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RESEARCH ARTICLE

Relative contribution of high and low elevation soil microbes and nematodes to ecosystem functioning

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Abstract

1. Ecosystem productivity is largely dependent on soil nutrient cycling which, in turn, is driven by decomposition rates governed by locally adapted below-ground microbial and soil communities. How climate change will impact soil biota and the associated ecosystem functioning, however, remains largely an open question.
2. To address this gap, we first characterized differences in soil microbial and nematode communities as well as functional characteristics from soils collected from the foothills or in sub-alpine elevations of the Alps. We next performed a full-factorial reciprocal transplant common garden experiment at two elevations, and asked whether elevation-related functional and taxonomic differences are maintained or can be altered depending on the local climatic conditions. For this, we separately transplanted soil microbial and nematode communities from low and high elevation in their home or opposite elevation in pots added with a common plant community.
3. We found evidence for taxonomic and functional differentiation of the microbial and nematode communities when collected at high or low elevation. Specifically, we observed a decrease in microbial diversity and activity at high elevation, and additionally, through nematodes' functional characterization, we found increased fungal-dominated energy channels at high elevation.
4. Moreover, according to the reciprocal transplant experiment, while we found little effect of soil biodiversity change based on elevation of origin on plant growth and plant community composition, soils inoculated with microbes originating from low elevation respired more than those originating from high elevation, particularly when at low elevation. This observation correlates well with the observed faster carbon degradation rates by the low elevation microbial communities.
5. Climate change can reshuffle soil communities depending on organism-specific variation in range expansion, ultimately affecting soil fertility and carbon-cycle dynamics.

KEYWORDS
alpine habitat, carbon cycling, ecosystem functioning, elevation gradient, reciprocal transplant, soil biota

1 | INTRODUCTION

Terrestrial ecosystem productivity is largely dependent on nutrient cycling in soil top layers (Bormann & Likens, 1967), which, in turn, is dependent on below-ground microbial and invertebrate biodiversity and activity (Bardgett & van der Putten, 2014). Soil microbes and invertebrates decompose organic matter into molecules that can be assimilated by plants (Wardle, 2002), and higher soil microbial and invertebrate activity generally translates in higher soil respiration, which is also responsible for vast releases of soil carbon back to the atmosphere (Yiqi & Zhou, 2010). Soil microbial decomposition of organic matter and the related microbial respiration is regulated by several abiotic factors, such as temperature, soil moisture and substrate availability (Curiel Yuste et al., 2007). Such an environmentally driven balance between what is entering the soil and can be assimilated by plants, and what is fully degraded and not available to plants, ultimately influences major ecosystem properties, such as vegetation productivity. Accordingly, even marginal future changes in global temperatures and precipitation rates are likely to alter terrestrial ecosystem dynamics (Heimann & Reichstein, 2008).

Climate change is not only modifying the distribution of species within and across ecosystems (Parmesan, 2006), but also how species within communities interact with each other (Tylianakis et al., 2008). Changes in climate could impact ecosystem processes by either directly increasing the transfer of energy from one trophic level to another (van der Putten et al., 2004) or by modifying the efficiency of the different trophic compartments via the arrival and/or evolution of more efficient novel organisms. Hence, climate change can form novel biotic interactions (Tylianakis et al., 2008), and also induce changes in ecosystem processes (Morin et al., 2018). A number of recent models have incorporated biotic interactions for predicting species distribution and abundance (Brooker et al., 2007); however, for fully comprehending the effect of climate change on ecosystem processes, manipulative experiments that measure the strength of local adaptation versus the degree of temperature-driven plasticity in trophic dynamics are still largely needed (Descombes et al., 2020). Accordingly, reciprocal transplant experiments have become standards for dissecting plant population divergences and how this phenomenon scale up to affect ecosystem processes (Johnson et al., 2021).

The composition and functioning of the soil microbial community can be impacted by the presence of other member of the soil biota, such as nematodes (Sánchez-Moreno et al., 2006). Nematodes occur in great numbers in soils, and represent one of the most diverse animal groups of terrestrial ecosystems (Yeates et al., 2009). Nematodes play a significant role in soil food webs, since they cover all the main trophic groups, including the herbivores, omnivores, predators, as well as microbial feeders (Ferris, 2010). Therefore, nematodes can impact microbial communities, as well as plant and soil health (Yeates et al., 2009). For instance, higher abundance of fungivore nematodes at one site can shift the energy flow from fungal- to bacterial-dominated decomposition pathway (Ferris et al., 2001). Moreover, the different functional groups, represented by different life-history and feeding strategies, can show vastly different responses to environmental disturbances and global change (Van Den Hoogen et al., 2019). While bacterivore nematodes, that are known as typical r-strategists or colonizers, might be able to benefit from enhanced nutrient availability and increased microbial biomass under fertilized, intensified land use, the more sensitive nematode groups consisting of K-strategists (i.e. persisters), such as the omnivores, may decline after perturbation, resulting in simplified and less structured soil food webs (Ferris et al., 2001). Such functional shifts can be captured by the calculation of nematode functional indices developed by Bongers (1990) and Ferris et al. (2001), which can, in turn, indirectly inform on the current successional and functional dynamics of any given soil food web compartment.

One way to address the effect of climate on ecosystem processes, including shifts in soil community composition and function, is to work along large-scale ecological gradients. Along elevation gradients, in particular, due to physiological trade-offs, species that have evolved to tolerate cold and harsh environments are bound to reduce their overall metabolism (Hille & Cooper, 2015). Consequently, the functioning of the alpine ecosystem should be slower than at low elevation (Stige & Kvile, 2017). Along these lines, soil-related properties also vary, and processes should be reduced at high elevation (Pellissier et al., 2014). Along elevation, soil depth, nutritive value and microbial diversity all tend to decrease, but carbon, nitrogen and root biomass per volume of soil tend to be higher at high elevation, indicating slower organic matter decomposition (Malhi et al., 2017). As elevation increases, the decomposition rate is expected to decrease as a result of a combined effect of lower temperature (Conant et al., 2011) and slowed down metabolic efficiency of cold-adapted decomposers (Rubenstein et al., 2017). Overall, there is evidence that plant productivity (Malhi et al., 2017), and decomposition from soil organisms (Looby & Treseder, 2018) all decrease with elevation, while soil organic matter content and carbon storage increases. However, whether changes in soil and vegetation processes along elevation are driven by plastic and modular enzymatic processes in the soil, or whether they are driven by differences in taxonomic composition of communities, or finally, whether they are driven by genetic or ecotypic differentiation in the same functional guilds adapted to different elevations, largely remains an open question.

To address whether variation in plant productivity and decomposition are driven by variation in microbe and nematode communities' changes along elevation, and whether such changes could affect ecosystem processes during climate change, we compared functional and taxonomic variation in microbe and nematode communities across two contrasted elevations in the Swiss Alps with a reciprocal transplant experiment. Specifically, we hypothesized that differences in elevation and their associated abiotic predictors generated divergence in the taxonomic and functional diversity of soil biota, which in turn would change levels of respiration rates and plant productivity. Specifically, we predicted that (a) high elevation soil biotas are composed of communities with intrinsic slower metabolic rates. Therefore, high elevation soil biotas would sustain lower soil respiration rates and a decrease in vegetation productivity.

(b) Based on previous soil surveys, we expected higher nematode abundances in alpine habitats (Kergunteuil et al., 2016), and, since with elevation decomposition rates decrease and soil organic matter increases, we expected a shift from fast- towards slow-energy flows, mediated by bacterial- to fungal-dominated decomposition channels. (c) High elevation soil biota should increase their metabolic activity when placed at low elevation, and mimicking direct climate change effects. Accordingly, the patterns we recorded in this study along elevation gradients will help predicting how climate changes may accelerate energy flows in particular biomes characterized by slow energy channels, such as in alpine or arctic habitats.

2 | MATERIALS AND METHODS

2.1 | Experimental design

To measure ecotypic differentiation, and the relative contribution of soil microbes and nematodes from low and high elevations on soil productivity and respiration, we performed a full-factorial soil biota reciprocal transplant experiment in the Swiss Prealps (see details in Figure 1, Figures S1–S2 and Supplementary Methods S1). The treatments consisted in inoculating about 1.5 L of the high and low elevations, autoclaved (two cycles of autoclave at 121°C) soils with high- or low elevation soil biota (nematodes or micro-organisms, separately). Soils were sieved at 2 cm prior autoclaving. The soil biota was added to the soils belonging to the same transects. All the soil-filled pots were then divided equally in two batches and placed in two common gardens at high and low elevations along transect 1 (N = 4 replicates × 2 common garden sites × 2 soil biota treatments × 2 elevations of origin for soil biota × 2 elevations of origin for the soils × 3 transects = 192 pots). At each site of collection, we also characterized soil physicochemical properties as described in Supplementary Methods S1.

Next, in order to measure the combined effect of elevation, origin of the soil, and the origin of soil organisms (nematodes and microbes) on plant productivity and soil respiration, we built one common garden at the colline vegetation stage (Vd-low site at 440 m above sea level (a.s.l.), and one at the sub-alpine vegetation (Vd-High sites at 1,700 m a.s.l., Figure 1, Figure S1). In addition, for the Vaud transect, where the common garden experiment took place, an additional set of pots were included for comparing the effect of the entire soil community on plant productivity and soil respiration against the two soil biota (nematodes only or soil microbes only) treatments (N = 8 replicates × 2 common garden sites × 2 elevation of origins for the soils = 32 pots). This treatment consisted in using the field collected soil, sieved at 2 mm, but without further manipulation, in order to represent as accurate as possible 'natural' soil communities' conditions.

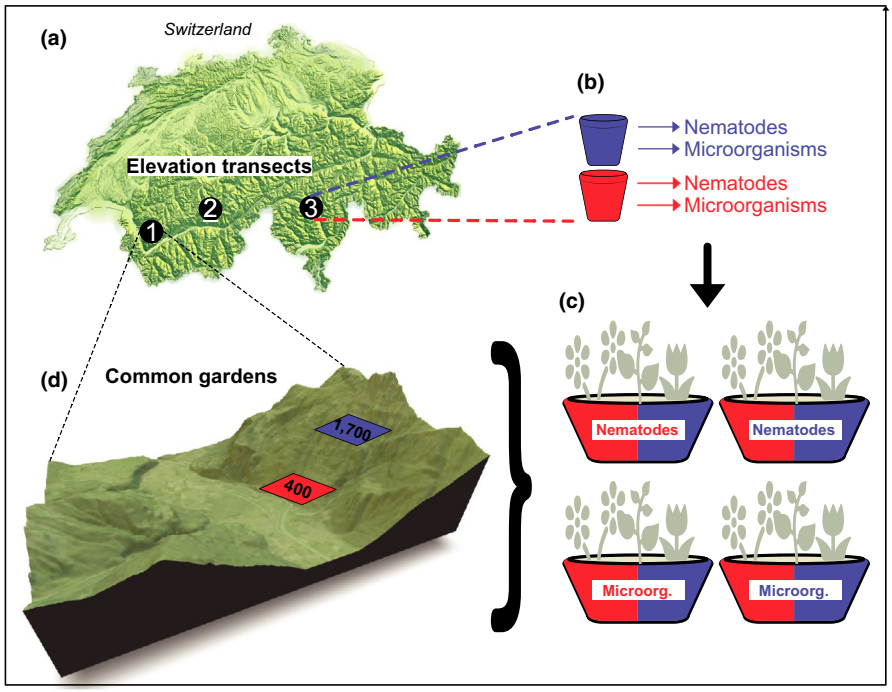

FIGURE 1 Experimental design. (a) Map of Switzerland showing the location of the three elevation transects where soils and sol biota were collected. 1: Vaud (Vd) transect in the Northern Alps, 2: Valais (Vs) transect in the Western Alps, 3: Ticino (Ti) transect in the Southern Alps. (b) Within each transect, we sampled at low (red colour) and at high (blue colour) elevation. Transect 1: Vd-Low (521 m; N: 46°11′53.302″, E: 7°1′34.758″) and Vd-High (1,794 m, N: 46°12′53.623″, E: 7°47′33.239″), transect 2: Vs-Low (657 m; N: 46°18′24.429″, E: 7°40′18.350″) and Vs-High (1,850 m, N: 46°20′15.029″, E: 7°32′6.388″), and transect 3: Ti-Low (820 m, N: 46°29′08.701″, E: 8°47′33.239″) and Ti-High (1,880 m, N: 46°30′29.273″, E: 8°46′33.515″). (c) Soil micro-organisms and nematodes from low and high elevation were then extracted and reciprocally inoculated in pots containing soils from low or high elevation, and then (d) everything was replicated in the two common gardens placed within the transect 1

2.2 | Nematodes' extraction and identification

Nematodes were extracted from multiple sub-samples of the initial bulk soil from each collection site using a modified Baermann's extraction method. Specifically, we extracted nematodes from 2 L soil volume per funnel by soaking it in 1 L water, and by adding an additional 350 ml of water after 24 hr to avoid too rapid desiccation. Once collected, nematodes were immediately stored in cell culture treated flasks with filter cap (Nunc™; Thermo Scientific) at 11°C until re-inoculation in the experimental soils (see below). From each collection site, a representative volume of water containing a subset of all nematodes collected was used for nematode identification under a stereomicroscope. Nematodes were identified to the nearest know taxonomical resolution (species, genus or family level), and the number of nematodes per gram of soil was finally calculated. Finally, nematodes were functionally characterized using the online web tool 'Nematode Indicator Joint Analysis (NINJA)' (Sieriebriennikov et al., 2014) (see details in Supplementary Methods S1).

2.3 | Micro-organisms' extraction

To extract the entire bacterial and fungal communities (hereafter broadly referred to; soil micro-organisms) from the six soils, 1 L volume of soil was placed in suspension in 1 L volume tap water (1:1 volume proportion) and mixed by hand for 2 min to break-down small aggregates. The suspension was divided into 450 ml containers and centrifuged at 3,000 RCF for 3 min. The supernatant was next sieved through a 2 μm mesh in order to keep only the microbial communities and filter out nematodes or other eukaryotes (Wagg et al., 2014). The microbial suspensions were stored at 4°C on an agitation table until soil re-inoculation. The taxonomic composition of the bacterial communities was assessed using next-generation sequencing of bacterial DNA markers, and the microbial communities' efficacy in degrading carbo-based resources was characterized EcoPlates from Biolog (Insam, 1997) (Supplementary Methods S1).

2.4 | Plant community manipulation

On 31 July, seed mixes were sowed to each pot. Specifically, we sowed 10 plant species based on the criteria of being generally highly abundant, well distributed from the colline to the sub-alpine zones, and representative of the natural environment and vegetation cover of dry grasslands (Mesobromion and Seslerion, at low and high elevation, respectively (Delarze et al., 2015)), and representative of major plant families: *Centaura montana* (Asteraceae), *Phyteuma orbiculare* (Campanulaceae), *Trifolium montanum* (Fabaceae), *Onobrychis vicifolia* (Fabaceae), *Anthyllis carpatica* (Fabaceae), *Bromus erectus* (Poacae), *Brachypodium pinnatum* (Poaceae), *Sesleria caerulea* (Poacae), *Plantago media* (Plantaginaceae) and *Sanguisorba minor* (Rosaceae). In total, we germinated five individuals per species in each pot. After 2 months of growth, on 21 September, each plant individual was identified and carefully removed from the soil, separated into roots and shoots, stored in paper envelopes and let dry at 40°C for 1 week before above- and below-ground biomasses were recorded. Roots were washed under tap water before drying and weighing.

2.5 | Soil respiration measurements

Following plant collection, soil microbial communities were allowed to re-establish for 24 hours before soil respiration measurements were taken. Soil CO_2 effluxes were measured with a portable LI-8100A Automated Soil Gas Flow System (LI-COR Biosciences GmbH). Once the measurements of respiration were completed, all soil samples were stored at 4°C until performing the same soil analyses as described above.

2.6 | Statistical analyses

We performed all statistical analyses with R software, version 3.5.1 (R Development Core Team, 2020).

2.6.1 | Soil properties

Initial bulk soil physicochemical properties were visualized using principal component analyses (PCA; ADE4 package (Dray & Dufour, 2007)). Subsequently, we measured the effect of all treatments combinations (full interaction between the soil biota treatment [two levels: microbes and nematodes], the origin of the soil biota [two levels: high and low], the elevation of the common garden [two levels: high and low elevation], and the soil provenance [two levels: high or low elevation]) on soil parameters using a four-way permutational ANOVA (PERMANOVA; *adonis* function in the VEGAN package (Oksanen et al., 2013), Euclidean distance estimation), and with transects included as strata in the model. We next assessed the effect of elevation of origin for each soil variable separately using a mixed-effect model, with elevation as fixed factor, and transect as random factor using LME4 (Bates et al., 2015) and LMERTEST (Kuznetsova et al., 2015) packages.

2.6.2 | Vegetation

The effect of soil biota treatment (two levels: microbes and nematodes), the origin of the soil biota (two levels: high and low), elevation of the common garden (two levels: high and low elevation), the soil provenance (two levels: high or low elevation) and all their interaction terms on plant total biomass and on root to shoot biomass ratio at the end of the growing period were assessed using a four-way mixed-effect ANOVA, by including transects are random factor in the model. Next, we assessed the effect of soil biota treatment, the origin of the soil biota, elevation of the common garden, the soil provenance and all their interaction terms on plant community composition (based total

biomass) at the end of the growing period using a four-way permutational ANOVA (PERMANOVA; *adonis* function in the VEGAN package (Oksanen et al., 2013)), and with transects included as strata in the model. Since, soil origin effect was strongest in the PERMANOVA above (see Section 3), we also addressed the effect of different soil variables on the community structure of plants. For this, we fitted the soil data matrix (six variables) onto the vegetation matrix (based on total biomass) using the *envfit* function in VEGAN (Oksanen et al., 2013). This analysis allows visualizing the soil factors that significantly correlate with the vegetation matrix. The analysis was visualized using non-metric multidimensional scaling (NMDS) implemented in the VEGAN package, and the Bray–Curtis metric was used to calculate dissimilarity among samples for both the NMDS and the PERMANOVA.

2.6.3 | Soil respiration

The effect of soil biota treatment (two levels: microbes and nematodes), the origin of the soil biota (two levels: high and low), the soil provenance (two levels: high or low elevation) and all their interaction terms on soil respiration were assessed using two (for both high and low elevation common gardens separately) three-way mixed-effect ANOVAs, by including transects are random factor in the model. In this case, the analyses for two common gardens were kept separate since the respiration measures were done over two consecutive days.

3 | RESULTS

3.1 | Soil physicochemical properties

Soils varied strongly across elevation and sites (Table S1; Figure S4), and we found no effect of any other treatment on soil properties besides elevation of origin after the reciprocal transplant experiment (Table S2). Overall, we found that soils from high elevation had 2.4 times more moisture content (Figure S5a), contained 2.5 times more organic matter (Figure S5b), including 2.3 times, and 2.4 times more carbon and nitrogen, respectively (Figure S5f,g), but had the same proportion of carbon to nitrogen (Figure S5h). Soils of high elevation had average pH of 6.11 compared to an average pH of 6.84 at low elevation (Figure S5c), and high elevation soils had 1.93 times higher cation exchange capacity than at low elevation (Figure S5e). Finally, we practically found no $CaCO_3$ in high elevation soils compared to low elevation soils (Figure S5d).

3.2 | Nematode community structure

Overall, 7,274 nematodes were extracted from the six 'initial soil' samples taken along the three transects. Of these 7,274 nematodes, 585 individuals were assigned to 27 genera, 3 families, 2 order and 1 to the species level, while the rest was assigned to functional groups and feeding types only (Table S3). The six soil samples displayed significant differences in term of nematode functional groups' composition (chi-sq = 247.75, $df = 20$, $p < 0.001$; Figure 2a, Figure S5). Although almost all feeding guilds are represented in each soil, it is interesting to note that, in general, the proportion of omnivorous nematodes increases at high elevation, the proportion of herbivores is higher at low elevation, and the other groups show overall similar trends but variables across transects (Figure 2a). Indeed, while Vs-Low and Ti-Low sheltered only few omnivorous nematodes, their presence was higher at high elevation, that is, in Vs-High and Ti-High, respectively. In general, we observed the highest percentage of herbivorous nematode in Ti-Low samples, fungivorous nematodes in Vd-Low samples, bacterivorous nematodes in Vs-Low samples and omnivorous nematodes in Ti-High samples (Figure S6a). We also observed that c-p2 class (basal, resistant nematodes) is dominant in all soil samples except in Ti-High soil samples where c-p4 class (large and long generation time nematodes) is the most represented (Table S4, Figure S6b). Overall, we observed a shift towards 'persisters' with elevation along two transects (Figure 2b). Indeed, while c-p4 were only recorded in Vs-High as compared to Vs-Low, Ti-High supports high proportion of c-p4 and c-p5 as compared to Ti-Low (Figure S6b). We also observed that for Vs-Low and Vd-High samples a *basal* food web (diminished due to stress), a *basal-structured* food web for Vs-High sample and a *basal-enriched* food web for Vd-Low sample. Finally, we observed that when considering all transects (except for Ticino, for which this index could not be calculated), the level of organic enrichment decreased with altitude, while decomposition channels switched from bacterial to fungal pathways in two of the transects studied (Table S4, Figure 2b).

3.3 | Microbial communities

Overall, we found the microbial communities to be functionally different between high and low elevations (Figure 3). Specifically, low elevation microbes consumed in average, across all sites, 12% more carbon sources than high elevation microbes (elevation effect; $F_{1,45} = 14.20$, $p < 0.001$), while the microbial functional diversity, in term of carbon degradation, was more similar among soils coming from either low or high elevation than across transects (see cluster dendrogram in Figure 3a). We also found that low elevation soils tended to display a greater diversity of bacterial actual sequence variants' (ASVs) (Figure 3b), with particularly 28% and 48% more Proteobacteria and Actinobacteria in low elevation soils compared to high elevation soils, but less so for the fungal ASVs (Figure S7).

3.4 | Vegetation productivity

The mixed-effect model indicated that only the common garden site had a significant effect on plant total biomass production (Table S5),

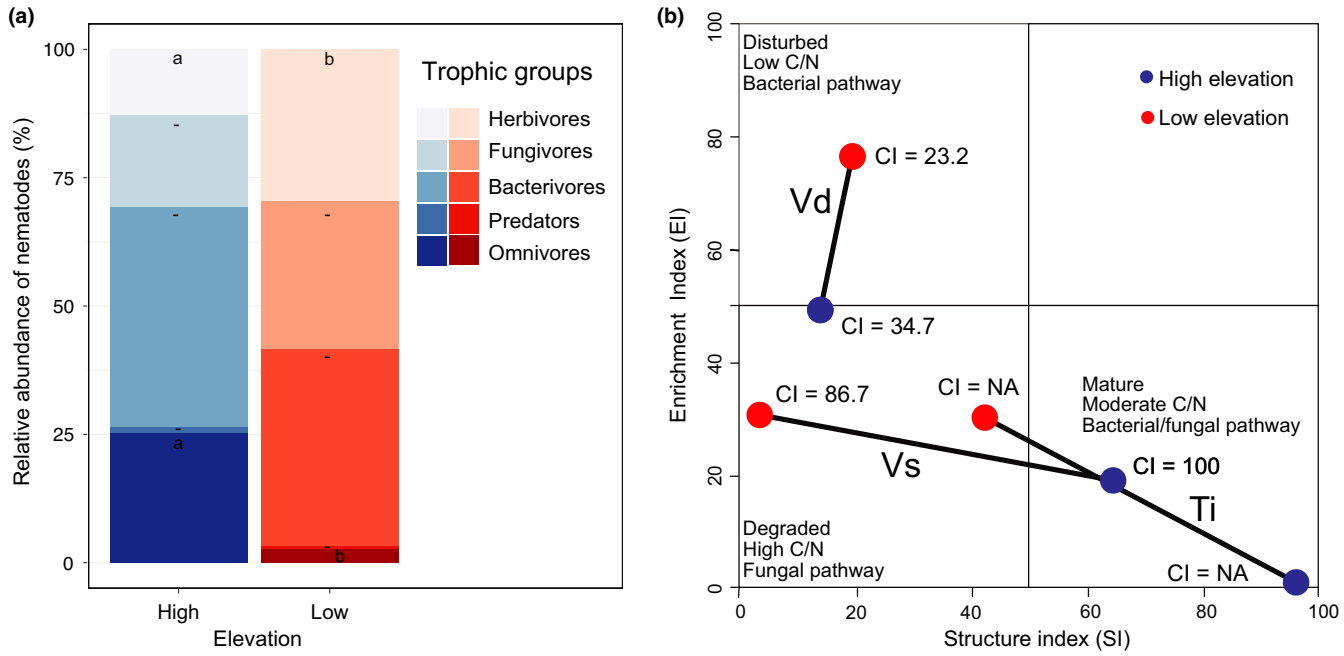

FIGURE 2 Survey of soil nematode functional diversity along elevation gradients. (a) The relative abundance of nematode trophic guilds; from darker to lighter colours: ominvores, predators, bacterivores, fungivores and herbivores found across three elevation transects. Different letters in similarly shaded rectangles represent significant differences between two same nematodes functional groups that are found in soils from low and high elevation (χ^2-test, $p < 0.05$). (b) Food web analysis of nematode communities sampled across two elevations and three transects in three Swiss cantons (Vaud (Vd), Valais (Vs) and Ticino (Ti); see also Figure S1). The bold black lines show that when considering each transect, carbon-to-nitrogen (C/N) ratio increases with elevation, and the decomposition channels (measured as channel index, CI) switch from bacterial to fungal pathways

with an average plants growing at low elevation being 36% heavier than their counterparts that grew at the high elevation common garden site (Figure 4a). Root to shoot biomass ratio (RS) was also significantly influenced by the common garden site (Table S5). Plants growing at low elevation allocated in average 47% more biomass to the roots than when growing at high elevation (Figure 4b). This effect was however modulated by the soil biota treatment (see significant interaction between common garden site and soil biota treatment in Table S5). At low elevation, nematodes increased the RS by 76%, while at high elevation they decreased it by 27% compared to the microbes' soil addition (Figure 4b).

3.5 | Plant community composition

We found that the site of growth, common garden sites and soil biota treatments all influenced independently plant community structure in terms of relative allocation of biomass across species (Table S6). Accordingly, the biomass of the nine species under investigation changed depending on site of growth, but also varying across species. For instance, *P. media* plants increased >400% their biomass when growing at low elevation, while *A. carpatica* producing the same biomass across sites (Table S2, Figure 4c). Soil type also influenced the community structure of the vegetation (Table S6), and the environmental fitting analysis indicated that only the pH was significantly correlated ($r = 0.31$, $p = 0.002$) with changes in vegetation community structures (Figure 4d). Specifically, *P. media*, *S. minor*, *B. pinnatum*, *P. orbiculare* grew more on more alkaline soils.

3.6 | Soil respiration

We found that the soil biota treatment strongly affects soil respiration (Table S7), with soils inoculated with micro-organisms respiring in average 3.5 times more than soils inoculated with nematodes only (Figure 5). Soils with intact soil microbial and nematode communities showed average respirations in between the two soil biota treatments (Figure 5). Finally, we observed that soils with microbes and nematodes from low origin had 13% and 28% higher respiration, respectively (Table S7, Figure 5a), but that this difference was only observed in the lower elevation common garden (Figure 5b).

4 | DISCUSSION

By using a full factorial reciprocal transplant experiment at two elevations, we found evidence for ecotypic and functional differentiation of the microbial and nematode communities growing in the foothills or in the sub-alpine soils of the Alps. Overall, we observed a decrease in microbial diversity and activity, and, through nematodes' functional characterization, we found an increase in fungal-dominated metabolic pathways with elevation. We also found that soils with microbes and

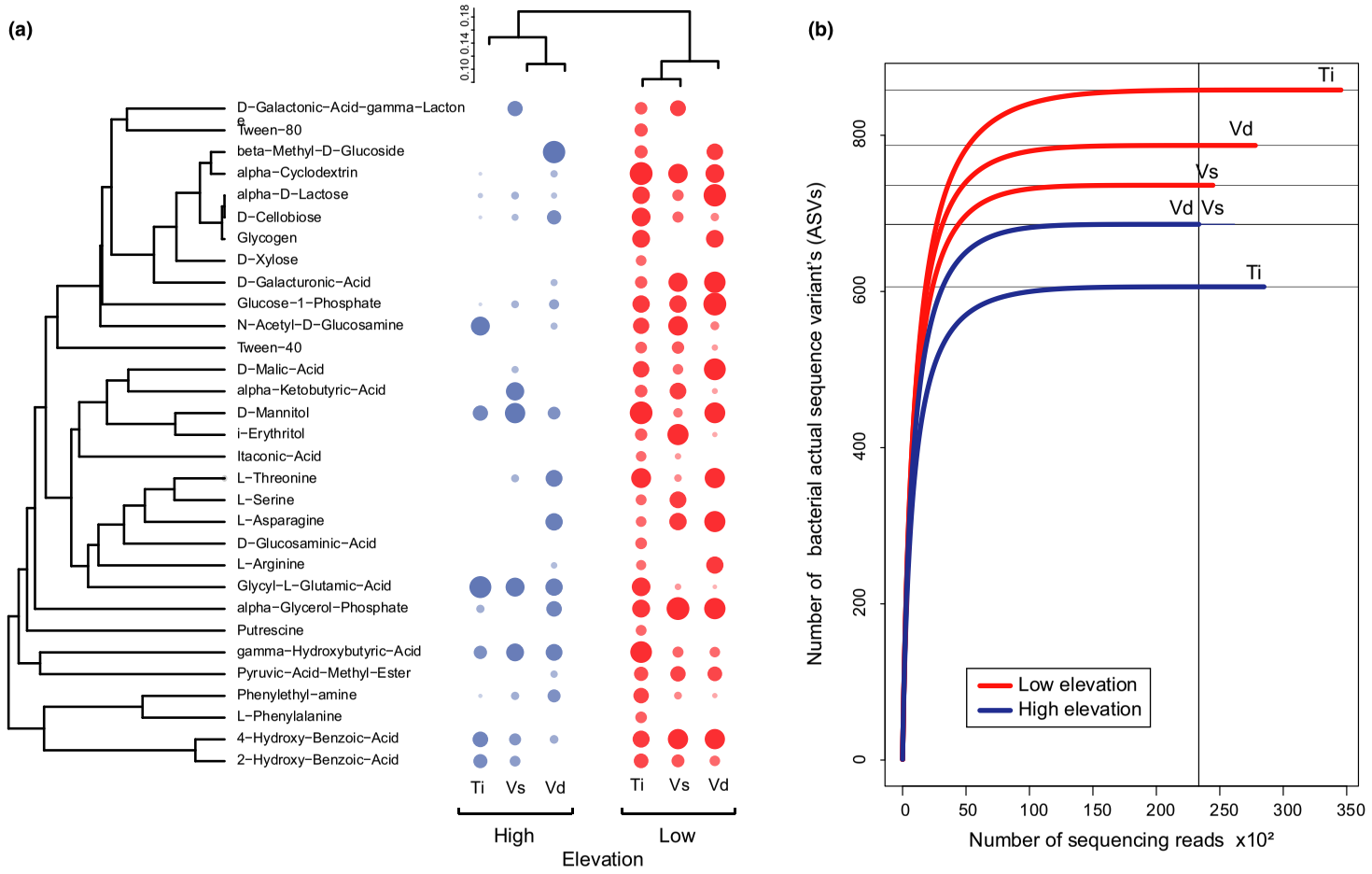

FIGURE 3 Survey of soil microbe functional and taxonomic diversity at two contrasted elevations. (a) Shown is a cluster dendrogram for separating the six 'natural soil' microbial communities, and showing differences between low (blue dots) and high (red dots) elevation microbial communities according to their metabolic activity (through carbon source utilization). Carbon substrates that are closely related to the distance tree have similar metabolic pathways. Overall, the average metabolic activity is 12% higher at low altitude (elevation effect; $F_{1,45} = 14.20$, $p < 0.001$), and (b) genetic difference (diversity of bacterial ASVs) of microbial communities from low and high elevation

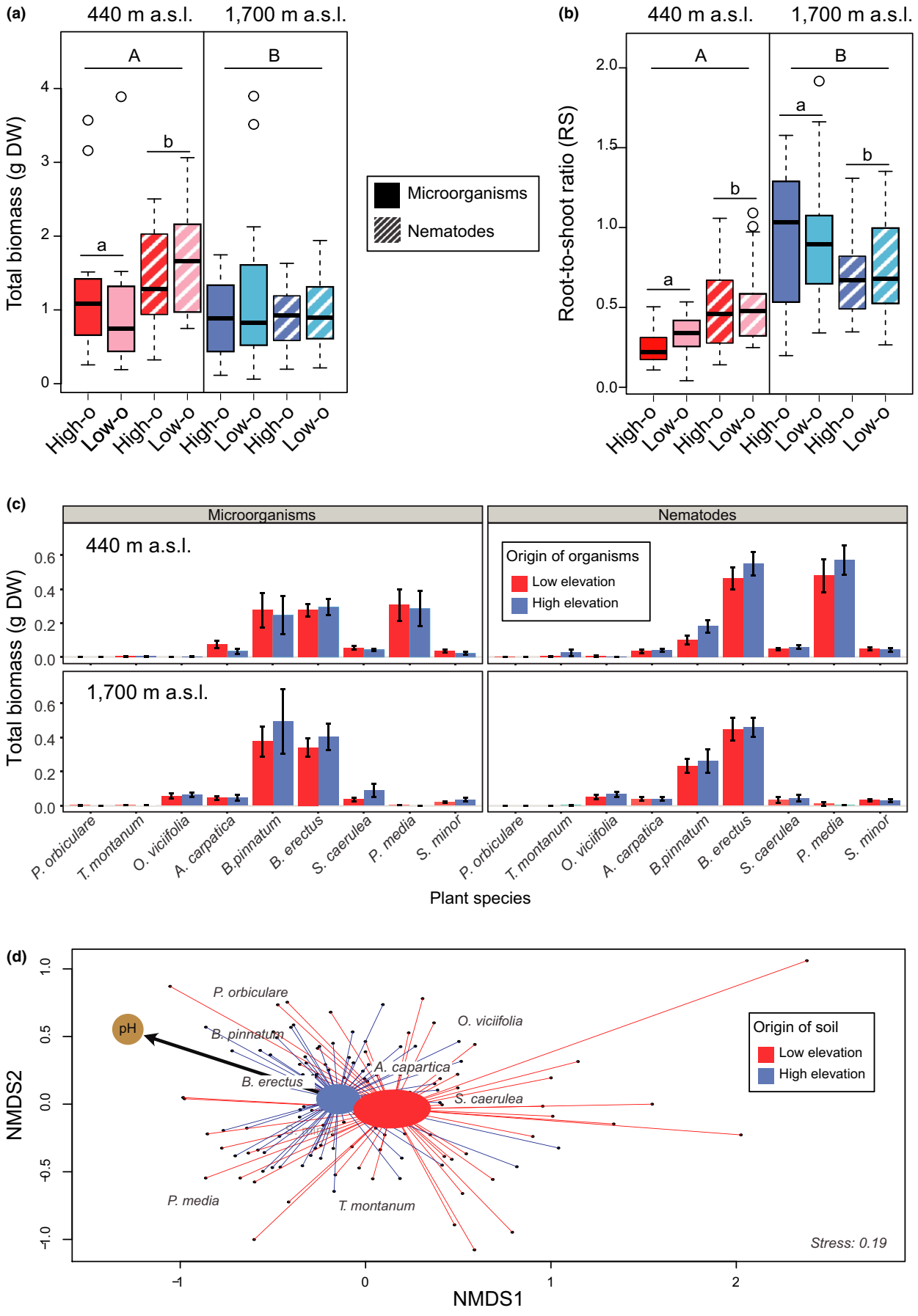
(a)
440 m a.s.l.
1,700 m a.s.l.
A
B
a
b
Total biomass (g DW)
Microorganisms
Nematodes
High-o
Low-o
(b)
Root-to-shoot ratio (RS)
(c)
Microorganisms
Nematodes
440 m a.s.l.
1,700 m a.s.l.
Origin of organisms
Low elevation
High elevation
P. orbiculare
T. montanum
O. viciifolia
A. carpatica
B.pinnatum
B. erectus
S. caerulea
P. media
S. minor
Plant species
(d)
NMDS1
NMDS2
pH
Origin of soil
Stress: 0.19

FIGURE 4 Effect of soil biota and elevation on plant biomass production based on the reciprocal transplant experiment. (a) Boxplots show the effect on total plant biomass, and (b) on root to shoot biomass ratio (RS) when plants grew at low elevation (red filling, Vd-Low; 440 m a.s.l.), or at high elevation (blue filling, Vd-High; 1,700 m a.s.l.). Plants also grew on soils inoculated with soil microbes only (plain filling), or with soil nematodes only (hatched filling). Letters above boxplots represent significant differences among main effects (Tuckey's post-hoc tests; $p < 0.05$). Panel (c) shows the effect of the different soil treatments for each plant species tested, and panel (d) the overall structure (based on total biomass) of the plant communities planted at high or low elevation common gardens. The pH arrow represents a statistical correlation (envift analysis; $p < 0.05$) with the plant community ordination

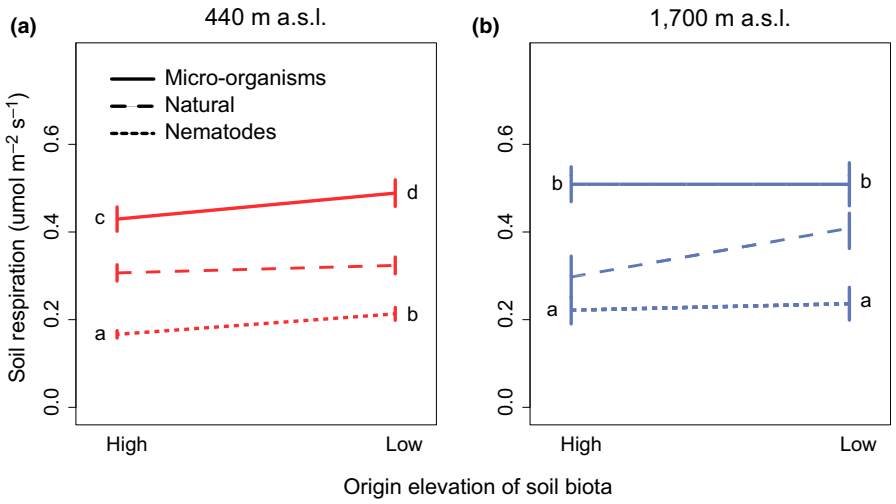

FIGURE 5 Effect of soil biota on soil respiration. Interaction plots show the effect of different soil micro-organisms (plain lines) and nematodes (finely hatched lines) on soil respiration. Soil biota were originated from six different soils (three at high elevation, and three at low elevation). Soil respiration was measured on soils placed at low elevation (red colours; Vd-Low, 440 m a.s.l.) and at high elevation (blue colours; Vd-High, 1,700 m a.s.l.). Letters besides lines represent significant differences (Tukey's post-hoc tests, $p < 0.05$). Shown are also average soil respirations obtained from soils with the intact soil biota community (Natural)

nematodes from low elevation had higher respirations than soils with microbes originating at high elevation. Together, these results indicate that climate-change-driven upward movement of soil biota could help foster CO_2 release and organic matter degradation in sub-alpine soils. Below, we expand on each of these points.

4.1 | Soil physicochemical changes along elevation gradients

We observed clear differences in soil physicochemical composition across three different bioclimatic zones and across two elevations. Soil functioning is generally related to a combination of variation in climatic conditions as well as to vegetation quality and the soil substrate (e.g. pH; Conant et al., 2011). Indeed, we showed that high elevation soils, where mean annual temperature is lower, precipitations are more abundant, and vegetation chemistry is more recalcitrant than at low elevation (Djukic et al., 2010), were richer in organic matter, and contained more carbon and nitrogen. These results confirm the literature of soil analyses along elevation gradients, which indicates that in general soil organic matter increases with elevation due to low decomposition rates (Djukic et al., 2010; Egli et al., 2009; Pellissier & Rasmann, 2018), and which in turn produces more acidic soils and with higher cation-exchange capacity. We indeed observed an increase in the cation exchange capacity with elevation, which indicates that at high elevation soil are indeed richer in soil organic matter. Also, noteworthy is that soil samples from low and high elevation maintain clear differences after the transplant experiment. These results suggest that biotic treatments applied during the experiment (about 8 weeks in total) did not significantly change the physico properties of soils, and thus suggesting that soil physicochemical properties are resilient to microbial biotic perturbation, at least in the short term of a growing season. However, further experiments are required to test over longer periods how the incursion of low elevation soil communities into high elevation soils, due to climate warming, might trigger a decline of soil organic matter, and potentially other physicochemical changes, such as an increase in pH, or a decrease in cation-exchange capacity.

4.2 | Nematode functional differentiation along elevation gradients

Nematode have been increasingly shown to play key role in soil food webs, nutrient cycling, and vegetation composition (Bardgett

et al., 1999). We found structural differentiation in nematode communities from high to low elevation, with higher numbers of herbivore nematodes at low elevation, but with higher omnivores at high elevation. Recently, along similar elevation transects, it was found that the overall abundance of nematodes increases with elevation, including the bacterivores, the fungivores and the omnivores, but also the herbivores (Kergunteuil et al., 2016). Such discrepancies in herbivorous nematodes might arise from site-specific variation in nematode community composition, regardless of elevation. Moreover, our results for nematode diversity and abundance show a high proportion of opportunistic enrichment nematode species (*Rhabditis* and *Cervidellus*), which are known to be increasing in number faster than non-opportunistic nematodes (*Diphtherophora*, *Metateratocephalus*, *Prismatolaimus*, *Tripyla*, Chromadoridae and Aporcelaimidae) in response to an increase in microbial activity caused by addition of organic matter (Bongers & Ferris, 1999). In line with Kergunteuil et al. (2016), persister nematodes were more abundant at high elevation, likely due to low temperatures and slow turnover of nutrients at high elevation as discussed above. Additionally, the nematode food web analysis showed that, when considering each transect, the decomposition channels switch from bacterial to fungal pathways (as inferred from low EI and high CI values) from low to high elevation. One explanation for this finding could be that low temperatures, as well as lower pH values, are more favourable for the growth of fungi rather than bacterial growth (Margesin et al., 2009), and that fungivore but also omnivore nematodes can profit of increased organic matter and also higher mycelia presence at high elevation. Indeed, elevation increases soil organic matter contents, a main driver of nematode abundance at a global scale (Van Den Hoogen et al., 2019). The complexity of the nematode community also increases with elevation, probably due to lower soil perturbation associated with elevation. Taken together, these results point to a nematode-mediated general slowdown of the functioning of the high elevation ecosystem (generally high reproduction rates, MI), which is also reflected in the decrease in soil organic matter degradation at high elevation.

4.3 | Microbial functional and ecotypic differentiation along elevation gradients

Heterotrophic microbial communities that inhabit soils control key processes that participate in the carbon and nitrogen cycle. We found clear differences in the microbial communities from low and high elevation, particularly the bacteria, which also showed more consistent ability to degrade organic matter when originating from low elevation. These differences could be driven by a direct link between strong beta diversity in vegetation communities from low and high elevation (Descombes et al., 2017), changes in organic matter composition or by changes in the abiotic environment (Zak et al., 2003). Since we observed that microbial community differences were maintained between low and high elevation, independently of the identity of the elevation transects, where vegetation differences are pronounced (Pitteloud et al., 2021), it suggests that elevation has a greater impact on shaping soil microbial communities than the geographical distances between sites of the same elevation. Accordingly, microbial community and metabolic differentiation could be explained by environmental filters such as temperature and pH (Fierer, 2017), which, when colder and more acidic, respectively, may limit the number of possible bacterial metabolic pathways and thereby favour specific groups of micro-organisms.

We also observed that microbial diversity from low elevation soils can utilize a greater spectrum of carbon substrates that microbes from high elevation. This finding is consistent with previous results obtained in the Austrian alps showing that soil microbial activity decreases with elevation (Margesin et al., 2009). These patterns go hand-in-hand with a reduced soil microbial respiration with high elevation microbes, which is particularly marked at low elevation, likely due to higher average temperature regimes at the Lavey site. Other studies similarly suggest a direct link between microbial community composition and soil respiration rates, which are likely linked to particular microbial life strategies and functional capabilities. Indeed, while multiple studies have shown that geographical locality, climate (García-Palacios et al., 2012), soil quality (Delgado-Baquerizo et al., 2015) and plant community structure (Knowles et al., 2015) are all strong predictors of soil respiration, it is clear that soil microbial biomass, diversity and enzymatic activity, all have also to be included in order to improve predictions of soil C fluxes at the global scales (Delgado-Baquerizo et al., 2016). Moreover, in addition to soil bacterial composition, fungal richness has also been shown to directly affect soil respiration, thus suggesting an additional fungal role in driving carbon cycling (Wagg et al., 2014). For instance, Trivedi et al. (2016) found a significant relationship between functional genes and their corresponding enzymatic activity, and showed that the variations of the enzymatic activity involved in the carbon degradation were predicted by the functional gene abundance of the soil bacterial and fungal community. Future detailed analyses for characterizing the different communities of soil bacteria and fungi are thus needed to complement our results and discriminate which taxa of the bacteria or fungal communities from high and low elevation soils could explain the differences in soil respiration rates.

4.4 | Effect of soil biota on plant communities

We observed that nematodes alone induced biomass production and increased root-to-shoot ratio, particularly, when vegetation communities grew at low elevation. We also found that overall, low elevation, more alkaline soils were more productive than high elevation soils, but this effect was plant-species specific. However, we did not detect a direct effect of elevation of origin of the micro-organisms on the vegetation. While our results are in agreement with previous studies showing that plant community composition is driven by the diversity and species composition of various groups of soil organisms (van der Heijden et al., 1998), soil properties can clearly also

influence plant communities (Klanderud et al., 2015). That said, it remains puzzling the fact that vegetation productivity was higher in soil with nematodes only. Nematode cuticles are known to carry active bacteria (Adam et al., 2014), so nematode inoculation could favour some level of microbial recolonization of the soils. Besides, primary and secondary metabolites produced by roots may result from the selective recruitment of the microbiome associated with the rhizosphere (Venturi & Keel, 2016). Therefore, we might speculate that nematode-driven microbial re-inoculation and chemical exudates involved in plant–microbe interactions may, for instance, have recruited plant growth-promoting rhizobacteria or other microbes that indirectly stimulate plant growth. Additionally, specific feeding guilds of nematodes such as bacterivores could act as biological agents reducing the presence of phytopathogens through their grazing activities, and enhance soil fertility through excretion of nitrogen forms (Standing et al., 2006). A number of bacteria are primarily regulated by predation by bacterivorous nematodes, whereas fungi are regulated more by substrate quantity and quality (Cheng et al., 2017). Therefore, by influencing the carbon and nitrogen cycle differently, variation in nematode and bacteria communities, as manipulated here, could effectively produce different soil qualities, and ultimately different vegetation productivities.

5 | CONCLUSIONS

Both carbon sequestration and soil respiration are critical processes controlling key ecosystem functions such as climate regulation, nutrient cycling and plant productivity. This study highlights the role of soil biota in the fine regulation of these ecosystem functions, showing that abiotic factors such as soil pH and elevation (indirectly temperature) affect the structure of the ecosystem by directly influencing the functional composition of soil communities. The observed elevation-specific ecotypic adaptation of soil biota can differently affect carbon incorporation dynamics and soil respiration. Climate change is likely to change these dynamics (Pellissier & Rasmann, 2018). For instance, warmer temperatures might favour the upward movement of some groups of soil biota over others, or spur thermal adaptation through rapid evolution, particularly for fast-growing micro-organisms. Future research along elevation gradients should thus address the combined effect of increased soil metabolic activity, coupled with novel species compositions and interactions in the context of climate change.

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CONFLICT OF INTEREST

Sergio Rasmann is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

AUTHORS' CONTRIBUTIONS

S.S., A.K. and S.R. conceived the idea; S.S. and A.K. performed the common garden experiment and collected the data; S.S.-M. classified the nematode communities; J.P., T.G. and R.G. analysed the microbial communities; S.R. and S.S. wrote the first draft of the manuscript, and all co-authors contributed to the writing.

DATA AVAILABILITY STATEMENT

All data for this paper are available from Dryad Digital Repository https://doi.org/10.5061/dryad.hhmgqnkhv (Rasmann et al., 2021).

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REFERENCES

Adam, M., Westphal, A., Hallmann, J., & Heuer, H. (2014). Specific microbial attachment to root knot nematodes in suppressive soil. *Applied and Environmental Microbiology*, *80*, 2679–2686. https://doi.org/10.1128/AEM.03905-13

Bardgett, R. D., Cook, R., Yeates, G. W., & Denton, C. S. (1999). The influence of nematodes on below-ground processes in grassland ecosystems. *Plant and Soil*, *212*, 23–33.

Bardgett, R. D., & van der Putten, W. H. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, *515*, 505–511. https://doi.org/10.1038/nature13855

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., & Singmann, H. (2015). *lme4: Linear mixed-effects models using Eigen and S4*, *2014*. R package version 1.1-9.

Bongers, T. (1990). The maturity index: An ecological measure of environmental disturbance based on nematode species composition. *Oecologia*, *83*, 14–19. https://doi.org/10.1007/BF00324627

Bongers, T., & Ferris, H. (1999). Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology & Evolution*, *14*, 224–228. https://doi.org/10.1016/S0169-5347(98)01583-3

Bormann, F. H., & Likens, G. E. (1967). Nutrient cycling. *Science*, *155*, 424–429. https://doi.org/10.1126/science.155.3761.424

Brooker, R. W., Travis, J. M., Clark, E. J., & Dytham, C. (2007). Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, *245*, 59–65. https://doi.org/10.1016/j.jtbi.2006.09.033

Cheng, Y., Wang, J., Wang, J., Chang, S. X., & Wang, S. (2017). The quality and quantity of exogenous organic carbon input control microbial NO_3^- immobilization: A meta-analysis. *Soil Biology and Biochemistry*, *115*, 357–363. https://doi.org/10.1016/j.soilbio.2017.09.006

Conant, R. T., Ryan, M. G., Ågren, G. I., Birge, H. E., Davidson, E. A., Eliasson, P. E., Evans, S. E., Frey, S. D., Giardina, C. P., Hopkins, F. M., Hyvönen, R., Kirschbaum, M. U. F., Lavallee, J. M., Leifeld, J., Parton, W. J., Megan Steinweg, J., Wallenstein, M. D., Martin Wetterstedt, J. Å., & Bradford, M. A. (2011). Temperature and soil organic matter decomposition rates–synthesis of current knowledge and a way forward. *Global Change Biology*, *17*, 3392–3404. https://doi.org/10.1111/j.1365-2486.2011.02496.x

Curiel Yuste, J., Baldocchi, D. D., Gershenson, A., Goldstein, A., Misson, L., & Wong, S. (2007). Microbial soil respiration and its dependency on

carbon inputs, soil temperature and moisture. *Global Change Biology*, *13*,2018–2035.https://doi.org/10.1111/j.1365-2486.2007.01415.x

Delarze, R., Gonseth, Y., Eggenberg, S., & Vust, M. (2015). *Guide des milieux naturels de Suisse*. Rossolis.

Delgado-Baquerizo, M., Gallardo, A., Covelo, F., Prado-Comesaña, A., Ochoa, V., & Maestre, F. T. (2015). Differences in thallus chemistry are related to species-specific effects of biocrust-forming lichens on soil nutrients and microbial communities. *Functional Ecology*, *29*, 1087–1098. https://doi.org/10.1111/1365-2435.12403

Delgado-Baquerizo, M., Maestre, F. T., Reich, P. B., Jeffries, T. C., Gaitan, J. J., Encinar, D., Berdugo, M., Campbell, C. D., & Singh, B. K. (2016). Microbial diversity drives multifunctionality in terrestrial ecosystems. *Nature Communications*, *7*, 1–8. https://doi.org/10.1038/ncomms10541

Descombes, P., Pitteloud, C., Glauser, G., Defossez, E., Kergunteuil, A., Allard, P.-M., Rasmann, S., & Pellissier, L. (2020). Novel trophic interactions under climate change promote alpine plant coexistence. *Science*, *370*, 1469–1473. https://doi.org/10.1126/science.abd7015

Descombes, P., Vittoz, P., Guisan, A., & Pellissier, L. (2017). Uneven rate of plant turnover along elevation in grasslands. *Alpine Botany*, *127*, 53–63. https://doi.org/10.1007/s00035-016-0173-7

Djukic, I., Zehetner, F., Tatzber, M., & Gerzabek, M. H. (2010). Soil organic-matter stocks and characteristics along an Alpine elevation gradient. *Journal of Plant Nutrition and Soil Science*, *173*, 30–38. https://doi.org/10.1002/jpln.200900027

Dray, S., & Dufour, A. B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.

Egli, M., Sartori, G., Mirabella, A., Favilli, F., Giaccai, D., & Delbos, E. (2009). Effect of north and south exposure on organic matter in high Alpine soils. *Geoderma*, *149*, 124–136. https://doi.org/10.1016/j.geoderma.2008.11.027

Ferris, H. (2010). Form and function: Metabolic footprints of nematodes in the soil food web. *European Journal of Soil Biology*, *46*, 97–104. https://doi.org/10.1016/j.ejsobi.2010.01.003

Ferris, H., Bongers, T., & de Goede, R. G. M. (2001). A framework for soil food web diagnostics: Extension of the nematode faunal analysis concept. *Applied Soil Ecology*, *18*, 13–29. https://doi.org/10.1016/S0929-1393(01)00152-4

Fierer, N. (2017). Embracing the unknown: Disentangling the complexities of the soil microbiome. *Nature Reviews Microbiology*, *15*, 579–590. https://doi.org/10.1038/nrmicro.2017.87

García-Palacios, P., Maestre, F. T., Bardgett, R. D., & De Kroon, H. (2012). Plant responses to soil heterogeneity and global environmental change. *Journal of Ecology*, *100*, 1303–1314. https://doi.org/10.1111/j.1365-2745.2012.02014.x

Heimann, M., & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, *451*, 289–292. https://doi.org/10.1038/nature06591

Hille, S. M., & Cooper, C. B. (2015). Elevational trends in life histories: Revising the pace-of-life framework. *Biological Reviews*, *90*, 204–213. https://doi.org/10.1111/brv.12106

Insam, H. (1997). A new set of substrates proposed for community characterization in environmental samples. In H. Insam & A. Rangger (Eds.), *Microbial communities: Functional versus structural approaches* (pp. 259–260). Springer.

Johnson, L. C., Galliart, M. B., Alsdurf, J. D., Maricle, B. R., Baer, S. G., Bello, N. M., Gibson, D. J., & Smith, A. B. (2021). Reciprocal transplant gardens as gold standard to detect local adaptation in grassland species: New opportunities moving into the 21st century. *Journal of Ecology*, (1), 1–18. https://doi.org/10.1111/1365-2745.13695

Kergunteuil, A., Campos-Herrera, R., Sánchez-Moreno, S., Vittoz, P., & Rasmann, S. (2016). The abundance, diversity and metabolic footprint of soil nematodes is highest in high elevation alpine grasslands. *Frontiers in Ecology and Evolution*, *4*, 1–12. https://doi.org/10.3389/fevo.2016.00084

Klanderud, K., Vandvik, V., & Goldberg, D. (2015). The importance of biotic vs. abiotic drivers of local plant community composition along regional bioclimatic gradients. *PLoS ONE*, *10*, e0130205.

Knowles, J. F., Blanken, P. D., & Williams, M. W. (2015). Soil respiration variability across a soil moisture and vegetation community gradient within a snow-scoured alpine meadow. *Biogeochemistry*, *125*, 185–202. https://doi.org/10.1007/s10533-015-0122-3

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2015). *Package 'lmerTest'*. R package version, 2.

Looby, C. I., & Treseder, K. K. (2018). Shifts in soil fungi and extracellular enzyme activity with simulated climate change in a tropical montane cloud forest. *Soil Biology and Biochemistry*, *117*, 87–96. https://doi.org/10.1016/j.soilbio.2017.11.014

Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., Huaraca Huasco, W., Silva-Espejo, J. E., Aguilla-Pasquell, J., Farfán Amézquita, F., Aragão, L. E. O. C., Guerrieri, R., Ishida, F. Y., Bahar, N. H. A., Farfan-Rios, W., Phillips, O. L., Meir, P., & Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: A whole carbon budget perspective. *New Phytologist*, *214*, 1019–1032. https://doi.org/10.1111/nph.14189

Margesin, R., Jud, M., Tscherko, D., & Schinner, F. (2009). Microbial communities and activities in alpine and subalpine soils. *FEMS Microbiology Ecology*, *67*, 208–218. https://doi.org/10.1111/j.1574-6941.2008.00620.x

Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., & Bugmann, H. (2018). Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports*, *8*, 5627. https://doi.org/10.1038/s41598-018-23763-y

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Wagner, H. (2013). *vegan: Community ecology package*. Retrieved from http://vegan.r-forge.r-project.org/

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pellissier, L., Niculita-Hirzel, H., Dubuis, A., Pagni, M., Guex, N., Ndiribe, C., Salamin, N., Xenarios, I., Goudet, J., Sanders, I. R., & Guisan, A. (2014). Soil fungal communities of grasslands are environmentally structured at a regional scale in the Alps. *Molecular Ecology*, *23*, 4274–4290. https://doi.org/10.1111/mec.12854

Pellissier, L., & Rasmann, S. (2018). The functional decoupling of processes in alpine ecosystems under climate change. *Current Opinion in Insect Science*, *29*, 126–132. https://doi.org/10.1016/j.cois.2018.07.005

Pitteloud, C., Walser, J. C., Descombes, P., Novaes De Santana, C., Rasmann, S., & Pellissier, L. (2021). The structure of plant–herbivore interaction networks varies along elevational gradients in the European Alps. *Journal of Biogeography*, *48*, 465–476. https://doi.org/10.1111/jbi.14014

R Development Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rasmann, S., Semeraro, S., Kergunteuil, A., Sánchez-Moreno, S., Puissant, J., Goodall, T., & Griffiths, R. (2021). Dataset for: Relative contribution of high and low elevation soil microbes and nematodes to ecosystem functioning. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.hhmgqnkhv

Rubenstein, M. A., Crowther, T. W., Maynard, D. S., Schilling, J. S., & Bradford, M. A. (2017). Decoupling direct and indirect effects of temperature on decomposition. *Soil Biology and Biochemistry*, *112*, 110–116. https://doi.org/10.1016/j.soilbio.2017.05.005

Sánchez-Moreno, S., Minoshima, H., Ferris, H., & Jackson, L. E. (2006). Linking soil properties and nematode community composition: Effects of soil management on soil food webs. *Nematology*, *8*, 703–715. https://doi.org/10.1163/156854106778877857

Sieriebriennikov, B., Ferris, H., & De Goede, R. G. M. (2014). NINJA: An automated calculation system for nematode-based biological monitoring. *European Journal of Soil Biology*, *61*, 90–93. https://doi.org/10.1016/j.ejsobi.2014.02.004

Standing, D., Knox, O. G. G., Mullins, C. E., Killham, K. K., & Wilson, M. J. (2006). Influence of nematodes on resource utilization by bacteria—An in vitro study. *Microbial Ecology*, *52*, 444–450. https://doi.org/10.1007/s00248-006-9119-8

Stige, L. C., & Kvile, K. Ø. (2017). Climate warming drives large-scale changes in ecosystem function. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 12100–12102. https://doi.org/10.1073/pnas.1717090114

Trivedi, P., Delgado-Baquerizo, M., Anderson, I. C., & Singh, B. K. (2016). Response of soil properties and microbial communities to agriculture: Implications for primary productivity and soil health indicators. *Frontiers in Plant Science*, *7*, 990. https://doi.org/10.3389/fpls.2016.00990

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*, 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Van Den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., de Goede, R. G. M., Adams, B. J., Ahmad, W., Andriuzzi, W. S., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Cares, J. E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., … Crowther, T. W. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature*, *572*, 194–198. https://doi.org/10.1038/s41586-019-1418-6

van der Heijden, M. G. A., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., & Sanders, I. R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, *396*, 69–72. https://doi.org/10.1038/23932

van der Putten, W. H., de Ruiter, P. C., Martijn Bezemer, T., Harvey, J. A., Wassen, M., & Wolters, V. (2004). Trophic interactions in a changing world. *Basic and Applied Ecology*, *5*, 487–494. https://doi.org/10.1016/j.baae.2004.09.003

Venturi, V., & Keel, C. (2016). Signaling in the rhizosphere. *Trends in Plant Science*, *21*, 187–198. https://doi.org/10.1016/j.tplants.2016.01.005

Wagg, C., Bender, S. F., Widmer, F., & van der Heijden, M. G. A. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 5266–5270. https://doi.org/10.1073/pnas.1320054111

Wardle, D. A. (2002). *Communities and ecosystems: Linking the aboveground and belowground components*. Princeton University Press.

Yeates, G. W., Ferris, H., Moens, T., & van der Putten, W. H. (2009). Role of nematodes in ecosystems. In M. J. Wilson & T. Kakouli-Duarte (Eds.), *Nematodes as environmental indicators* (pp. 1–44). CAB International.

Yiqi, L., & Zhou, X. (2010). *Soil respiration and the environment*. Elsevier.

Zak, D. R., Holmes, W. E., White, D. C., Peacock, A. D., & Tilman, D. (2003). Plant diversity, soil microbial communities, and ecosystem function: Are there any links? *Ecology*, *84*, 2042–2050. https://doi.org/10.1890/02-0433

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