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Meta-analysis

A meta-analysis of the effects of climate change-related abiotic factors on aboveground and belowground plant-associated microbes

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The abiotic environment exerts strong effects on plant-associated microbes, shaping their interactions with plants and resulting ecosystem processes. However, these abiotic effects on plant–microbe interactions are often highly specific and contingent on the abiotic driver or microbial group, requiring synthesis work describing general patterns and from this generate hypotheses and guide mechanistic work. To address this, we conducted a meta-analysis of the effects of climate change-related abiotic factors, namely warming, drought, and eCO_2, on plant-associated microbes distinguishing by microbial taxonomic or biological group (bacteria, fungi or virus) and the plant part where microbes are found or associated with (phyllosphere or rhizosphere). We found abiotic driver-specific patterns, whereby drought significantly reduced microbial abundance, whereas warming and eCO_2 had no significant effects. In addition, these abiotic effects were contingent on the microbial taxonomic group, with fungi being negatively affected by drought but positively affected by warming (eCO_2 enrichment had no effect), whereas bacteria and viruses were not significantly affected by any factor. Likewise, rhizospheric microbes were negatively affected by drought but positively affected by warming (eCO_2 enrichment had no effect), whereas phyllospheric microbes were not significantly affected by any factor. Collectively, these findings point to important implications for global change research by highlighting contrasting effects of climate change-related abiotic drivers on plant-associated microbes and the contingency of such effects on microbe life histories and the nature of their interactions with plants.

Keywords: climate change, drought, eCO_2, phyllosphere, plant-associated microbes, rhizosphere, warming

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Introduction

Plants are closely associated with a wide variety of microbes (e.g. fungi, bacteria, protists, viruses) which often specialize on plant tissues or compartments such as the phyllosphere (i.e. the region surrounding the aerial part of the plant) and the rhizosphere (i.e. the narrow region of soil surrounding plant roots) (Coleman-Derr et al. 2016, Dong et al. 2019). These microorganisms play a pivotal role in regulating ecosystem processes (e.g. water and nutrient cycling, energy flux and community dynamics) and services (e.g. plant productivity and biodiversity) directly or indirectly via their interactions with plants (Bulgarelli et al. 2013, Philippot et al. 2013).

The abiotic environment exerts strong effects on plant-associated microbes and resulting microbe-mediated ecosystem processes (Delgado-Baquerizo et al. 2020, Zhu et al. 2022). Such effects have presumably become increasingly important to understand global change impacts given substantial changes in abiotic variables such as atmospheric CO_2 concentration (eCO_2), air temperature, and precipitation (IPCC 2022). These climate change-related abiotic factors can affect plant-associated microbes directly (Hashizume et al. 2008, Peñuelas et al. 2012, Tedersoo et al. 2012), as well as indirectly via effects on soil properties or plant phenotypes (Schortemeyer et al. 2002, Haase et al. 2007, Drigo et al. 2010). We have good evidence, however, that such effects vary depending on the microbial group studied (e.g. fungi, virus, bacteria) (Compant et al. 2010, Velásquez et al. 2018, Cheng et al. 2019). For example, studies have shown that warming, drought, and increases in eCO_2 promote leaf- and soil-borne pathogens (Trebicki et al. 2015, Sinha et al. 2019, Delgado-Baquerizo et al. 2020, Amari et al. 2021), and in some cases reduce the abundance of mycorrhizal fungi and nitrogen-fixing bacteria (Monz et al. 1994, Godbold et al. 1997, Aydogan et al. 2018, Duarte and Maherali 2022). Similarly, abiotic effects are also contingent on the plant part or tissue where they are found and interact with the plant. For example, climate change-related abiotic factors are predicted to have stronger effects on microbes living on above ground plant surfaces (i.e. phyllosphere) which are exposed to environmental conditions that fluctuate more compared to more buffered or stable belowground conditions found in the rhizosphere (Dastogeer et al. 2020, Trivedi et al. 2022). In addition, the impacts of climate change-related abiotic drivers have also been shown to exhibit highly variable outcomes, many times contingent on host- or microbe-species or group-specific characteristics (Naylor et al. 2017, Panneerselvam et al. 2020, Lozano et al. 2021). Efforts to synthesize and quantitatively analyze these patterns can be of great value to identify general trends in abiotic responses of different microbial groups as well as test or generate new hypotheses while guiding mechanistic experiments to test for candidate mechanisms.

Here we conducted a meta-analysis testing the effects of climate change-related abiotic factors on plant-associated microbes. To this end, we analyzed studies involving experimental manipulations of climate change-related abiotic factors (e.g. warming, drought, and eCO_2) and measuring abundance of microbes (e.g. virus, bacteria, fungus) in the phyllosphere or rhizosphere. We aimed at: 1) describing the overall magnitude and direction of effects of abiotic factors on plant-associated microbes, and 2) testing whether such abiotic effects were contingent on the type of microbe, namely bacteria, fungus or virus, and plant part where microbes are found, namely the phyllosphere or rhizosphere. In doing so, this study furthers our understanding of climate change-related abiotic forcing on plant-associated microbes and its implications for ecosystem responses to global change threats.

Material and methods

Data collection

We carried out an extensive literature search in Scopus database in May 2022 using a combination of the following keywords: ((plant OR tree OR shrub) AND (drought OR warming OR co2 OR flooding OR wind OR salt OR salin OR deposit) AND (microb OR bacter OR fung OR virus OR protist OR alga OR nematod OR mycorrhiz)). We retained only articles, book chapters, reviews, theses, dissertations and abstracts published in English. To further limit the search to relevant papers, we filtered outputs to consider only the following research areas: Agricultural and Biological science, Biochemistry, Genetics and Molecular biology, Environmental science, Immunology and Microbiology. This search spanned published work from 1967 to 2022. In addition, we also surveyed the references in review articles on climate change and interactions between plants and microbes (Compant et al. 2010, Singh et al. 2020, Sharma et al. 2022, Trivedi et al. 2022, Zhu et al. 2022) and included any studies that were missed in our Scopus search. In total, our initial search yielded 5450 papers (see the PRISMA flow chart in the Supporting information).

To be included in our analysis, studies had to meet the following criteria: 1) provide a measure of plant-associated microbial abundance (e.g. amount, frequency, disease intensity, transmission rate, virus load) in the phyllosphere or rhizosphere of plants growing under experimental manipulation of climate change-related abiotic conditions (eCO_2, warming, drought, etc.), and 2) report treatment level means (abiotic manipulation vs unmanipulated control), variability (i.e. variance, SE or SD), and the sample size in either the text, figures, tables or appendices. When needed, we extracted data from figures following digitalization using WebPlotDigitizer software. We excluded studies that applied two or more different abiotic manipulations together on the same plants. After applying these criteria, the resulting dataset consisted of 513 case studies from 96 studies (out of the original 5450) from the primary literature published between 1975 and 2021 in 47 scientific journals (Fig. 1; see also the list of references in the Supporting information). Study cases represented data points, i.e. treatment versus control comparisons, drawn from a single primary study, where a single study may have one or more study cases. The occurrence of

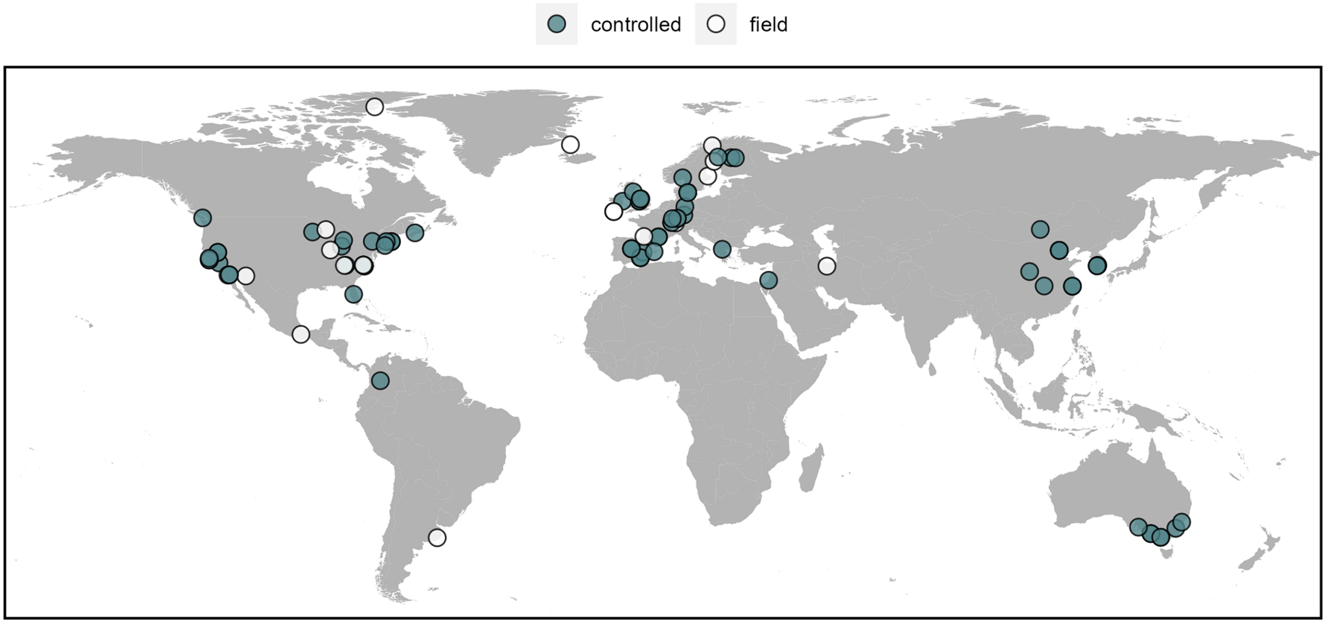

Figure 1. Map showing the location of the 96 studies included in this meta-analysis. Blue and white dots represent studies performed under controlled (i.e. greenhouse or laboratory) and field conditions, respectively.

more than one study case in a given study took place when more than one response was measured and/or more than one abiotic treatment was tested (against a control), in which case the number of study cases in a given study equaled the number of responses by the number of treatment level versus control comparisons. We used different approaches to account for both sources of non-independence in our analyses and assessed the robustness of our conclusions to the inclusion of multiple study cases per primary study.

For each study case, we compiled the following moderators: plant species and growth form (herbaceous or woody), experimental conditions (field or controlled, i.e. greenhouse or laboratory), climate change-related abiotic factors (warming, drought, eCO_2), microbial taxonomical group (i.e. bacteria, fungus or virus), and the plant part where microbes were found (phyllosphere or rhizosphere).

Statistical analyses

For each study case, we estimated effect sizes using Hedges' *d* metric and a confidence interval (Hedges 1981) using the 'metafor' package ver. 3.8-1 in R 2022.07.2 (Viechtbauer 2010, www.r-project.org). Hedges' *d* is calculated as the standardized mean difference between plants subjected to the abiotic manipulation and control (unmanipulated) plants, such that negative values indicate that microbial abundance had lower mean values on abiotically-manipulated plants compared to control plants, whereas positive values indicate the inverse.

We first estimated the grand mean effect size and 95% confidence interval (CI) across all studies to assess whether there was an overall effect of abiotic factors on microbial abundance (Koricheva et al. 2013). This grand effect size does not separate the effects of different types of climate change-related abiotic factors. Rather, the purpose of this analysis was to estimate the degree of consistency among studies by means of the between-studies heterogeneity (τ^2 and associated Q statistics), an important overall estimator for our analysis. High heterogeneity can be accounted for by using explanatory variables (referred to as 'moderators' in meta-analysis literature). Total heterogeneity is split into among-group heterogeneity (i.e. among abiotic factors) and within-group heterogeneity (i.e. variance of effect sizes within moderator level). The τ^2 and associated Q statistics for heterogeneity aim at determining whether among-group heterogeneity is large enough as compared to within-group heterogeneity to conclude on the significant effect of the moderator tested. Because τ^2 is dependent on sample size, we also calculated I^2 value which is a standardized estimate of total heterogeneity ranging from 0 and 1 (Koricheva et al. 2013, Nakagawa et al. 2017).

We next evaluated the effects of the type of climate change-related abiotic factor (eCO_2, warming, and drought) on the abundance of plant-associated microbes by estimating mean effect sizes and 95% CIs for each abiotic factor and running models with the type of abiotic factor as a moderator. Then, we tested whether effects of the type of climate change-related abiotic factor on the abundance of plant-associated microbes were contingent on the microbial taxonomic group (bacteria, fungus or virus), and the plant part with which microbes were associated (phyllosphere or rhizosphere). For this, we ran models including as moderators: the type of climate change-related abiotic factor, one of the above-mentioned factors (microbial taxonomic group or plant region of colonization), and the two-way interaction between the type of abiotic factor and the microbe grouping factor. We note that there was not enough replication to test for the three-way interaction between abiotic forces, microbial group, and plant region of colonization. We reported results from the omnibus test (i.e. overall effect of all moderators) as well as from the coefficient parameter estimate and associated confidence interval. In all the above models, we performed multi-level error meta-analyses (Nakagawa et al. 2017) with the *rma.mv* function of the R package 'metafor' ver. 2.0-0 (Viechtbauer 2010, www.r-project.org), and included the primary study and study case nested within primary study as random factors in order to account for non-independence among multiple effect sizes drawn from a single primary study. Multiple comparisons of abiotically-manipulated plants with the same control plant were accounted for by computing the variance–covariance matrix among all effect sizes. We considered an effect size as significant if its 95% confidence interval did not overlap with zero (Koricheva et al. 2013). Preliminary analyses testing for an effect of plant growth form (herbaceous or woody) and experimental conditions (field or controlled conditions) indicated that these factors did not significantly influence the abundance of plant-associated microbes (plant growth form: $Q_M = 0.26$, $p = 0.878$, $k = 513$; experimental conditions: $Q_M = 0.09$, $p = 0.765$, $k = 513$). Similarly, the two-way interactions between experimental conditions and plant growth form with microbial group and plant region of colonization did not significantly influence the abundance of plant-associated microbes (experimental conditions × microbial group: $Q_M = 2.16$, $p = 0.707$, $k = 513$; experimental conditions × plant region: $Q_M = 0.09$, $p = 0.993$, $k = 513$; plant growth form × microbial group: $Q_M = 1.46$, $p = 0.962$, $k = 513$; plant growth form × plant region: $Q_M = 0.34$, $p = 0.987$, $k = 513$). We therefore pooled all data and did not further consider these factors.

To ensure that our findings were robust, we conducted a sensitivity analysis in which we sequentially removed one primary study at a time. This analysis was aimed at testing whether the main result could have emerged from the inclusion of any particularly influential study, for instance one providing a large number of study cases. For each of the 95 runs, corresponding to removing each of the 95 primary studies included in the main analysis, we checked that model parameter estimates for each treatment (abiotic manipulated vs unmanipulated control plants) were comparable, regardless of whether each study was later included or not in the analyses. This analysis indicated that our findings were robust and unbiased by non-independence among effect sizes (Supporting information). In addition, we used several approaches to verify that our results were not affected by publication bias (Nakagawa et al. 2022): 1) inspection of funnel plots, 2) exploration of the relationship between effect-sizes and journal impact factor and 3) cumulative meta-analysis. These analyses indicated that our findings were robust to selective reporting and dissemination bias (Supporting information).

Results

The grand mean effect size (± 95% CI) for the effect of abiotic factor (across all drivers) on plant-associated microbes was positive (0.055 ± [−0.196; 0.306]) but not significantly different from zero ($p = 0.665$). This overall test also indicated a substantial amount of total heterogeneity, most of which was attributable to among-study heterogeneity ($I^2 = 98.1$).

Moderator models indicated a significant effect of the type of climate change-related abiotic factor on the abundance of plant-associated microbes ($Q_M = 10.94$, $p = 0.004$, $k = 513$). Specifically, drought significantly reduced microbial abundance, whereas warming and eCO_2 had no significant influence (Fig. 2). However, these effects were found to be further contingent on the microbial group (i.e. significant abiotic factor by microbial group interaction; $Q_M = 11.64$, $p = 0.003$, $k = 513$), whereby fungi were negatively influenced by drought and positively affected by warming (Fig. 3a), whereas bacteria and viruses were not significantly affected by either factor (Fig. 3a); eCO_2 did not affect any microbial group (Fig. 3a).

Likewise, climate change-related abiotic effects were also contingent on the plant part where microbes are found (i.e. significant abiotic factor by plant part interaction; $Q_M = 9.02$, $p = 0.011$, $k = 513$). Here, rhizospheric microbes were negatively affected by drought and positively influenced by warming, whereas phyllospheric microbes were not affected by either factor (Fig. 3b); eCO_2 did not influence either microbial group (Fig. 3b).

Discussion

Our findings indicate that climate change-related abiotic forcing on plant-associated microbes is contingent on the

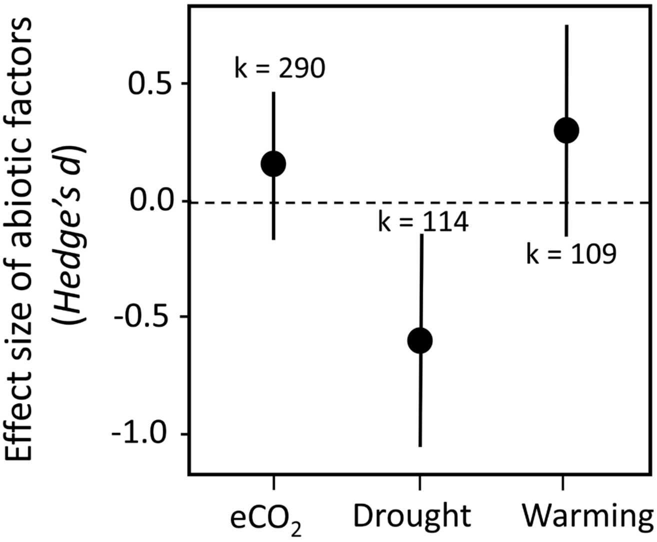

Figure 2. Mean effect size of climate change-related abiotic factors (eCO_2, warming and drought) on the abundance of plant-associated microbes. Dots and error bars represent model parameter estimates and corresponding 95% confidence intervals. $k =$ number of study cases. The vertical dashed line centred on zero represents the null hypothesis (i.e. no difference in microbial abundance between unmanipulated control and abiotically-manipulated plants). The effect size is significant if the 95% CI does not include zero.

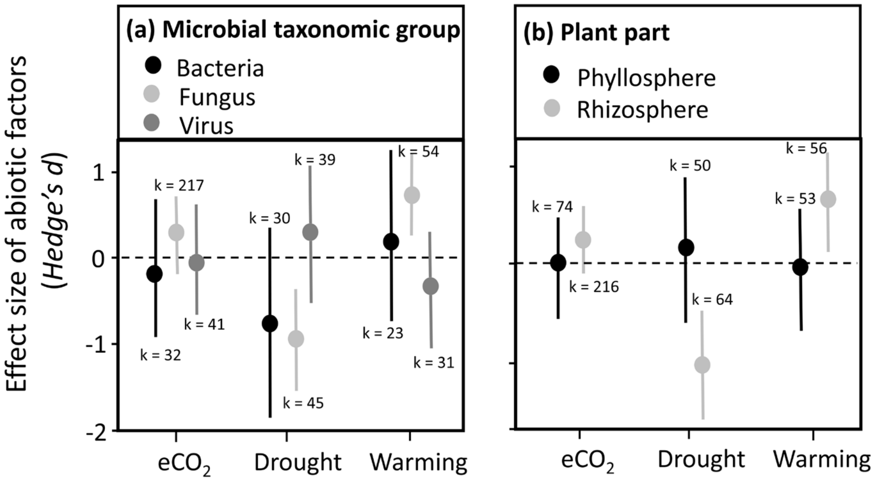

Figure 3. Mean effect size of climate change-related abiotic factors (eCO$_2$, warming and drought) on the abundance of plant-associated microbes depending on (a) microbial taxonomic group (bacteria, fungus or virus), and (b) plant part where associations take place (phyllosphere versus rhizosphere). Dots and error bars represent model parameter estimates and corresponding 95% confidence intervals. k = number of study cases. The vertical dashed line centred on zero represents the null hypothesis (i.e. no difference in microbial abundance between unmanipulated control and abiotically-manipulated plants). The effect size is significant if the 95% CI does not include zero.

factor looked at. Whereas drought significantly reduced overall microbial abundance, warming and eCO$_2$ had weak or inconsistent effects. These results are consistent with work showing that drought disrupts key nutrient cycles and drastically reduces soil and leaf water content (Kaisermann et al. 2017, Malik and Bouskill 2022), negatively affecting below- and above-ground plant-associated microbes (Nilsen et al. 1998, Valdés et al. 2006). On the other hand, while warming and eCO$_2$ effects have been shown to enhance microbial activity under moderate stress levels (Alberton et al. 2005, Bradford et al. 2008, Chung et al. 2017), negative effects have also been reported (Clemmensen et al. 2013, Aydogan et al. 2018) and variability in their effects (including many times non-significant outcomes; Markkola et al. 1996, Cordier et al. 2012) have often been the norm. Collectively, these findings call for further experimental work investigating the mechanisms (e.g. metabolic changes in host plants, microbial community changes) by which drought appears to exert stronger and more consistent controls on plant-associated microbes compared to warming and eCO$_2$.

We further found that effects of climate change-related abiotic factors on plant-associated microbes varied depending on the type of plant-associated microbe. Results indicated that fungi were overall negatively affected by drought (presumably driving or at least contributing to the overall negative effect of this factor) but positively affected by warming, whereas bacteria and viruses were, on average, not significantly affected by either factor. It is known that fungi exhibit rapid population and species turnover which could confer higher (and more rapid) responsiveness to environmental changes (e.g. through species evolutionary change or shifts in species composition) compared to other microbial taxa such as bacteria (Kaisermann et al. 2015). Warming, on the other hand, has been shown to increase respiration rates and abundance of plant-associated fungi (Pietikäinen et al. 2005, Schindlbacher et al. 2011), a response that could be at least partly mediated, in the case of pathogenic fungi, by changes (e.g. reductions) in the expression of biotic resistance-related plant genes under elevated temperatures (Wang et al. 2009). By comparison, again neither of these abiotic drivers affected bacteria or viruses, which tended to exhibit overall more variable responses compared to fungi. Bacteria often live in concealed niches (e.g. solitary cells in leaves), and could therefore be less affected by environmental fluctuations than fungi (Ding et al. 2019). In addition, studies have reported environmental stress affects viral transmission rates and virulence, but that these effects are not necessarily coupled with changes in viral load (Bergès et al. 2018), possibly leading to buffering mechanisms that explain non-significant effects on this group. It should be noted, however, that even though bacterial and viral abundances often remain unresponsive or weakly responsive to abiotic changes, there could be underlying shifts in community structure in these microbial groups affecting plants and ecosystem function (Lesaulnier et al. 2008, Xu et al. 2018).

Climate change-related abiotic forcing on plant-associated microbes was also contingent on the plant compartment to which microbes are associated with. Unexpectedly, microbes found in the rhizosphere were more affected by abiotic manipulations compared to their phyllospheric counterpart. Specifically, we found that microbes in the rhizosphere were negatively affected by drought but positively influenced by warming, whereas those found in the phyllosphere were, on average, not significantly affected by either factor. Previous work has found that reductions in plant photosynthetic rates under drought alters carbon output to the rhizosphere (Karlowsky et al. 2018, Wang et al. 2021), a possible mechanism explaining the observed negative effect of this factor on soil microbes found in this plant compartment. Decreases in soil moisture due to drought can also have a direct negative impact on soil microbes due to reduced nutrient mobility, potentially also explaining the observed pattern (Naylor and Coleman-Derr 2018). On the other hand, warming often has a direct positive effect on microbial respiration rates which leads to increases in microbial abundance in the rhizosphere (Bradford et al. 2008, Hawkes et al. 2008), in agreement with observed patterns. By contrast, microbes found in the phyllosphere were not significantly affected by any of the studied abiotic factors. Together, the overall stronger influence of abiotic factors on rhizospheric compared to phyllospheric microbes depicted by our results could be explained, at least in part, by effects on pathogenic soil microorganisms, whereby environmental stress leads to higher the transmission rates and/or pathogenicity as observed in some systems (Velásquez et al. 2018, Sharma et al. 2022). Nonetheless, this affirmation remains speculative as has been relatively little work addressing the impacts of abiotic manipulations on phyllospheric microbial communities (Zhu et al. 2022), thus warranting further studies to test this idea and yield more robust generalizations.

Research limitations and future work

Our study only considered effects on microbial abundance, as this was the most widely available response measured. While dominant microbial species or groups largely explaining effects on ecosystem function or resistance expectedly drive overall abundance (Orland et al. 2019), an explicit consideration of effects on other microbial community features (e.g. evenness, species composition, etc.) is strongly warranted. For instance, microbial communities often exhibit functional redundancy, such that changes in abundance may not necessarily impact ecosystem function (Allison and Martiny 2008). Therefore, observed changes in abundance in our analyses may not necessarily lead to effects (at least not ecologically significant ones) on ecosystems. Likewise, changes in microbial community traits such as dominance or evenness can in some cases better predict resistance to environmental perturbations than overall abundance alone (Powell et al. 2015). Our review clearly points to the need for more studies measuring species- or functional group-specific changes in microbial relative abundances in response to abiotic manipulations, particularly those pertaining climate change drivers.

Another important consideration is that we were only able to test for effects of each abiotic driver individually. There is good evidence that climate change drivers act in concert, often leading to synergistic effects on ecosystems (Reich et al. 2020). Unfortunately, the number of studies involving abiotic manipulations is not large enough to test for these interactive effects, leading to likely limited assessment of climate change effects on microbial communities. Besides more microbial studies involving abiotic manipulations, our review of the literature also highlights the need for individual studies simultaneously testing for different abiotic factors in order to achieve a more robust and realistic understanding of climate change effects on ecosystems via changes in microbial community structure.

Finally, we recognize the need for further work to shed light on the mechanisms underlying the observed abiotic effects on plant-associated microbes. This potentially involves untested factors acting at different scales which are associated with or interact with the tested abiotic drivers (e.g. broad-scale factors such as latitude, elevation or biome type and local-scale factors such as soil type o microhabitat conditions; Orwin 2010, Aqeel et al. 2024). On the one hand, we ran into a limitation in the number of studies to properly test for some of these factors. On the other, many studies lacked information on these factors and available data bases do not have a high-enough resolution to confidently test for them, particularly at local scales).

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Author contributions

Gabriela Quiroga: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Writing – original draft (lead); Writing – review and editing (equal). **Bastien Castagneyrol:** Formal analysis (lead); Writing – review and editing (equal). **Luis Abdala-Roberst:** Writing – review and editing (equal). **Xoaquín Moreira:** Conceptualization (equal); Funding acquisition (lead); Writing – original draft (equal); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dfn2z3594 (Quiroga et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Alberton, O., Kuyper, T. W. and Gorissen, A. 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. – New Phytol. 167: 859–868.

Allison, S. D. and Martiny, J. B. H. 2008. Resistance, resilience, and redundancy in microbial communities. – Proc. Natl Acad. Sci. USA 105: 11512–11519.

Amari, K., Huang, C. and Heinlein, M. 2021. Potential impact of global warming on virus propagation in infected plants and agricultural productivity. – Front. Plant Sci. 12: 649768.

Aqeel, M., Khalid, N., Noman, A., Ran, J., Manan, A., Hou, Q., Dong, L., Sun, Y., Deng, Y., Lee, S. S., Hu, W. and Deng, J.

2024. Interplay between edaphic and climatic factors unravels plant and microbial diversity along an altitudinal gradient. – Environ. Res. 242: 117711.

Aydogan, E. L., Moser, G., Müller, C., Kämpfer, P. and Glaeser, S. P. 2018. Long-term warming shifts the composition of bacterial communities in the phyllosphere of *Galium album* in a permanent grassland field-experiment. – Front. Microbiol. 9: 144.

Bergès, S. E., Vile, D., Vazquez-Rovere, C., Blanc, S., Yvon, M., Bédiée, A., Rolland, G., Dauzat, M. and van Munster, M. 2018. Interactions between drought and plant genotype change epidemiological traits of cauliflower mosaic virus. – Front. Plant Sci. 9: 703.

Bradford, M. A., Davies, C. A., Frey, S. D., Maddox, T. R., Melillo, J. M., Mohan, J. E., Reynolds, J. F., Treseder, K. K. and Wallenstein, M. D. 2008. Thermal adaptation of soil microbial respiration to elevated temperature. – Ecol. Lett. 11: 1316–1327.

Bulgarelli, D., Schlaeppi, K., Spaepen, S., Ver Loren van Themaat, E. and Schulze-Lefert, P. 2013. Structure and functions of the bacterial microbiota of plants. – Annu. Rev. Plant Biol. 64: 807–838.

Cheng, Y. T., Zhang, L. and He, S. Y. 2019. Plant–microbe interactions facing environmental challenge. – Cell Host Microbe 26: 183–192.

Chung, B. N., Koh, S. W., Choi, K. S., Joa, J. H., Kim, C. H. and Selvakumar, G. 2017. Temperature and CO_2 level influence potato leafroll virus infection in *Solanum tuberosum*. – Plant Pathol. J. 33: 522–527.

Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A. and Lindahl, B. D. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. – Science 339: 1615–1618.

Coleman-Derr, D., Desgarennes, D., Fonseca-Garcia, C., Gross, S., Clingenpeel, S., Woyke, T., North, G., Visel, A., Partida-Martinez, L. P. and Tringe, S. G. 2016. Plant compartment and biogeography affect microbiome composition in cultivated and native *Agave* species. – New Phytol. 209: 798–811.

Compant, S., van der Heijden, M. G. and Sessitsch, A. 2010. Climate change effects on beneficial plant–microorganism interactions. – FEMS Microbiol. Ecol. 73: 197–214.

Cordier, T., Robin, C., Capdevielle, X., Fabreguettes, O., Desprez-Loustau, M. L. and Vacher, C. 2012. The composition of phyllosphere fungal assemblages of European beech (*Fagus sylvatica*) varies significantly along an elevation gradient. – New Phytol. 196: 510–519.

Dastogeer, K. M. G., Tumpa, F. H., Sultana, A., Akter, M. A. and Chakraborty, A. 2020. Plant microbiome – an account of the factors that shape community composition and diversity. – Curr. Plant Biol. 23: 100161.

Delgado-Baquerizo, M., Guerra, C. A., Cano-Díaz, C., Egidi, E., Wang, J., Eisenhauer, N., Singh, B. K. and Maestre, F. T. 2020. The proportion of soil-borne pathogens increases with warming at the global scale. – Nat. Clim. Change 10: 550–554.

Ding, X., Chen, S., Zhang, B., Liang, C., He, H. and Horwath, W. R. 2019. Warming increases microbial residue contribution to soil organic carbon in an alpine meadow. – Soil Biol. Biochem. 135: 13–19.

Dong, C. J., Wang, L. L., Li, Q. and Shang, Q. M. 2019. Bacterial communities in the rhizosphere, phyllosphere and endosphere of tomato plants. – PLoS One 14: e0223847.

Drigo, B., Pijl, A. S., Duyts, H., Kielak, A. M., Gamper, H. A., Houtekamer, M. J., Boschker, H. T., Bodelier, P. L., Whiteley, A. S., van Veen, J. A. and Kowalchuk, G. A. 2010. Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. – Proc. Natl Acad. Sci. USA 107: 10938–10942.

Duarte, A. G. and Maherali, H. 2022. A meta-analysis of the effects of climate change on the mutualism between plants and arbuscular mycorrhizal fungi. – Ecol. Evol. 12: e8518.

Godbold, D. L., Berntson, G. M. and Bazzaz, F. A. 1997. Growth and mycorrhizal colonization of three north American tree species under elevated atmospheric CO_2. – New Phytol. 137: 433–440.

Haase, S., Neumann, G., Kania, A., Kuzyakov, Y., Römheld, V. and Kandeler, E. 2007. Elevation of atmospheric CO_2 and N-nutritional status modify nodulation, nodule-carbon supply, and root exudation of *Phaseolus vulgaris* L. – Soil Biol. Biochem. 39: 2208–2221.

Hashizume, Y., Sahashi, N. and Fukuda, K. 2008. The influence of altitude on endophytic mycobiota in *Quercus acuta* leaves collected in two areas 1000 km apart. – For. Pathol. 38: 218–226.

Hawkes, C. V., Hartley, I. P., Ineson, P. and Fitter, A. H. 2008. Soil temperature affects carbon allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. – Global Change Biol. 14: 1181–1190.

Hedges, L. V. 1981. Distribution theory for Glass's estimator of effect size and related estimators. – J. Educ. Behav. Stat. 6: 107–128.

IPCC 2022. Contribution of working group II to the sixth assesment report of the intergovernmental panel on climate change. – In: Pörtner, H.-O. et al. (eds), Climate change. Cambridge Univ. Press, pp. 37–118.

Kaisermann, A., Maron, P. A., Beaumelle, L. and Lata, J. C. 2015. Fungal communities are more sensitive indicators to non-extreme soil moisture variations than bacterial communities. – Appl. Soil Ecol. 86: 158–164.

Kaisermann, A., de Vries, F. T., Griffiths, R. I. and Bardgett, R. D. 2017. Legacy effects of drought on plant–soil feedbacks and plant–plant interactions. – New Phytol. 215: 1413–1424.

Karlowsky, S., Augusti, A., Ingrisch, J., Hasibeder, R., Lange, M., Lavorel, S., Bahn, M. and Gleixner, G. 2018. Land use in mountain grasslands alters drought response and recovery of carbon allocation and plant–microbial interactions. – J. Ecol. 106: 1230–1243.

Koricheva, J., Gurevitch, J. and Mengersen, K. 2013. Handbook of meta-analysis in ecology and evolution. – Princeton Univ. Press.

Lesaulnier, C., Papamichail, D., McCorkle, S., Ollivier, B., Skiena, S., Taghavi, S., Zak, D. and van der Lelie, D. 2008. Elevated atmospheric CO_2 affects soil microbial diversity associated with trembling aspen. – Environ. Microbiol. 10: 926–941.

Lozano, Y. M., Aguilar-Trigueros, C. A., Roy, J. and Rillig, M. C. 2021. Drought induces shifts in soil fungal communities that can be linked to root traits across 24 plant species. – New Phytol. 232: 1917–1929.

Malik, A. A. and Bouskill, N. J. 2022. Drought impacts on microbial trait distribution and feedback to soil carbon cycling. – Funct. Ecol. 36: 1442–1456.

Markkola, A. M., Ohtonen, A., Ahonen-Jonnarth, U. and Ohtonen, R. 1996. Scots pine responses to CO_2 enrichment – I. Ectomycorrhizal fungi and soil fauna. – Environ. Pollut. 94: 309–316.

Monz, C. A., Hunt, H. W., Reeves, F. B. and Elliott, E. T. 1994. The response of mycorrhizal colonization to elevated CO_2 and climate change in *Pascopyrum smithii* and *Bouteloua gracilis*. – Plant Soil 165: 75–80.

Nakagawa, S., Noble, D. W., Senior, A. M. and Lagisz, M. 2017. Meta-evaluation of meta-analysis: ten appraisal questions for biologists. – BMC Biol. 15: 18.

Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar, A., Yang, Y. and O'Dea, R. E. 2022. Methods for testing publication bias in ecological and evolutionary meta-analyses. – Methods Ecol. Evol. 13: 4–21.

Naylor, D. and Coleman-Derr, D. 2018. Drought stress and root-associated bacterial communities. – Front. Plant Sci. 8: 2223.

Naylor, D., DeGraaf, S., Purdom, E. and Coleman-Derr, D. 2017. Drought and host selection influence bacterial community dynamics in the grass root microbiome. – ISME J. 11: 2691–2704.

Nilsen, P., Børja, I., Knutsen, H. and Brean, R. 1998. Nitrogen and drought effects on ectomycorrhizae of Norway spruce *Picea abies* L.(Karst.). – Plant Soil 198: 179–184.

Orland, C., Emilson, E. J. S., Basiliko, N., Mykytczuk, N. C. S., Gunn, J. M. and Tanentzap, A. J. 2019. Microbiome functioning depends on individual and interactive effects of the environment and community structure. – ISME J. 13: 1–11.

Orwin, K. H., Buckland, S. M., Johnson, D., Turner, B. L., Smart, S., Oakley, S. and Bardgett, R. D. 2010. Linkages of plant traits to soil properties and the functioning of temperate grassland. – J. Ecol. 98: 1074–1083.

Panneerselvam, P., Kumar, U., Senapati, A., Parameswaran, C., Anandan, A., Kumar, A., Jahan, A., Padhy, S. R. and Nayak, A. K. 2020. Influence of elevated CO_2 on arbuscular mycorrhizal fungal community elucidated using Illumina MiSeq platform in sub-humid tropical paddy soil. – Appl. Soil Ecol. 145: 103344.

Peñuelas, J., Rico, L., Ogaya, R., Jump, A. S. and Terradas, J. 2012. Summer season and long-term drought increase the richness of bacteria and fungi in the foliar phyllosphere of *Quercus ilex* in a mixed Mediterranean forest. – Plant Biol. 14: 565–575.

Philippot, L., Spor, A., Hénault, C., Bru, D., Bizouard, F., Jones, C. M., Sarr, A. and Maron, P. A. 2013. Loss in microbial diversity affects nitrogen cycling in soil. – ISME J. 7: 1609–1619.

Pietikäinen, J., Pettersson, M. and Bååth, E. 2005. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. – FEMS Microbiol. Ecol. 52: 49–58.

Powell, J. R., Welsh, A. and Hallin, S. 2015. Microbial functional diversity enhances predictive models linking environmental parameters to ecosystem properties. – Ecology 96: 1985–1993.

Quiroga, G., Castagneyrol, B., Abdala-Roberts, L. and Moreira, X. 2024. Data from: A meta-analysis of the effects of climate change-related abiotic factors on aboveground and belowground plant-associated microbes. – Dryad Digital Repository, https://doi.org/10.5061/dryad.dfn2z3594.

Reich, P. B., Hobbie, S. E., Lee, T. D., Rich, R., Pastore, M. A. and Worm, K. 2020. Synergistic effects of four climate change drivers on terrestrial carbon cycling. – Nat. Geosci. 13: 787–793.

Schindlbacher, A., Rodler, A., Kuffner, M., Kitzler, B., Sessitsch, A. and Zechmeister-Boltenstern, S. 2011. Experimental warming effects on the microbial community of a temperate mountain forest soil. – Soil Biol. Biochem. 43: 1417–1425.

Schortemeyer, M., Atkin, O. K., McFarlane, N. and Evans, J. R. 2002. N_2 fixation by *Acacia* species increases under elevated atmospheric CO_2. – Plant Cell Environ. 25: 567–579.

Sharma, B., Singh, B. N., Dwivedi, P. and Rajawat, M. V. S. 2022. Interference of climate change on plant–microbe interaction: present and future prospects. – Front. Agron. 3: 725804.

Singh, B. K., Trivedi, P., Egidi, E., Macdonald, C. A. and Delgado-Baquerizo, M. 2020. Crop microbiome and sustainable agriculture. – Nat. Rev. Microbiol. 18: 601–602.

Sinha, R., Irulappan, V., Mohan-Raju, B., Suganthi, A. and Senthil-Kumar, M. 2019. Impact of drought stress on simultaneously occurring pathogen infection in field-grown chickpea. – Sci. Rep. 9: 5577.

Tedersoo, L., Bahram, M., Toots, M., Diédhiou, A. G., Henkel, T. W., Kjøller, R., Morris, M. H., Nara, K., Nouhra, E., Peay, K. G., Põlme, S., Ryberg, M., Smith, M. E. and Kõljalg, U. 2012. Towards global patterns in the diversity and community structure of ectomycorrhizal fungi. – Mol. Ecol. 21: 4160–4170.

Trebicki, P., Nancarrow, N., Cole, E., Bosque-Pérez, N. A., Constable, F. E., Freeman, A. J., Rodoni, B., Yen, A. L., Luck, J. E. and Fitzgerald, G. J. 2015. Virus disease in wheat predicted to increase with a changing climate. – Global Change Biol. 21: 3511–3519.

Trivedi, P., Batista, B. D., Bazany, K. E. and Singh, B. K. 2022. Plant–microbiome interactions under a changing world: responses, consequences and perspectives. – New Phytol. 234: 1951–1959.

Valdés, M., Asbjornsen, H., Gómez-Cárdenas, M., Juárez, M. and Vogt, K. A. 2006. Drought effects on fine-root and ectomycorrhizal-root biomass in managed *Pinus oaxacana* Mirov stands in Oaxaca, Mexico. – Mycorrhiza 16: 117–124.

Velásquez, A. C., Castroverde, C. D. M. and He, S. Y. 2018. Plant–pathogen warfare under changing climate conditions. – Curr. Biol. 28: R619–R634.

Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. – J. Stat. Softw. 36: 1–48.

Wang, Y., Bao, Z., Zhu, Y. and Hua, J. 2009. Analysis of temperature modulation of plant defense against biotrophic microbes. – Mol. Plant Microbe Interact. 22: 498–506.

Wang, R., Cavagnaro, T. R., Jiang, Y., Keitel, C. and Dijkstra, F. A. 2021. Carbon allocation to the rhizosphere is affected by drought and nitrogen addition. – J. Ecol. 109: 3699–3709.

Xu, L. et al. 2018. Drought delays development of the sorghum root microbiome and enriches for monoderm bacteria. – Proc. Natl Acad. Sci. USA 115: E4284–E4293.

Zhu, Y. G., Xiong, C., Wei, Z., Chen, Q. L., Ma, B., Zhou, S. Y., Tan, J., Zhang, L. M., Cui, H. L. and Duan, G. L. 2022. Impacts of global change on the phyllosphere microbiome. – New Phytol. 234: 1977–1986.