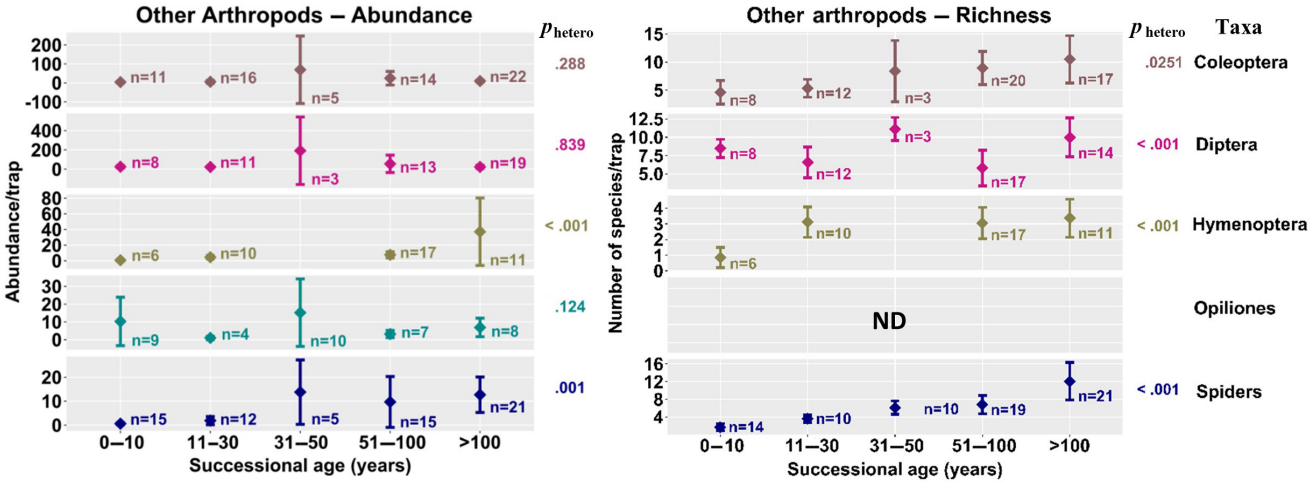

FIGURE 8 Successional patterns of abundance and richness of insects, Opiliones, and spiders along the chronosequence. Each panel represents different taxa. Mean values indicate summary effect sizes, error bars indicate standard errors, and *n* is the number of studies within each successional age. $p_{hetero} < .05$ indicates significant differences among successional age groups within each taxon. ND, no data [Colour figure can be viewed at wileyonlinelibrary.com]

intermediate soils may be associated with the increase in uptake of TK by increased vegetation. In older soils, TK is added back to soils through the leaching of foliage by rainfall and increased incorporation of organic matter into the soil. The increase in soil moisture content in the older soils is probably due to increased plant abundance and richness, which increases the water-holding capacity of the soil through pronounced root penetration (Brankatschk et al., 2011). Moisture and conductivity are inversely correlated as the increase in water content reduces salt concentrations in the soil (Bajerski & Wagner, 2013). Soil pH gradually declined over successional time, likely due to litter input, the release of organic acids from organic matter degradation, and the release of root exudates into the soil (Bernasconi et al., 2011; Knelman et al., 2012).

4.2 | Plant and lichen succession

Plants and soil organisms are physically connected through the soil and mutually benefit each other (Wardle et al., 2004). Plant succession in glacier forefields enhances resources, which will be used by soil organisms through root exfoliates, exudates, and litter input into the soil (Brown & Jumpponen, 2014; Duc et al., 2009; Hahn & Quideau, 2013; Kazemi et al., 2016; Miniaci et al., 2007; Tscherko et al., 2003). In turn, soil organisms convert the immobilized nutrients in plant organic matter into mobile forms, which can be assimilated by plants (Bonkowski, 2004; Clarholm, 1985). Below-ground communities are tightly linked to plant communities through symbiosis, herbivory, and

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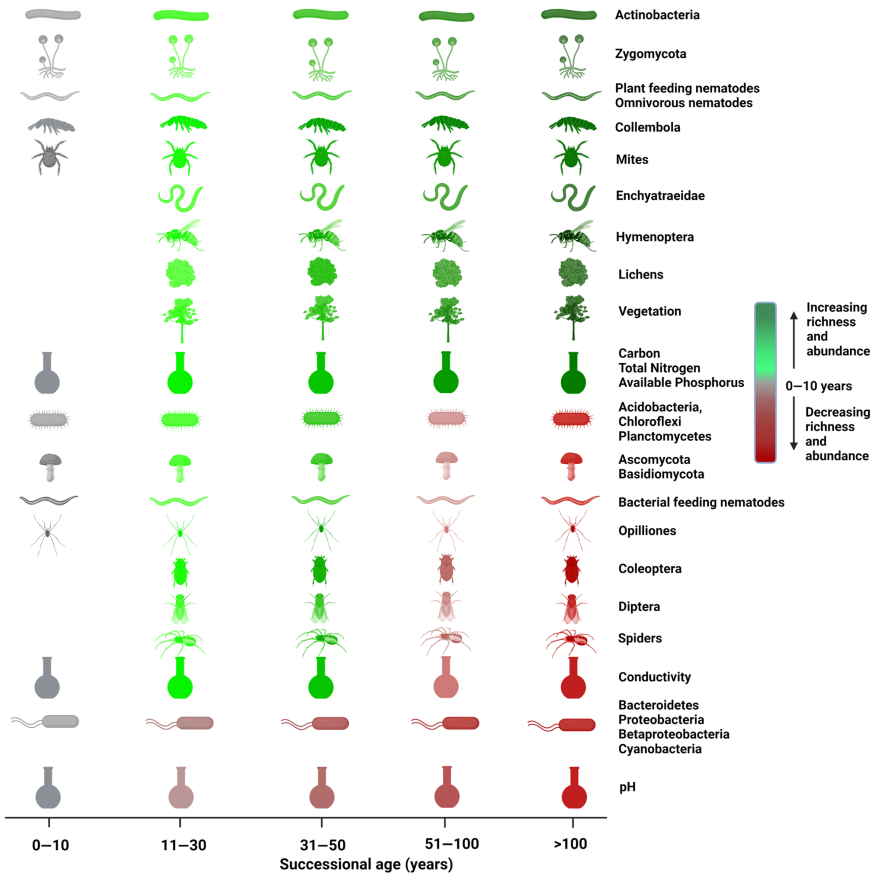

FIGURE 9 Patterns of glacial forefield community succession. Grey indicates community diversity and abundance at 0–10 years successional age. Increase in the intensity of green (becoming darker green) indicates increased organismal abundance and richness. Increase in the intensity of red (becoming darker red) indicates decreased organismal abundance and richness. Only statistically significant trends are depicted, thus not all analyzed taxa appear in the figure. [Colour figure can be viewed at wileyonlinelibrary.com]

decomposition of dead plant material (Sylvain & Wall, 2011). Several studies report that vegetation composition and the relative dominance of different plant species strongly structure below-ground communities (De Deyn et al., 2004; Hodkinson et al., 2003; Kaufmann, 2001; Stephan et al., 2000). The cover percentage and richness of total vegetation, vascular plants, and non-vascular plants increases along the chronosequence, a pattern reported by several plant primary succession studies (Jones & Del Moral, 2005; Jones & Henry, 2003). The increase in cover percentage and richness of plants may be due to an increase in the availability of resources that accumulate with soil age. Similarly, analysis of plant classes revealed that the abundance and richness of Magnoliopsida, Pinopsida, and Bryopsida increase over successional time. Lichens initiate succession on rock surfaces by weathering the rocks and releasing inorganic nutrients that can be eventually used by plants (Adamo & Violante, 2000; Garibotti et al., 2011). The increase in lichens may be due to the gradual increase in the growth of crustose lichens on plant debris and decaying terricolous mosses, which increases along the chronosequence (Bilovitz, Nascimbene, et al., 2014; Bilovitz, Nascimbene, & Mayrhofer, 2015; Bilovitz, Wallner, et al., 2014, 2015). The association of plants and lichens is supported by the significant positive correlation between lichen cover percentage and the abundance of vascular plants (Mantel tests; Supplemental Information 1).

4.3 | Microbial succession

Microbial communities are important drivers of terrestrial ecosystem processes (Bradley et al., 2016). Microbes contribute to mineral weathering and decomposition of organic matter, which accelerates soil formation and facilitates the establishment of more complex soil organisms and plant communities (Bradley et al., 2016; Devetter et al., 2021; Jiang et al., 2018). The observed increase in bacterial overall OTU richness over time in glacial forefields could be due to increased plant richness and availability of organic matter (Hu et al., 2021; Liu et al., 2012; Nemergut et al., 2007; Schmidt et al., 2008; Sigler & Zeyer, 2002). The drop in overall OTU richness at 31–50 years age might be an effect of the lower number of studies for this time period ($n = 4$). Acidobacteria grow well under oligotrophic conditions and are generally considered acidophilic organisms (Dion, 2008). The abundance and richness of Acidobacteria increased as soil pH decreased over the first 50 years. This negative correlation has been reported in many studies (Jones et al., 2009; Kim et al., 2017; Kwon et al., 2015; Lauber et al., 2009; Rousk et al., 2010). However, the declining trend in abundance and richness of Acidobacteria after 50 years likely reflects the abundant availability of nutrients, which favor copiotrophs compared to oligotrophic taxa (Knelman et al., 2012). The high abundance of Actinobacteria in newly deglaciated soils that are characterized by poor nutrient availability may be due to their ability to form hyphae, which can access

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water and nutrients from more distant soil pore spaces (Dion, 2008; Schütte et al., 2010). Actinobacteria are abundant in soils that are close to the glaciers, becoming less abundant as soils became older and more acidic. This trend has been observed in several studies (Fernández-Martínez et al., 2017; Kwon et al., 2015; Rime et al., 2015; Zumsteg et al., 2012). Nevertheless, in our analysis, the relative abundance of Actinobacteria started gradually increasing after 50 years. Actinobacteria are capable of decomposing organic matter and metabolizing a wide range of substrates (Bajerski & Wagner, 2013; Fernández-Martínez et al., 2017; Větrovský et al., 2014). The successful establishment of Actinobacteria in older soils (>50 years) is likely due to the increase in the availability of organic matter as the soil matures. Proteobacteria are consistently predominant among bacteria throughout successional stages, probably because they represent such high functional diversity (phototrophs, photoheterotrophs, and chemolithotrophs; Fernández-Martínez et al., 2017; Kersters et al., 2006). The relative abundance of Proteobacteria decline with the successional age of the soil, a pattern consistent with several studies (e.g. Wu et al., 2012; Zumsteg et al., 2012). Cyanobacteria are photoautotrophic and play crucial functional roles under oligotrophic conditions by fixing carbon and nitrogen, allowing for the colonization of bare rocks and soils (Fermani et al., 2007; Schmidt et al., 2008; Schulz et al., 2013). Photosynthetic Cyanobacteria ramp up the nutrient status of soil, further facilitating colonization by heterotrophic organisms (Fernández-Martínez et al., 2017; Freeman et al., 2009; Frey et al., 2013; Kaštovská et al., 2005; Kwon et al., 2015; Rime et al., 2015; Schmidt et al., 2008; Tscherko et al., 2003; Wojcik et al., 2021; Zumsteg et al., 2012). The relative abundance and richness of Cyanobacteria are initially high in young soils and decline in older soils because the colonization of plants increases the availability of carbon for heterotrophs, which reduces the abundance and richness of autotrophic Cyanobacteria along the chronosequence (Knelman et al., 2012). This declining trend has been reported previously (Fernández-Martínez et al., 2017; Kwon et al., 2015; Zumsteg et al., 2012). Similar to Proteobacteria, the relative abundance of Bacteroidetes declined significantly over successional time. Initially, Bacteroidetes are highly abundant in soils adjacent to glaciers as the meltwater provides suitable habitat (Wu et al., 2012). Moreover, a positive correlation exists between the relative abundance of Bacteroidetes and soil pH (Lauber et al., 2009; Liu et al., 2012; Philippot et al., 2009, 2011). As with Proteobacteria and Bacteroidetes, the relative abundance of Betaproteobacteria is significantly reduced as soil age increases. Its high abundance and richness in young soils may be due to highly versatile Betaproteobacteria physiology (Kim et al., 2017). The observed declining trend over successional time is positively correlated with soil pH (Liu et al., 2012; Philippot et al., 2011). On the other hand, the rise in Betaproteobacteria richness in older soils is probably due to the increase in copiotroph richness, which is well supported by the already available nutrients (Fierer et al., 2007).

Shifts in fungal communities are strongly associated with plant colonization (Brown & Jumpponen, 2014; Jumpponen, 2003; Zumsteg et al., 2012). Diverse plant communities support diverse fungal taxa (McGuire et al., 2012; Tian et al., 2017). Several studies report that fungal richness increases with soil age (Hodkinson et al., 2004; Jones & Henry, 2003). However, in our analysis, the decline in overall fungal richness in older soils may also be due to strong biotic interactions, such as competition (Blaalid et al., 2012; Tian et al., 2017). Among fungal communities, Ascomycota is the predominant taxon throughout the successional age. The relative abundance and richness of most fungal taxa are not significantly heterogeneous among successional ages due to the low number of studies. Even though there were no statistically significant differences across the successional ages, we found evident patterns in Ascomycota, Basidiomycota, and Zygomycota. The relative abundance of Ascomycota and Basidiomycota and richness of Ascomycota increased in soils from 0 to 50 years after deglaciation, probably due to accumulation of resources and decrease in soil pH along with the soil development, which increases habitat suitability for a wide range of fungal species (Fujiyoshi et al., 2011; He & Tang, 2008; Kabala & Zapart, 2012). However, the declining trend of relative abundance of Ascomycota and Basidiomycota and richness of Ascomycota after 50 years may be due to increased competition among soil biota, resulting from increased availability of organic matter and nutrients (Dong et al., 2016). On the other hand, Zygomycetes were the least abundant fungal taxon of deglaciated soils and generally live on decomposing plant material (Raven et al., 2005). The dependence of Zygomycota on plant communities is supported by a significant positive correlation between the relative abundance of Zygomycota and the abundance of plant communities along the chronosequence.

4.4 | Nematode succession

Soil formation and vegetation succession are the major factors that influence soil invertebrate succession (Gobbi et al., 2006, 2011; Kaufmann, 2001; Kaufmann & Raffl, 2019). Among nematode trophic groups, the relative abundance of omnivores significantly increases over successional time, probably because higher organic matter and nutrients during the mature stage lead to increases in nematode abundance and richness (Lei et al., 2015; Pothula et al., 2022). Although the relative abundance of other nematode trophic groups does not significantly differ across successional ages, the relative abundance of plant feeders does increase with the abundance of plant communities as a function of successional age (Bokhorst et al., 2017; Lei et al., 2015). The association of plant feeders with plant communities is supported by the significant positive correlation from the Mantel test. The increase in the relative abundance of bacterial feeders and predators in soils that had been deglaciated for 50 years may be due to the high availability of organic matter content and resources in mid-aged soils (Doblas-Miranda et al., 2008), gradually decreasing after 50 years, probably due to increased competition among invertebrates (Vater, 2012; but not that nematode richness data are not available for the successional age of 11–30 years). Additionally, the low number of studies produces a high standard error, especially for the 0–10 year time period. Thus,

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we do not detect clear patterns until after 30 years. The richness of bacterial feeders gradually increased from 31 years with increasing soil age, probably due to the high availability of organic matter content and resources (Doblas-Miranda et al., 2008). The richness of plant feeders and omnivores increased in soils that were exposed for 500 and 100 years respectively since deglaciation, probably due to increases in vegetation and available nutrients, but these declined during subsequent stages of ecological succession.

4.5 | Arthropod and enchytraeid succession

Arthropod succession is tightly linked with the gradual accumulation of organic matter and plant succession (Gobbi et al., 2006, 2011; Hågvar et al., 2017; Kaufmann, 2001; Kaufmann & Raffl, 2019). Collembola and mites are the earliest arthropod colonizers along retreating glaciers (Hågvar, 2010; Hågvar et al., 2009). Collembola are more abundant than mites along the successional age of the soil. The increase in Collembola, mite, and enchytraeid abundance and richness along the chronosequence is likely due to a simultaneous increase in vegetation cover and the development of a deep organic layer in older soils (Gryziak, 2009; Hågvar et al., 2017; Hodkinson et al., 2004). This trend is strongly supported by the positive correlation of abundance and richness of Collembola and mites with abundance and richness of plant communities and TOC. Further analyses of Collembola families indicate that Isotomidae is the most abundant and diverse group across the successional ages. Moreover, the increased abundance and richness of Istomidae and the abundance of Sminthuridae with successional age might be due to the accumulation of organic matter and soil microbiota. However, the abundance of Hypogastruridae increased up to 100 years and then declined. The latter decline of Hypogastruridae may be associated with increased competition among invertebrates (Vater, 2012). Hymenopterans act as herbivores relying on plants for their food resources or predators and parasites relying on other insects, spiders, and dead animals (Hyodo et al., 2011). The abundance and richness of Hymenoptera significantly increase along the chronosequence, likely due to increases in vegetation cover and abundance of Collembola, Enchytraeidae, and spiders. The colonization of Coleoptera in soils that were exposed for 50 years after a glacial retreat may be due to the increase in decomposing organic matter, lichens, and other arthropods (Bråten et al., 2012). The decline in abundance of Coleoptera after 50 years is probably due to increased competition among soil invertebrates rather than a response to vegetation succession (Vater, 2012). We also analyzed the succession of different families of Coleoptera. Among Coleopterans, Carabidae and Staphylinidae are the most abundant and diverse families. The families of Coleoptera are not significantly different across the successional age except for the richness of Carabidae and Staphylinidae, which significantly increase with increasing soil age. Carabids, most of which are predators of Collembola and adult chironomids, are early colonizers (Hågvar et al., 2017; Lencioni & Gobbi, 2018; Raso et al., 2014). Our Mantel test results also supported the correlation between the abundance of Carabidae and the abundance of Diptera. Increased Carabidae richness along the chronosequence may be due to either increase in Collembola or vegetation cover and plant species richness. Increased vegetation cover is correlated with diverse carabid species having longer larval development periods (Gobbi et al., 2011). However, such correlations were not evident in our results from the Mantel test. On the contrary, Staphylinidae are late colonizers. The increase in the richness of Staphylinidae over successional time is likely favored by an increased organic soil layer, which arises from the increased decomposition of plant matter (Bråten et al., 2012). The abundance and richness of Diptera follow a zigzag pattern indicating no correlation with vegetation succession. However, analysis of families of Diptera reveals a significant increase in richness of Empididae and Muscidae along the chronosequence which might be attributed to the development of supporting food chains (Kaufmann et al., 2002). The richness of spiders increased with increasing soil age; however, their abundance gradually increases in soils exposed for 50 years after the glacial retreat and then decreased in subsequent years. Spider colonization is favored by increased vegetation, which impedes wind, maintains humidity, and creates a stable shelter (Hågvar et al., 2017). Our Mantel test results also supported the correlation of the abundance and richness of spiders with the abundance and richness of plant communities. The decline in spider abundance in soils after 50 years is probably due to increased competition among soil invertebrates than a response to vegetation succession (Vater, 2012). Additional analysis of Spiders at the family level reveals that Linyphiidae and Lycosidae are more abundant than other groups. The abundance of Phalangiidae and richness of Gnaphosidae, Linyphiidae, and Lycosidae increase with successional age, probably due to the increase in vegetation cover. However, Linyphiidae and Lycosidae abundance increases for up to 50 years and then declines. The initial increase of Linyphiidae abundance could be due to the transport of these spiders by wind along with their prey (Hodkinson et al., 2002). As with the aforementioned taxa with similar functional traits, the decline after 50 years may be due to an increase in resource competition among invertebrates.

Our analyses indicate that most of the research on glacier forefield succession is focused on plants and bacteria while research on fungi and invertebrates is more limited. This results in decreased confidence in identifying patterns of succession for many of the less explored taxa, by increasing their standard errors and contributing to statistically non-significant differences. Further research emphasizing the less explored soil biota in studies of this nature, particularly microeukaryotes and microfauna, is much needed.

5 | CONCLUSIONS

Our synthesis of the ecological and soil physicochemical succession concomitant with glacial recession reveals two main patterns. The first conspicuous pattern is one of increased taxonomic abundance and richness over time: Actinobacteria (bacteria), Zygomycota (fungi), plant feeding and omnivorous nematodes, Isotomidae and

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Sminthurididae (Collembola), Mites, Enchytraeidae, Hymenoptera, Carabidae and Staphylinidae (Coleoptera), Empididae and Muscidae (Diptera), Phalangiidae and Gnaphosidae (spiders), lichens, and plant communities. Additionally, soil nutrients such as carbon, TN, and AP increase with successional age. The second pattern shows increased abundance and richness for other taxa, peaking at around 50 years followed by a gradual decline (in abundance and richness): Acidobacteria, Chloroflexi, and Planctomycetes (bacteria); Ascomycota and Basidiomycota (fungi); bacterial feeding nematodes; Hypogastruridae (Collembola); Coleoptera, Opiliones, Spiders, Linyphiidae, Lycosidae, electrical conductivity. Apart from these two patterns, the abundance and diversity of a few bacterial taxa, such as Bacteroidetes, Proteobacteria, Betaproteobacteria, and Cyanobacteria, decline as the pH of the soil decreases along the chronosequence (Figure 9).

The organisms and soil properties that are intimately tied to vegetation follow the first pattern. This observation is consistent with several studies showing that above-ground plant communities can strongly structure below-ground communities (De Deyn et al., 2004; Hodkinson et al., 2003; Kaufmann, 2001; Stephan et al., 2000). The second pattern, which shows an initial increase in taxonomic diversity and abundance followed by a gradual decline may be due to nutrient availability and plant richness and abundance during the first 50 years, after which increased biotic interactions, such as resource competition, result in a gradual decline in the abundance and diversity of select taxa.

Overall, our work provides a synthesis of how past and present terrestrial ecosystems are responding to deglaciation, informing predictions of how contemporary soil ecosystems will respond to future environmental change. Given the intimate relationship between below-ground communities and patterns of above-ground vegetation, much will be gained by future research that tests hypotheses associated with the processes that drive this relationship. This may be true especially as it pertains to how these processes occur in the context of climate-driven environmental changes that influence the spatial scale of available habitat, nutrient cycling, and dispersal. With increasing rates of terrestrial ice mass loss, we expect that the universal patterns and processes of ecological succession we have uncovered will continue as described, but over larger spatial scales, and perhaps more rapidly. For example, increased hydrological and aeolian connectivity could accelerate the rate of dispersal of organisms and nutrients, facilitating more rapid colonization and buildup of organic matter. Additionally, shifts in the frequency and magnitude of extreme temperature and precipitation events may lead to increased or decreased species richness and diversity, depending on how these pulse and press events impact the ecological amplitude of each species. The effects of these cascading changes will likely have important implications for ecological succession not only in periglacial ecosystems but also in terrestrial ecosystems globally.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data set generated during the current study is available in Dryad at https://doi.org/10.5061/dryad.stqjq2c6d.

ORCID

Satyendra K. Pothula https://orcid.org/0000-0002-3073-0990
Byron J. Adams https://orcid.org/0000-0002-7815-3352

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SUPPORTING INFORMATION

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