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A Large Fraction of Soil Microbial Taxa Is Sensitive to Experimental Warming

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ABSTRACT

Global warming is expected to significantly impact the soil fungal and bacterial microbiomes, yet the predominant ecological response of microbial taxa—whether an increase, decrease, or no change—remains unclear. It is also unknown whether microbial taxa from different evolutionary lineages exhibit common patterns and what factors drive these changes. Here, we analyzed three mid-term (> 5 years) warming experiments across contrasting dryland and temperate-boreal ecosystems, encompassing over 500 topsoil samples collected across multiple time points. We found that warming altered the relative abundance of microbial taxa, with both increases and decreases over time. For instance, the relative abundance of bacterial and fungal taxa responding to warming (increase or decrease) accounted for 35.9% and 42.9% in the dryland ecosystem, respectively. Notably, taxa within the same phylum exhibited divergent responses to warming. These ecological shifts were linked to factors such as photosynthetic cover and fungal lifestyle, both of which influence soil functions. Overall, our findings indicate that soil warming can reshape a significant fraction of the microbial community across ecosystems, potentially driving changes in soil functions.

1 | Introduction

Global warming is one of the main components of ongoing climate change, and its social, ecological, and economic impacts constitute one of the major challenges facing humanity (Rosenzweig et al. 2008). The Paris Climate Agreement, based on climate scenarios that predict a minimum global warming of 2°C over this century (Roberts et al. 2022), makes it clear that even a small increase in temperature can have critical consequences for human welfare and for the sustainability of ecosystems on Earth. The magnitude of ongoing global warming is particularly important for soil-atmosphere carbon feedback, which is mainly regulated by microbial communities (de Vries and Griffiths 2018). Yet, despite the critical importance of warming for soil microbial communities, we still lack the most basic information on what proportion of individual soil microbial taxa respond to mid-term (> 5 years) warming across different ecosystems.

A considerable number of studies have examined how increased temperature alters soil microbial communities in field experiments (Nottingham et al. 2019; Purcell et al. 2023; Ruan et al. 2023). For example, a recent study on long-term soil warming (+6°C) found that warming increased the number of active bacterial taxa rather than simply accelerating overall population growth (Metze et al. 2024). However, there are no measurements spanning from weeks to years that focus on how individual soil taxa of contrasting evolutionary origins respond to soil warming across longitudinally distributed experiments. Moreover, most studies conducted so far have coarsely grouped their responses at the community or phyla level (Guo et al. 2018; Liang et al. 2015). This clustering into higher groups leads to large uncertainties regarding whether the effects of warming on individual microbial taxa could be taxon specific. Emerging evidence also suggests that soil communities show phylogenetically conserved responses to other global change factors (e.g., nitrogen addition and drought) (Amend et al. 2016; Isobe et al. 2019; Yu et al. 2023). However, whether similar patterns are observed in response to soil warming remains largely unknown under field experimental conditions (Oliverio et al. 2017). Filling these knowledge gaps is key because soils harbor highly diverse microbial communities that regulate essential ecosystem processes and services, from nutrient cycling to climate regulation (Bardgett and van der Putten 2014; Delgado-Baquerizo et al. 2016). Finally, since short-term experiments (weeks to months) might fail to capture some of the mechanisms occurring over longer timescales (Hartmann et al. 2017), data from multiple years are needed to draw solid conclusions on the responses of microbial communities to soil warming.

Here, we studied the response of soil bacterial and fungal communities to warming in a dryland ecosystem (2.5°C) and two temperate-boreal forest ecotones (1.8°C and 3.4°C). These three longitudinally distributed experiments were sampled multiple times for 5 years or more. To investigate whether individual soil taxa show general patterns to warming, we characterized three ecological responses based on changes in the relative abundance of zOperational Taxonomic Units (zOTUs defined at 100% sequence similarity): non-significant ('unchanged'), significant increases ('opportunistic'), or significant decreases ('vulnerable') (see Figure 1A for the conceptual framework and ref. (Evans and Wallenstein 2014) for a similar approach based on drought effects). Our sampling design accounted for temporal variation by incorporating a nested permutational multivariate analysis of variance (PERMANOVA) stratified by years (random factor). This approach allowed us to control for temporal variability without explicitly exploring interactions between warming and time, ensuring that the classification of each zOTU was based solely on its response to warming.

Soil microbiome might exhibit high resistance to soil warming due to its extensive genetic diversity and short generation times enabling their rapid evolution (Chase et al. 2021), but the potential for microbial evolution and adaptation to environmental changes is vast and contradictory (Alster et al. 2023; Romero-Olivares et al. 2017). In fact, previous studies indicate that the soil microbiome is sensitive to mid-term severe warming (5°C) (DeAngelis et al. 2015), yet a comprehensive understanding of the underlying mechanisms driving these changes remains unknown. We posit that experimental warming could lead to significant increases or decreases in the presence and/or abundance of multiple individual soil taxa, driven by differences in microbial physiology (e.g., fungal lifestyle) (Bradford 2013) or to changes in environmental factors (e.g., rising temperatures modifying the cover of photosynthetic organisms, which could ultimately disrupt the link between soil microbial communities and vegetation: Bragazza et al. 2015). For instance, the most recent evidence indicates that warmer temperatures will increase the relative abundance of soil-borne potential fungal plant pathogens on a global scale (Singh et al. 2023). As such, the taxa comprising the new soil microbial community could be at least partially responsible for changes in ecosystem functions in response to soil warming. Toward this aim, we explored whether fungal lifestyle following opportunistic and vulnerable responses could be linked to important soil functions (enzyme activities and soil respiration rates). The use of multiple experiments with multiple sampling years offers a unique opportunity to understand how individual microbial taxa respond to warming in different contexts.

2 | Materials and Methods

2.1 | Study Area

This research was conducted in three sites, one located in central Spain (Aranjuez, dryland ecosystem) and two in northern Minnesota (Cloquet and Ely, old mixed aspen-birch-fir forests of 40–60 years representing the transition from temperate to boreal biomes) (Figure S1). In Aranjuez (Maestre et al. 2013), we implemented a fully factorial design with three treatment factors, each comprising two levels: biocrust cover (poorly developed biocrust communities with cover < 20% vs. well-developed biocrust communities with cover > 50%), warming (control vs. 2.5°C), and rainfall exclusion (control vs. 33% rainfall reduction). The full experiment has been running continuously since August 2008, with two soil samplings conducted in 2012 and 2017. To minimize sampling disturbance, soil collection points were randomly selected. At each sampling, composite soil samples were obtained by taking five (0–1 cm depth) soil cores. In total, there were 80 surface samples (40 samples × 2 years) that were sieved through a 2 mm mesh. At both USA sites (see refs.

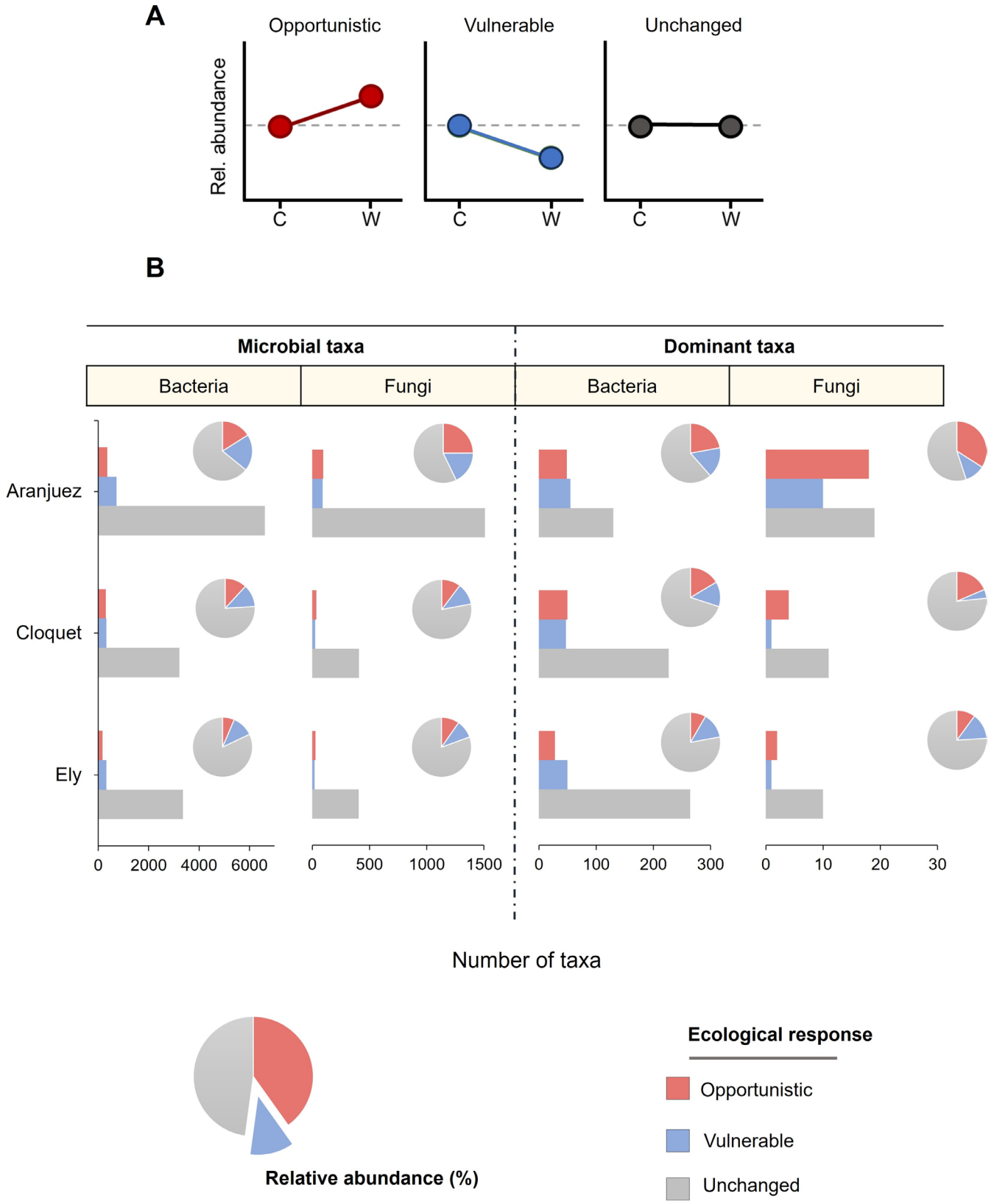

FIGURE 1 | Ecological responses of soil microbes across experimental sites. Panel A encompasses three ecological responses included in our study, which are based on changes in the relative abundance of microbial taxa (C = control; W = warming). Panel B depicts the number of taxa and the percentage of relative abundance (pie chart) for three ecological responses included in our research. Pie charts represent the sum of the three ecological responses (opportunistic, vulnerable, and unchanged) across all years for each site. The dominant taxa are defined as the top 10% most common phylotypes (sorted by their percentage) that are found in more than half of the evaluated soil samples.

Reich et al. 2015, 2016; Rich et al. 2015 for further details), the overall experimental design was a 3 three-level warming treatment (control, +1.8°C, +3.4°C)×2 understory and open conditions (~5%–10% and 40%–60% of full light, respectively)×2 rainfall treatment (control vs. ≈40% exclusion implemented only in open canopy conditions). Our experimental design consisted of six blocks per site and has been running continuously since August 2010. Each block included two replicates per warming level (control, +1.8°C, and +3.4°C). We collected six samples per block annually, repeating this process over 6 years (sampling years: 2010, 2012, 2013, 2015, 2016, and 2017). This resulted in a total of 216 samples per site (6 blocks×6 samples×6 years) that were sieved through a 2 mm mesh. However, 4 soil samples were lost due to handling issues (2 per site), reducing the total number of samples available for analysis to 214 per site. At each sampling, composite soil samples were obtained by taking three soil cores (0–7 cm depth). Data sources can be found in Sáez-Sandino and Delgado-Baquerizo n.d. (2025): https://figshare.com/articles/dataset/A_large_fraction_of_soil_microbial_taxa_is_sensitive_to_experimental_warming/27691290 https://figshare.com/s/eea8b456782c3d152397

At the Aranjuez site, warming was achieved using hexagonal open-top chambers (40 cm × 50 cm × 32 cm). Air and shallow soil (0–2 cm) temperatures were recorded continuously with automated sensors (HOBO U23 Pro v2 Temp/RH and TMC20-HD, Onset Corp., USA). To simulate changes in rainfall, we set up passive rainfall shelters that do not modify the frequency of rainfall events but effectively reduce the total amount of rainfall reaching the soil surface (average reduction of 33%). B4WarmED (Cloquet and Ely sites) is an open-air warming experiment featuring 3 m diameter circular plots planted with a mix of boreal and temperate tree seedlings (11–17 species per cohort, varying by canopy type). Each plot contains 8–10 replicates per species, arranged in a randomized 30 cm grid. Annual warming treatments, applied from early spring to late fall, combine infrared lamp heaters and soil heating cables to elevate temperatures. An automated microprocessor-based feedback system maintains target aboveground (leaf-level) and belowground (10 cm depth) temperatures. This system continuously monitors sensor data, calculates real-time heating requirements, and adjusts power output via dimmer-controlled heaters to sustain consistent warming differentials relative to ambient plots. In 2012, a drought treatment was added to half of the open-canopy plots, reducing summer precipitation (June 1–September 30) by ~40% using retractable rainout shelters. Each shelter consists of a 4.5×4.5 m tarp suspended 4 m aboveground, deployed manually ~15 min before precipitation events and retracted immediately afterward to minimize shading effects.

2.2 | Cover of Photosynthetic Organisms

In Aranjuez, the cover of bryophytes and lichens was measured at each plot using a PVC collar (20 cm diameter, 8 cm height) inserted 5 cm into the soil. We then used high-resolution photographs to estimate the total cover of the biocrust community within each collar at various time intervals, with yearly samplings conducted between 2012 and 2017. To determine the proportion of lichen and moss cover, we mapped their areas using software tools such as GIMP (http://www.gimp.org/) and ImageJ (http://rsb.info.nih.gov/ij/) from these photographs. Cover estimates obtained with this method were highly related to those measured directly in the field (Maestre et al. 2013; Ladrón de Guevara et al. 2018). In Cloquet and Ely, the plant cover was determined by two independent surveys performed yearly approximately at the end of the peak of the growing season. During the first survey, we censused all transplanted seedlings for their presence and survival in those plots. In the second survey, we estimated the occurrence and % of cover of all plants present in our research plots. We then calculated the percentage of ectomycorrhizal using the FungalRoots database (Soudzilovskaia et al. 2020), which determines mycorrhizal status for plant genera.

2.3 | Soil Respiration Rates

In Aranjuez, soil respiration rates were measured in situ since the beginning of the experiment (2010) and continuously every 1–4 months using PVC collars with a closed dynamic system (Li-8100 Automated Soil CO2 Flux System, Li-COR, Lincoln, NB, USA). Here, we used the average annual respiration rates that coincide with the years of soil sampling (2012 and 2017). These measurements encompassed both the biocrusts living on their surface and the entire soil community associated with them. The chamber employed for these measurements effectively prevents any radiation from reaching the biocrusts, and given these conditions, we anticipate that carbon fixation, if it occurs at all, would be minimal. Moreover, due to the generally low CO_2 efflux rates in regions like the ones we studied (as documented in ref. Rey et al. 2011), each measurement period lasted 120 s to ensure reliable measurements. For further details, see ref. (Maestre et al. 2013). In Cloquet and Ely, soil respiration was measured biweekly since the inception of the experiment throughout the warming season (from April to November, approximately) using a LI-COR 6400 (LI-COR Biosciences Inc.). The measurements were done at each research plot (a total of 72) on two randomly installed PVC collars. Before each measurement of soil respiration, we ensured that living plants and litterfall inside the PVC collar were removed.

2.4 | Enzyme Activities

We assessed the activity of two extracellular enzymes in every soil sample: β-glucosidase (sugar degradation) and phosphatase (phosphorus mineralization). These activities were determined using 1 g of soil through fluorometry (Bell et al. 2013).

2.5 | Soil Molecular Analyses

For Aranjuez samples, soil DNA was extracted from 1 g of defrosted soil samples using the Canvax Soil DNA Isolation Kit (Canvax Biotech, S.L., Córdoba, Spain), and for Cloquet and Ely, 0.5 g of defrosted soil samples were extracted using the Power soil DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, CA, USA), according to the instructions provided by the manufacturers. For bacterial communities, the V3-V4 region of the 16S rRNA gene was amplified using 341F (CCTACGGGNGGCWGCAG) and 805R (GACTACHVGGGTATCTAATCC) (Ihrmark et al. 2012).

For fungal communities, the ITS2 region was amplified with primers fITS7 (GTGARTCATCGAATCTTTG) and ITS4 (TCCTCCGCTTATTGATATGC). DNA extracts (PCR parameters detailed in Table S6) were sequenced on an Illumina MiSeq platform (Caporaso et al. 2012) at the Next Generation Genome Sequencing Facility at Western Sydney University (NSW, Australia). Initial sequence processing and diversity analyses for both bacterial 16S rDNA and fungal ITS2 region were performed using the QIIME package (Caporaso et al. 2010). Taxonomy for 16S rDNA zOTUs and fungal ITS sequences was assigned using UCLUST against the Greengenes database (DeSantis et al. 2006; McDonald et al. 2012) and BLAST (Altschul et al. 1990) against the UNITE database (Version 6.9.7; Amelung et al. 2020), respectively. Sequences were clustered into soil phylotypes (i.e., zOperational Taxonomic Units; zOTUs) using a 100% identity level, and the number of phylotypes (richness) was measured from zOTUs read tables: 8550 (bacteria via 16S rRNA gene in Aranjuez), 4576 (bacteria via 16S rRNA gene in Cloquet and Ely), 2155 (fungi via ITS2 region in Aranjuez), and 576 (fungi via ITS2 region in Cloquet and Ely). Fungal lifestyles were determined using the FungalTraits database (http://www.stbates.org/guilds/app.php; accessed December 2022) (Põlme et al. 2020). A complete list of the soil phylotypes, ecological responses, and fungal lifestyles included in this study can be found in Supporting Information Data S1.

2.6 | Phylogenetic Analysis

Amplicon sequences, taxonomy data, and phylogenetic tree were used for community analyses using "Phyloseq" package (McMurdie and Holmes 2013). We show the relationship between ecological responses of microbial taxa to warming with two phylogenetic trees (bacterial and fungal communities) with colored rings with a cladistic perspective (Figure 3). For this, sequences were aligned using the online tool Silva Incremental Aligner (Pruesse et al. 2012) enabling the options "Search and Classify" and "Compute Tree" to search and obtain the most similar sequences (closest neighbors) from Silva SSU database (Silva SSU 138 release). We then reconstruct phylogenetic trees using the tree of neighbor sequences as a reference. This method is recommended to obtain a more robust and consistent tree hypothesis when the sequences are short. Visualization and annotation of the trees were made with the online tool iTol (Letunic and Bork 2019).

2.7 | Statistical Analyses

2.7.1 | Ecological Responses Classification

First, we analyzed each experiment separately due to methodological differences among stations (e.g., Ely and Cloquet lack biocrust cover). Rather than merging the data, our goal was to determine whether microbial taxa responses to warming were consistent across the three experiments. To quantify the responses of microbial taxa considered in our study (opportunistic, vulnerable, and unchanged), we grouped bacteria and fungi assigned to operational taxonomical units (zOTUs, at 100% similarity). We first rarefied (3500 reads) to ensure our choice is not obscuring our results and calculated the relative abundance (%) as the number of zOTU reads divided by the total number of reads (and multiplied by 100) for each soil sample. We used permutational multivariate analysis of variance (PERMANOVA with 'adonis2' function in the "vegan" R package) (Oksanen 2020) and the term "strata" (time) to classify the ecological responses of each zOTU to soil warming. PERMANOVA analyses can be applied to both multivariate and univariate data (Anderson 2001), do not require the assumption of homogeneity of variances (homoscedasticity), and have fewer assumptions (e.g., they do not require data to follow normal distributions). Moreover, PERMANOVA analyses allow for the examination of the individual response of each zOTU to warming using distance matrices. The independent evaluation of each zOTU (i.e., individualized analyses generate a unique set of permutations for each zOTU) and the control of temporal heterogeneity through stratification reduce the likelihood of false positives. In this context, our time-stratified analyses allow us to account for temporal variability in the response of microbial communities to warming. By stratifying the data by year, we controlled temporal variability uniformly across sites (soil samples were collected in different years at each experimental location), thereby enhancing the interpretability of our results. Here, we also used Euclidean distance (the same distance metric employed in Labouyrie et al. 2023, and Metze et al. 2024) due to several reasons: (i) our analysis focuses on assessing the response of each taxon individually (univariate data) to warming, and (ii) Bray-Curtis can produce very low or even indeterminate dissimilarities when some values in the dataset are zero, a common issue in soil microbiome studies (e.g., see GlobalFungi database available at https://globalfungi.com/). In our dataset, some microbial taxa were present in only a few samples, which means that dissimilarity calculations may not accurately capture real differences and could distort the interpretation of variation between samples.

No significant changes were defined as 'unchanged' ($p > 0.05$). If the zOTUs showed a significant response to warming ($p < 0.05$), we applied generalized linear models (GLM) to calculate their coefficients and determine whether the responses of each zOTU were positive or negative in relation to warming (Figure 2). Thus, zOTUs that showed significant responses to warming with a positive (increase in relative abundance) or negative (decrease in relative abundance) coefficient were classified as 'opportunistic' and 'vulnerable', respectively. We excluded any zOTUs that showed a significant interaction between warming and treatment (e.g., warming × rainfall exclusion) from our analyses to focus only on those taxa related to soil warming. We excluded any zOTUs that exhibited a significant interaction between warming and treatment (e.g., warming × rainfall exclusion, warming × canopy) from our analyses to focus solely on taxa directly related to soil warming. Including such interactions would obscure the direct relationship between the relative abundance of microbial taxa and soil warming.

To further test the robustness of our results, we also repeated our analysis for Cloquet and Ely using block as a stratification variable (Aranjuez site lacked a block control design). Our results using block as a stratification variable still support the idea that a substantial fraction of microbial taxa is sensitive to temperature increases (Figure S9). Moreover, our results based on the block-stratification approach also indicate that bacteria and fungi belonging to the same phylum can exhibit

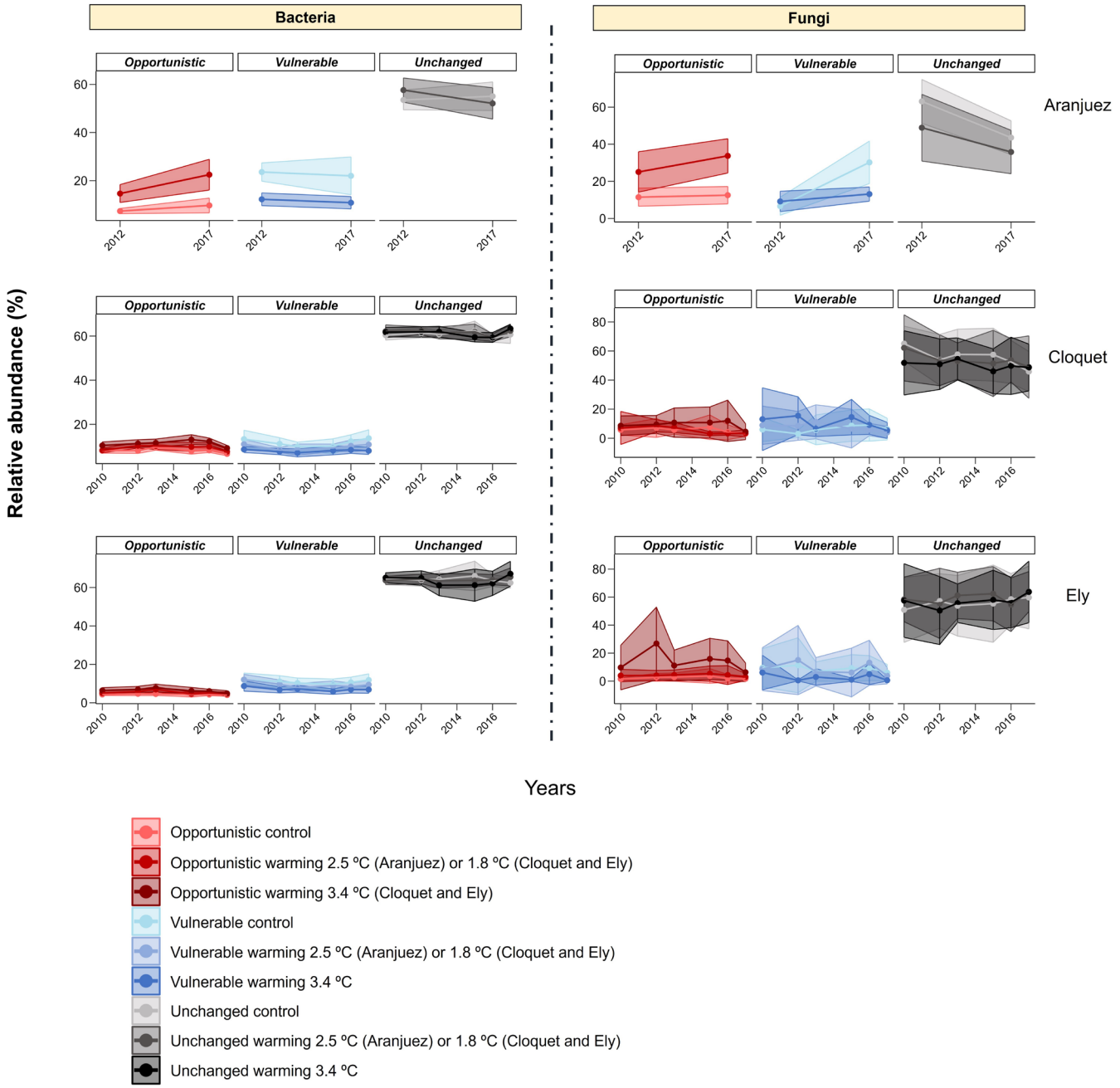

FIGURE 2 | Soil ecological responses across treatment and experimental sites. The *y*-axis shows the sum of the relative abundance (%) in each year (*x*-axis) across all soil samples in our study. The color scheme represents the relative abundance of each ecological response (shading indicating the standard deviation for each year).

different ecological responses to survive warming stress (Figure S10). We then found that Pearson correlation analyses ($p < 0.05$) showed a strong relationship between the relative abundance of microbial communities when either year or block was used as the stratification variable (Figure S11). Our findings indicated that microbial taxa responding to warming (opportunistic and vulnerable) always showed a positive and significant correlation. For instance, bacterial taxa with opportunistic ($\rho = 0.853$ in Cloquet; $\rho = 0.724$ in Ely) and vulnerable responses ($\rho = 0.889$ in Cloquet; $\rho = 0.799$ in Ely) showed near-perfect correlations. These findings confirm that our year-stratified approach is robust and that both methods effectively capture microbial responses to warming. While we acknowledge that spatial dependence is not fully eliminated using year as a stratification variable, microbial communities and soil properties are known to shift over time due to warming effects in our experimental sites (e.g., Fernandez et al. 2023; Thakur et al. 2018), likely introducing substantial interannual variability among samples.

2.7.2 | Relationships Between Cover of Photosynthetic Organisms and Ecological Responses

We first used PERMANOVA to determine if soil warming causes significant changes in the cover of photosynthetic

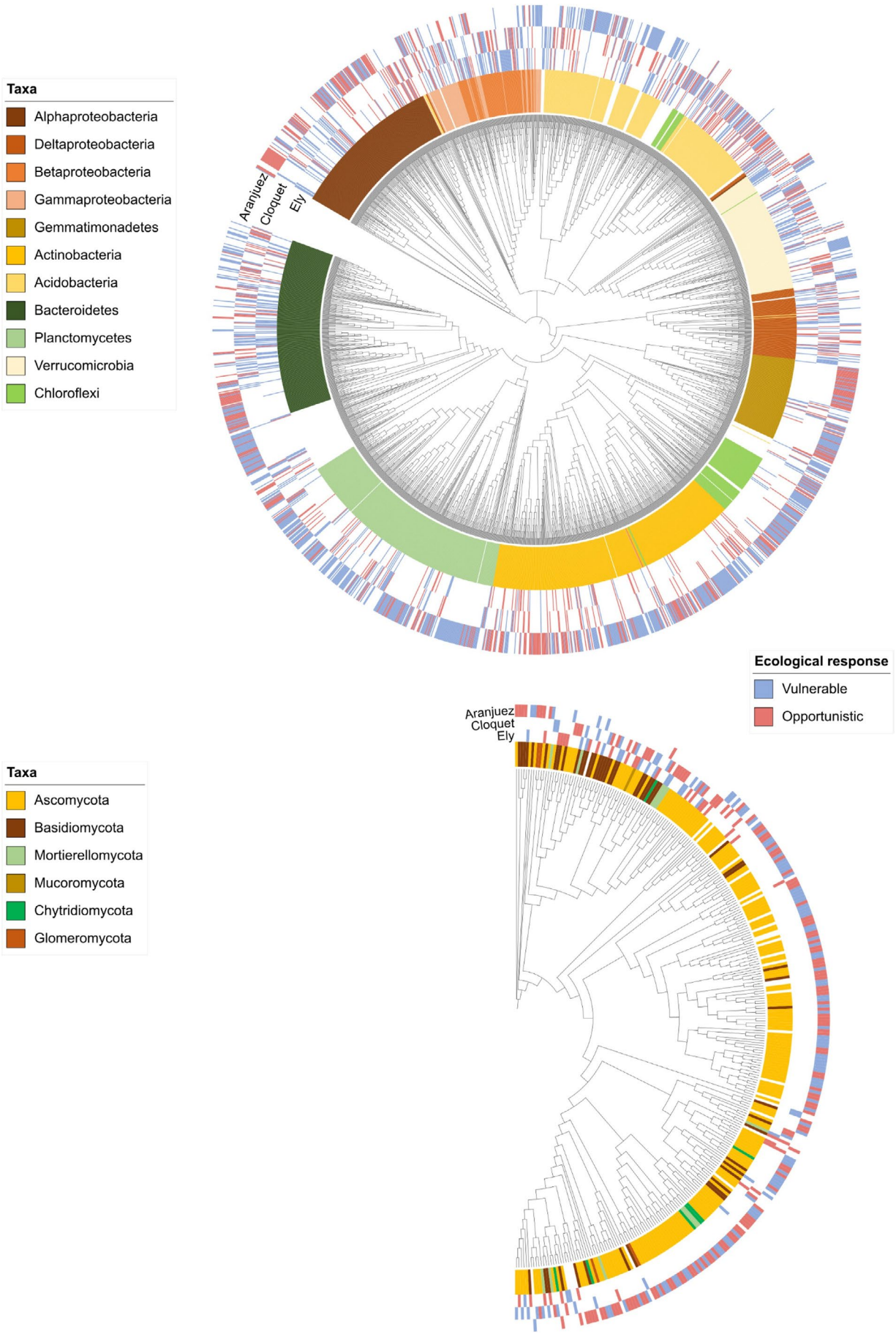

FIGURE 3 | Legend on next page.

FIGURE 3 | Phylogenetic distribution across experimental sites. Bacterial and fungal phylotypes from Aranjuez (outer ring), Cloquet (middle ring), and Ely (inner ring) are shown. The different rings show the phylum-level taxonomy of zOTUs (see Methods).

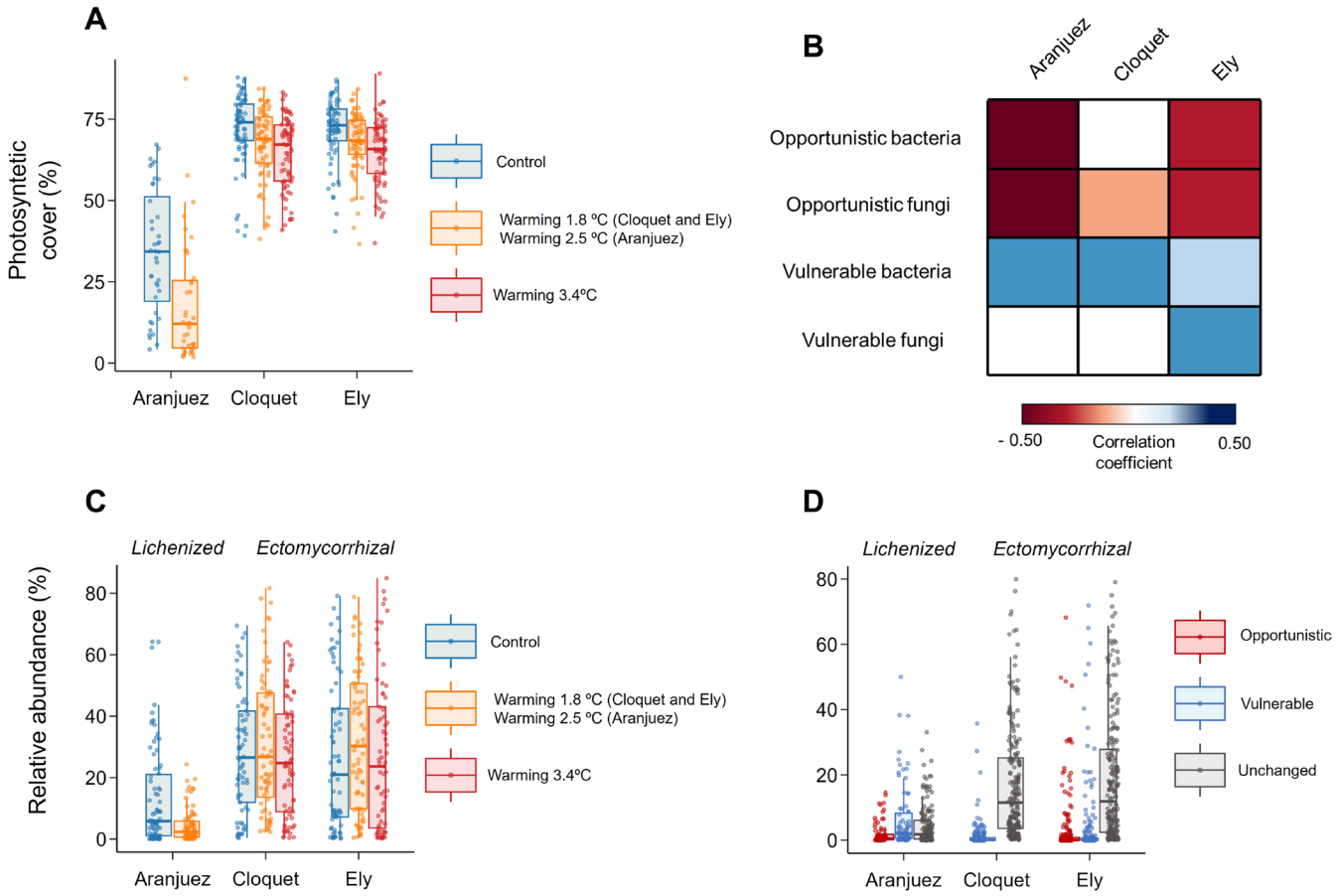

FIGURE 4 | Contribution of the cover of photosynthetic organisms and fungal lifestyle to ecological responses. Panel A shows the percentage of cover of photosynthetic organisms across different treatments (control vs. warming) and sites. Panel B shows Spearman correlations between the cover of photosynthetic organisms and the relative abundance of opportunistic and vulnerable responses across sites. Panel C shows the relative abundance of two fungal lifestyles across different treatments (control vs. warming) and sites. Panel D shows the relative abundance of two fungal lifestyles across ecological responses (opportunistic, vulnerable, and unchanged) and sites. See Tables S1–S5 for statistical analysis.

organisms across experimental sites (Figure 4A). We then used non-parametric Spearman rank correlations, which do not require the normality of data or homogeneity of variances, to observe the relationship between the cover of photosynthetic organisms and ecological responses with changes to warming (i.e., opportunistic and vulnerable) (Figure 4B). Significant correlations between both variables suggest that changes in the cover of photosynthetic organisms caused by warming could be directly related to the ecological responses of soil microbes.

2.7.3 | Relationships Between Fungal Lifestyle and Ecological Responses

We also conducted PERMANOVA to determine whether fungal lifestyles exhibited significant changes in relative abundance under warming (Figure 4C and Figure S7) across experimental sites. The same statistical analysis was used to determine which ecological response is most dominant within each fungal lifestyle (Figure 4D and Figure S8).

2.7.4 | Links Between Soil Functions and Fungal Lifestyle Exhibiting Different Ecological Responses

We further employed Spearman rank correlations to explore the potential associations between fungal lifestyle and opportunistic and vulnerable responses and soil functions (enzyme activities and soil respiration rates) (Figure 5A). By using Spearman correlations, we aimed to identify the most important trends in our results and measure the strength and direction of the association between these two ranked variables.

3 | Results & Discussion

3.1 | Ecological Responses of Soil Microbes Under Warming Scenarios

Our analyses revealed that the mid-term increases in temperature promoted by experimental warming can alter a significant portion of the individual taxa within the soil

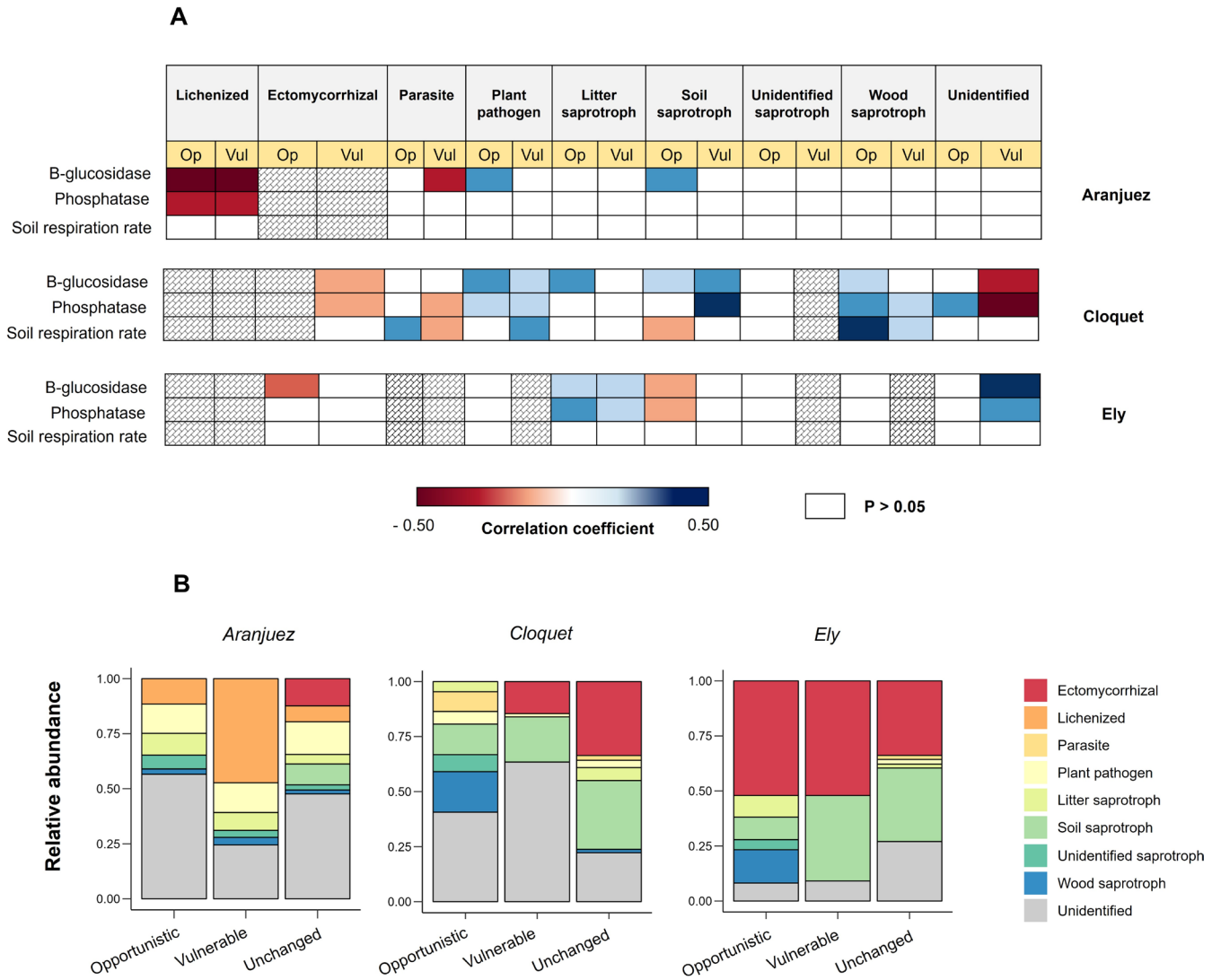

FIGURE 5 | Relationships between fungal lifestyles with opportunistic and vulnerable responses to warming and soil functions. Panel A displays the strength and direction of the Spearman correlation coefficients. Crossed-out cells indicate that no microbes (zOTUs) showed the fungal lifestyle with vulnerable or opportunistic responses at that experimental site. Yellow cells denote ecological responses (Op = opportunistic; Vul = vulnerable). Panel B presents stacked bars representing the relative abundance across all samples and treatments (control and warming). Each bar is normalized to 1, representing 100% total abundance. Each segment within a bar illustrates the proportion of total abundance attributable to each fungal lifestyle, with segment height reflecting the relative contribution of each lifestyle at each experimental site. Fungal lifestyles comprising less than 1% relative abundance are omitted for graphical clarity.

microbiome across contrasting ecosystems. To reach this conclusion, we first clustered ecological responses of microbial taxa and characterized both the biodiversity (number of zOTUs within each ecological response) and community composition (by summing the relative abundance of zOTUs belonging to each ecological response) of bacteria and fungi across contrasting ecosystems. We found that the number of microbial taxa with unchanged response (i.e., no significant changes with soil warming) was always higher than that of opportunistic or vulnerable (i.e., significant increases and decreases with soil warming, respectively), regardless of the community type (bacterial and fungal) and ecosystem (drylands and temperate-boreal ecotones) considered (Figure 1B). In this regard, we also observed that, while the number of bacterial taxa with an opportunistic response varied across ecosystems (358 in Aranjuez, 298 in Cloquet, and 168 in Ely), the number of vulnerable taxa was approximately twice as high in the arid ecosystem (729 in Aranjuez, 326 in Cloquet, and 326 in Ely). In addition, the dryland ecosystem exhibited nearly four times the number of fungal taxa with opportunistic (96 in Aranjuez, 35 in Cloquet, and 29 in Ely) and sensitive (90 in Aranjuez, 27 in Cloquet, and 20 in Ely) responses compared to temperate-boreal ecotones. Moreover, the relative abundance of bacterial and fungal taxa responding to warming accounted for 35.9% (15.9% opportunistic and 20% vulnerable) and 42.9% (25.2% opportunistic and 17.7% vulnerable) in the dryland ecosystem (Aranjuez; Figure 1B), respectively. In contrast, ecosystems located at temperate-boreal ecotones (Cloquet and Ely) showed a lower percentage of microbial taxa responding to experimental warming. For example, at Cloquet, the relative abundance of bacterial and fungal taxa was 24.1% (11.9% opportunistic and 12.2% vulnerable) and 22.1% (10.3%

opportunistic and 11.8% vulnerable), respectively. Similarly, at Ely, the percentages were even lower, with bacterial taxa showing 17.9% (6.4% opportunistic and 11.5% vulnerable) and fungal taxa showing 19.4% (9.7% opportunistic and 9.7% vulnerable). Despite variations in the number and relative abundance of microbial taxa responding to warming between dryland and temperate-boreal ecosystems, we consistently observed that microbial taxa with unchanged responses exhibited a higher number and relative abundance (always > 50%) across all ecosystems. The same patterns were found in dominant taxa—those that are both highly abundant (top 10% most common phylotypes sorted by their percentage) and ubiquitous (found in more than half of the soil samples evaluated) (Delgado-Baquerizo et al. 2018) (Figure 1B). The changes of the dominant taxa reinforce our idea that a substantial number of microbial taxa will be sensitive (increase or decrease) to the expected increases in temperature.

We then illustrated the ecological responses (opportunistic, vulnerable, and unchanged) across treatments (warming vs. control) over time (years) at each experimental site (Figure 2). By summing the relative abundance of microbial taxa within each ecological response for each year, we observed how opportunistic and vulnerable taxa increased and decreased in the warming treatment compared to the control, respectively. We observed microbial taxa displaying both opportunistic and vulnerable responses over a 5-year period (2012–2017) in the dryland ecosystem. Similar patterns emerged over a shorter 2-year period (2010–2012) in temperate-boreal ecotones (Cloquet and Ely), with changes in relative abundance persisting over time. For example, bacterial and fungal taxa with opportunistic responses consistently showed higher relative abundance under warming treatments (+1.8°C) compared to the control. Together, these results support a previous field study showing that a higher level of soil warming (5°C) is a key factor in modulating the relative abundance of microbial communities in temperate forests (DeAngelis et al. 2015), but also demonstrate that soil warming (1.8°C) over the medium term is sufficient to shape individual microbial taxa in contrasting dryland and temperate-boreal ecosystems.

3.2 | Key Factors Explaining the Ecological Responses of Soil Microbes to Warming

We explored the influence of microbial phylogeny in explaining the responses of soil individual taxa to warming scenarios (Figure 3). We observed that a single microbial phylum can belong to different ecological responses (Figure S2; and see Figures S3 and S4 for relative abundance patterns of microbial phyla across experimental sites and treatments). For instance, we found that Actinobacteria exhibited vulnerable responses to soil warming (Figure S5B), a pattern previously reported in a warming experiment after 12 years (DeAngelis et al. 2015). However, the same phylum also exhibited unchanged and opportunistic responses (e.g., half of the relative abundance of the opportunistic responses in Aranjuez belongs to this phylum; see Figures S2 and S5B). A similar pattern was observed for fungi (Figure S6), with the Ascomycota phylum exhibiting the highest relative abundance in the dryland ecosystem (Aranjuez) and Basidiomycota in the temperate-boreal forest ecotones (Cloquet and Ely), regardless of the ecological responses. Our findings suggest that these responses were not phylogenetically conserved, indicating that relying solely on groups sharing phylogenetic traits may not be the best approach for predicting microbial responses to warming. This result is consistent with a 100-day laboratory incubation from 18 sites throughout North America, where the temperature responses were not predictable in soil bacterial communities (Oliverio et al. 2017), but differs from previous studies demonstrating a strong phylogenetic signal from fungal communities (order level) in boreal forest (Treseder et al. 2016). Previous studies have reported phylogenetically conserved responses of bacteria to disturbances such as water addition (Evans and Wallenstein 2014; Placella et al. 2012), carbon addition (Morrissey et al. 2016), and drought (Amend et al. 2016). Similarly, changes in the relative abundance of certain fungal groups, such as increases in ectomycorrhizal fungi (Clemmensen et al. 2006) and decreases in Basidiomycota (Treseder et al. 2016) have been reported in response to warming. However, our results suggest that predicting changes in microbial communities at the phylum level could introduce large biases and uncertainties in global estimates of microbial-supported ecosystem functions under warming scenarios.

It is plausible that the link between microbes and the cover of photosynthetic organisms—defined here as the organism forming biocrust (bryophytes and lichens) in Aranjuez, and plants forming associations with ectomycorrhizal fungi in Cloquet and Ely—or life strategy (fungal lifestyle) could explain the observed microbial responses. We found contrasting patterns in the relationship between the cover of photosynthetic organisms, which decreased significantly with increasing warming (Figure 4A), and such responses. Interestingly, while the cover of photosynthetic organisms was positively correlated with vulnerable taxa, it was negatively correlated with opportunistic taxa. Such a pattern suggests a close relationship between aboveground and belowground communities under warming, where the presence of photosynthetic organisms may create favorable conditions for the survival of specific microbial taxa. We then found that fungal lifestyle, characterized using the FungalTraits database (Põlme et al. 2020) at the highest level of resolution, was closely aligned with the ecological responses of microbes to soil warming. For instance, the strong decrease in lichenized fungi (key taxa forming part of biocrusts) in response to warming observed in Aranjuez (Figure 4C) may be related to the higher percentage of relative abundance of microbes following vulnerable responses (Figure 4D). Similarly, we found that the relative abundance of ectomycorrhizal fungi did not change in response to increasing temperatures at Cloquet and Ely sites. This could be explained by the fact that most symbiotic fungi exhibited tolerant responses. Moreover, fungal genera classified as putative plant or human pathogens (e.g., members of the genera *Fusarium* and *Alternaria*, Summerell et al. 2010; Friedman and Schwartz 2019) and parasites were generally resistant or responded positively to warming across ecosystems (Figures 5B and S8). Lastly, we also noted that unidentified fungal lifestyles represent a significant percentage of relative abundance across ecological responses and experimental sites (e.g., unclassified fungi comprised over 50% of opportunistic taxa in Cloquet and Ely; Figure 5B). This result hampers our ability to assess the functional capabilities of fungi and

indicates that future efforts must focus on isolating and classifying unknown taxa to further advance our understanding of their roles and functions in soils. Although future experimental work should further investigate the influence of phenotypic plasticity (the ability to tolerate warming is not strictly determined by genetics) (Evans and Wallenstein 2014) and horizontal transfer of genes related to temperature tolerance (Isobe et al. 2019), our study suggests that ecological lifestyle may be an important factor in determining the dominance of fungal lineages in soils, and that the cover of photosynthetic organisms (biocrust and plants) can be crucial in supporting microbial survival under soil warming.

3.3 | Linking Fungal Lifestyle With Opportunistic or Vulnerable Responses and Soil Functions

Moreover, if we assume that the dominant microbial community likely comprises taxa with important soil functions due to their success (Delgado-Baquerizo et al. 2018), our findings suggest that changes in their relative abundance under expected warming scenarios may alter ecosystem functioning in our soils. For instance, the relative abundance of fungal taxa with vulnerable responses decreased under warming scenarios in the dryland ecosystem, whereas a marked increase was observed in the control treatment from 2012 to 2017 (Figure 2). This pattern suggests that, under undisturbed environmental conditions, these fungi may experience natural growth or microbial succession over time. Our results align with Guo et al. (2018), who demonstrated that warming could drive increasingly divergent succession patterns in soil microbial communities in a tallgrass prairie ecosystem, likely due to deterministic environmental filtering induced by warming. Lastly, we observed that fungal taxa with vulnerable responses classified as lichenized (the most abundant fungal lifestyle with vulnerable response in our dryland ecosystem; Figure 5B) were correlated with all measured enzymatic activities (Figure 5A). This indicates that shifts in these microbial communities could have cascade effects on soil functions (de Vries et al. 2012), such as organic matter decomposition dynamics, in response to rising temperatures.

We also found that fungal lifestyles with opportunistic taxa had a higher number of positive correlations with various enzymatic activities and soil respiration compared to vulnerable taxa (Figure 5A). For instance, we observed that soil respiration was positively correlated with fungal lifestyle following opportunistic response (wood saprotroph, soil saprotroph, unidentified saprotroph, parasite, and plant pathogen) but negatively correlated with vulnerable responses (soil saprotroph and parasite) at the Cloquet site. Moreover, different fungal lifestyles (wood and litter saprotrophs, parasites, and plant pathogens) with opportunistic responses were positively correlated with β-glucosidase (BG; an enzyme that catalyzes one of the later steps of cellulose degradation) and acid phosphatase activity (PHOS; responsible for phosphorus mineralization, which plays a fundamental role in the recycling of soil phosphorus). Our findings align with a global meta-analysis suggesting that changes in soil enzymes caused by soil warming are correlated with microbial traits and communities (Meng et al. 2020). Together, our findings suggest that fungal lifestyles associated with opportunistic responses could promote microbial enzyme activity under warming scenarios. Since soil extracellular enzymes serve as the proximate agents of organic matter decomposition in soils (Conant et al. 2011), we also posit that an increased potential for the microbial community to metabolize carbon could be expected in a warmer world.

Here we present experimental evidence that a substantial number of microbial taxa in dryland and temperate-boreal forest ecotone ecosystems are sensitive (i.e., their relative abundance will either increase or decrease) to soil warming. Our results indicate that bacteria and fungi belonging to the same phylum can exhibit different ecological responses to survive warming stress, suggesting that soil microbial taxa should be classified individually to better predict microbial responses to ongoing climate change. Even so, we identified that the cover of photosynthetic organisms and fungal lifestyles might help explain the ecological responses of soil microbes to warming. For instance, the cover of photosymbiotic organisms may establish conditions that enhance the survival of microbes exhibiting vulnerable responses to warming. Fungal lifestyles classified as soil-borne fungal pathogens exhibited either opportunistic or unchanged responses, whereas lichenized fungi showed vulnerable responses to warming. Moreover, we observed that fungal lifestyles associated with opportunistic taxa could enhance microbial enzymatic activity under warming scenarios and, ultimately, increase the potential for metabolizing carbon stored in our soils. Such information can enhance our ability to predict microbial feedback to climate change and their potential impacts on ecosystem functions and services that support human well-being.

Author Contributions

Tadeo Sáez-Sandino: formal analysis, writing – original draft, writing – review and editing. **Peter B. Reich:** conceptualization, data curation, funding acquisition, investigation, methodology, writing – original draft, writing – review and editing. **Fernando T. Maestre:** conceptualization, data curation, funding acquisition, investigation, methodology, writing – original draft, writing – review and editing. **Concha Cano-Díaz:** formal analysis, writing – original draft, writing – review and editing. **Artur Stefanski:** data curation, investigation, writing – original draft, writing – review and editing. **Raimundo Bermudez:** data curation, investigation, writing – original draft, writing – review and editing. **Juntao Wang:** formal analysis, writing – original draft, writing – review and editing. **Avinash Dhar:** data curation, writing – original draft. **Brajesh K. Singh:** conceptualization, data curation, investigation, methodology, writing – original draft, writing – review and editing. **Antonio Gallardo:** funding acquisition, writing – original draft, writing – review and editing. **Manuel Delgado-Baquerizo:** conceptualization, funding acquisition, methodology, writing – original draft, writing – review and editing. **Pankaj Trivedi:** conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Figshare at https://figshare.com/articles/dataset/A_large_fraction_of_soil_microbial_taxa_is_sensitive_to_experimental_warming/27691290. Raw sequencing data for the B4WarmED experiment is available from the NCBI sequence read archive (SRA) under the BioProject accession PRJNA1249504 and PRJNA1249103 for fungi and bacteria, respectively. Raw sequencing data for the Aranjuez experiment is available from the NCBI sequence read archive (SRA) under the BioProject accession PRJNA1254974.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.