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Fine-root functional trait responses to experimental warming: a global meta-analysis

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Summary

- Whether and how warming alters functional traits of absorptive plant roots remains to be answered across the globe. Tackling this question is crucial to better understanding terrestrial responses to climate change as fine-root traits drive many ecosystem processes.
- We carried out a detailed synthesis of fine-root trait responses to experimental warming by performing a meta-analysis of 964 paired observations from 177 publications.
- Warming increased fine-root biomass, production, respiration and nitrogen concentration as well as decreased root carbon : nitrogen ratio and nonstructural carbohydrates. Warming effects on fine-root biomass decreased with greater warming magnitude, especially in short-term experiments. Furthermore, the positive effect of warming on fine-root biomass was strongest in deeper soil horizons and in colder and drier regions. Total fine-root length, morphology, mortality, life span and turnover were unresponsive to warming.
- Our results highlight the significant changes in fine-root traits in response to warming as well as the importance of warming magnitude and duration in understanding fine-root responses. These changes have strong implications for global soil carbon stocks in a warmer world associated with increased root-derived carbon inputs into deeper soil horizons and increases in fine-root respiration.

Introduction

Functional traits of the narrowest, most absorptive plant roots reflect plant acquisition of soil resources and drive ecosystem processes such as nutrient cycling and organic matter decomposition (De Deyn *et al.*, 2008; Freschet *et al.*, 2013; McCormack *et al.*, 2017; Wurzburger *et al.*, 2017; Ma *et al.*, 2018; Solly *et al.*, 2018; McCormack & Iversen, 2019; Myers-Smith *et al.*, 2019). Moreover, root functional traits are commonly considered as good predictors of plant adaptations and ecosystem functions in response to environmental changes (Freschet *et al.*, 2021). Fine-root diameter, root tissue density (RTD), specific root length (SRL), and root nitrogen (N) concentration are aspects of root size and construction commonly measured to describe the acquisitive capacity of fine roots (Weemstra *et al.*, 2016; Li *et al.*, 2017).

Fine-root production and turnover account for *c.* 22% of global terrestrial net primary productivity, and carbon (C) inputs from fine roots are the dominant inputs to soil organic C stocks compared with aboveground litter-derived C inputs (Clemmensen *et al.*, 2013; Bardgett *et al.*, 2014; McCormack *et al.*, 2015a; Adamczyk *et al.*, 2019). Consequently, improving our functional understanding of fine-root responses to climate change drivers is central to predicting the response of terrestrial ecosystems to global changes.

Global syntheses on observational data have improved our knowledge of temperature effects on fine-root trait expression. These syntheses have shown a positive effect of temperature on fine-root diameter and a negative or neutral effect on SRL (Ostonen *et al.*, 2007; Freschet *et al.*, 2017; Valverde-Barrantes *et al.*, 2017; Fort & Freschet, 2020). Previous studies also suggest that fine-root production and turnover tend to be higher in warmer than in colder sites (Gill & Jackson, 2000; Yuan & Chen, 2010; Finér *et al.*, 2011). By contrast, fine-root life span has been found to decrease with temperature (Chen & Brassard, 2013). While these global endeavors have advanced our quantitative understanding of fine-root trait expression along temperature gradients, they have not been able to disentangle the effect of temperature from the effect of soil environments or plant functional types (Freschet *et al.*, 2017; Wang *et al.*, 2019).

To date, manipulative warming experiments have been widely used to assess fine-root trait responses to elevated temperature while keeping other environmental conditions and representative species consistent between the control and warming treatments. Based on these studies, the responses of fine-root traits to experimental warming appear inconsistent, showing increases, decreases or no change among individual experiments or biomes (Arndal *et al.*, 2018; Parts *et al.*, 2019; Malhotra *et al.*, 2020; Salazar *et al.*, 2020). Although not previously tested, we suggest that these various results could depend upon the warming magnitude, the duration of warming treatment, or the variations in potential modifiers of responses (e.g. the depth at which the soil is sampled, background climate and the warming method). Nevertheless, the influence of these moderators and their interactions on the warming responses of fine-root traits have not been comprehensively evaluated at the global scale.

Warming magnitude and duration probably interact with each other to impact fine-root traits, and these interactions may vary with other environmental factors (e.g. mean annual temperature, mean annual precipitation, annual aridity index or soil depth). Although less often assessed, the duration of warming treatment should regulate the fine-root functional trait responses as biological processes change with time, which may result in further strengthening or weakening of plant responses. For instance, it is suggested that drought coupled with prolonged warming can increase root mortality (Eissenstat & Yanai, 1997). Additionally, warming duration effects may be associated with greater warming magnitude as higher temperatures can aggravate drought stress and dramatically influence soil nutrient availability and C inputs at longer timescales. Thus, assessing how magnitude and duration interact is vital to improve our ability to assess the impacts of future scenarios of global warming.

The complexity in fine-root trait responses to elevated temperature makes it challenging to forecast ecosystem processes under future global warming. Here, we conducted a meta-analysis to investigate the effects of experimental warming on a suite of fine-root trait expression. We hypothesized that experimental warming would increase fine-root biomass. Furthermore, we expected that warming-induced increases in soil N availability and decreases in soil water content (Bai *et al.*, 2013; Xu *et al.*, 2013) would result in the production of thinner roots with higher SRL and higher root N concentration to improve their acquisitive capacity. We also expected increases in fine-root production, mortality, turnover and respiration rate, as well as a decrease in fine-root life span as a result of enhanced root activity, increasing soil nutrient availability and drought stress under warming (Yuan & Chen, 2012; Xiong *et al.*, 2018; Liese *et al.*, 2019). The main goals of this study were to investigate the global patterns in the responses of fine-root functional traits to warming; to examine whether and how warming effects are modulated by warming magnitude and duration; and to explore whether and how warming effects are dependent on environmental conditions (e.g. background climate and soil depth) and warming methods used (e.g. open-top chamber (OTC), heating cables, glasshouse, infrared radiators and reflective curtains).

Materials and Methods

Data collection

We searched peer-reviewed publications between January 1990 and September 2019 that investigated the effects of experimental warming on fine-root functional traits using the Web of Science, Google Scholar and China Knowledge Resource Integrated Databases (CNKI). We used the following combination of keywords for our systematic search: (temperature OR warming OR elevated temperature OR global change OR climate change) AND (root OR belowground) AND (biomass OR diameter OR length OR area OR density OR carbon OR nitrogen OR phosphorus OR nonstructural carbohydrate OR growth OR production OR mortality OR life span OR longevity OR turnover OR respiration OR morphology OR chemistry OR physiology OR dynamic OR trait OR function). Publications that were included in our meta-analysis met the following criteria: only field studies that reported the warming magnitude and duration as well as the means, the number of replications and the standard deviations of fine-root functional traits were considered; only studies in which the control and experimental warming treatments had the same initial conditions were considered; for multifactorial experiments, only the control and experimental warming treatment data were used and their interactions were excluded. Following Freschet *et al.* (2017), fine roots were defined as all roots with a diameter ≤ 2 mm because this root sampling category was the most common in field studies.

Data extraction

We extracted the following fine-root functional traits from each study: root system traits (root biomass and total root length), morphological traits (diameter and SRL), chemical traits (root C, root N, root phosphorus (P), root C : N ratio and root nonstructural carbohydrates), dynamics (root production, root mortality, belowground net primary production, root life span and root turnover) and one physiological trait (root respiration). In the studies included in our analysis, fine-root production and mortality data were mainly obtained using minirhizotrons. Belowground net primary production was estimated from ingrowth cores and mainly derived from grasslands (Supporting Information Dataset S1). Fine-root respiration referred to specific root respiration (i.e. respiration rate per unit root biomass). We extracted the means, sample size and standard deviation from each study. Data were extracted directly from tables or using PLOT DIGITIZER v.2.6.8 (http://plotdigitizer.sourceforge.net). If experiments were performed at multiple sites in one study, they were treated as independent observations.

We also extracted warming magnitude (°C), duration (number of yr between the initiation of the experiment and the measurements), ecosystem type, soil depth (midpoint of each sampling depth intervals; Chen & Brassard, 2013), latitude (°), longitude (°), mean annual temperature (MAT, °C), and mean annual precipitation (MAP, mm yr^{-1}). Elevated soil temperature was either directly reported or estimated using the median if a range of soil temperatures was provided. Based on the geographic locations, any missing MAT or MAP data were extracted using the WorldClim v.2 dataset (Fick & Hijmans, 2017). The annual aridity index (AI; MAP divided by mean annual potential evapotranspiration) was derived from the CGIAR-CSI Global-Aridity Database (Zomer *et al*., 2008), where a lower AI represents more arid conditions and a higher AI indicates lower aridity. The site characteristics can be found in Tables S1 and S2.

Data analysis

All statistical analyses were conducted in R 3.5.2 (R Core Team, 2018). The natural log-transformed response ratio ($\log_e$RR) was used to evaluate the responses of fine-root traits to warming following Hedges *et al*., (1999):

$$\mathrm{Log_eRR} = \log_e \overline{X}_{\mathrm{treatment}} - \log_e \overline{X}_{\mathrm{control}} \qquad \text{Eqn 1}$$

where $\overline{X}_{\mathrm{treatment}}$ and $\overline{X}_{\mathrm{control}}$ are the mean values of a given fine-root trait (e.g. diameter) in the warming treatment and in the control group, respectively.

Effect size estimates and subsequent inferences in the meta-analyses may be dependent on how individual observations were weighted (Ma & Chen, 2016). More importantly, weighting based on sampling variances could assign extreme importance to only a few individual observations, and consequently average $\log_e$RR would be determined predominantly by a small number of studies. We thus used the replication number for weighting, based on previous studies (Zhang *et al*., 2018; Chen & Chen, 2019; Chen *et al*., 2019):

$$W_{\mathrm{response\ ratio}} = (N_{\mathrm{control}} \times N_{\mathrm{treatment}})/(N_{\mathrm{control}} + N_{\mathrm{treatment}}) \qquad \text{Eqn 2}$$

where $W_{\mathrm{response\ ratio}}$ is the weight associated with each $\log_e$RR observation, N_{control} and $N_{\mathrm{treatment}}$ are the replication numbers in the control and warming treatment, respectively.

We used linear mixed effect models to test whether the response of individual fine-root traits to warming differed from zero, and whether $\log_e$RR varied with warming magnitude (M), warming duration (D) and ecosystem type (E) using the following model structure:

$$\begin{aligned}\mathrm{Log_eRR} = {} & \beta_0 + \beta_1 M + \beta_2 D + \beta_3 M \times D + \beta_4 E \\ & + \beta_5 M \times E + \beta_6 D \times E + \beta_7 M \times D \times E \qquad \text{Eqn 3} \\ & + \pi_{\mathrm{study}} + \varepsilon\end{aligned}$$

where β is a coefficient; π_{study} is the random effect of 'study', accounting for the autocorrelation among observations within each study; and ε is sampling error. Mixed effect models were fitted with maximum likelihood using the LME4 package with $W_{\mathrm{response\ ratio}}$ as the weight for each corresponding $\log_e$RR observation (Bates *et al*., 2017). To prevent overfitting (Johnson & Omland, 2004), we selected the most parsimonious model among all alternative models with the condition to retain M and D, as they were key aspects of the warming treatment to be tested. The model selection was performed by using the 'dredge' function of the MUMIN package (Barton, 2018). All terms associated with ecosystem type (E) were excluded in the most parsimonious models (Table S3). We thus conducted an alternative analysis with the ecosystem type as only fixed factor and the study as random factor (Table S4). We also compared linear and log-linear responses using three other alternative models, and all alternative models resulted in similar or higher Akaike information criterion (AIC) values (Table S5).

As in previous studies (Chen & Chen, 2019; Chen *et al*., 2019), we scaled the continuous predictors (M and D, observed values minus the mean and divided by 1 SD) in Eqn 3 to facilitate the comparison among fine-root traits that had variable M and D. When the continuous predictors were scaled, β_0 is the overall mean $\log_e$RR at the mean M and D (Cohen *et al*., 2013). To graphically illustrate whether the effect of warming magnitude on $\log_e$RR differed with warming duration, we calculated warming duration-dependent magnitude effects following the method proposed by Cohen *et al*., (2013) at warming durations of 1, 2, 4, 10 and 18 yr, respectively. The trend for warming duration over 10 yr was not shown as only one study reported the effect of warming duration longer than 10 yr on belowground net primary production (i.e. significant $M \times D$ effect).

To further investigate whether $\log_e$RR varied with environmental conditions, we selected the most parsimonious models using the method described by substituting E in Eqn 3 with soil depth, MAT and AI, respectively. The environmental variables were modeled individually for the following reasons. First, these predictors (e.g. ecosystem type, MAT and AI) were inherently correlated, and simultaneous modelling would result in strong multicollinearity (Zuur *et al*., 2010). Second, simultaneous modeling of these variables would lead to the number of predictors being greater than the number of studies in our database (Chen *et al*., 2021). The terms associated with soil depth were excluded during model selection with the exception of fine-root biomass (Table S6). As the terms associated with MAT or AI were insignificant for most fine-root traits in Eqn 3, to inspect the effects of these two predictors further (Chen *et al*., 2019), we performed an analysis with MAT or AI as the only fixed effect and the study as the random effect (Table S6). For ease of interpretation, $\log_e$RR and its corresponding confidence intervals (CIs) were transformed back to the percentage change as follows:

$$\left(e^{\log_e \mathrm{RR}} - 1\right) \times 100\% \qquad \text{Eqn 4}$$

Results

Overview of dataset

The constructed dataset included 964 paired observations from 177 published studies (Dataset S1). Ecosystems were classified into five distinct types: cropland (10 studies), grassland (75 studies), forest (62 studies), tundra (19 studies) and wetland (11 studies) (Table S2). The data were mainly collected from Asia (91 studies), followed by North America (40 studies), Europe (37 studies) and Oceania (six studies) (Fig. 1). The methods used for warming were either glasshouse (i.e. enclosed and transparent film covered on the plants in the field, 16 studies), heating cables (30 studies), infrared radiators (77 studies), OTC (48 studies) or reflective curtains (five studies) (Fig. S1). In the dataset, fine-root biomass was the most frequently reported (134 studies), while fine-root life span and turnover were the least frequently reported (four studies).

Effects of experimental warming on fine-root functional traits

Fine-root system, chemistry and morphology Fine-root biomass was increased by, on average, 8.7% (95% confidence intervals, 2.8–14.7%; $P = 0.004$, $n = 363$, Table S3) with warming as compared to the controls (Fig. 2). Total fine-root length showed no significant response to warming ($P = 0.483$, $n = 67$). Under warmer conditions, fine-root N was increased by, on average, 13.3% (3.8–22.8%, $P = 0.009$, $n = 80$), whereas fine-root C : N ratio was decreased by 16.4% (−24.9 to −7.8%, $P = 0.004$, $n = 37$; Table S3) and fine-root nonstructural carbohydrates was decreased by 10.6% (−17.8 to −3.2%, $P = 0.035$, $n = 37$; Table S3; Fig. 2). Fine-root morphological traits (i.e. root diameter and SRL) and root C and P concentrations showed no significant responses to warming ($P > 0.05$; Fig. 2; Table S3). We also found that the warming methods presented a significant effect on response ratios of fine-root biomass, length and N concentration (Table S7). Although results varied widely among studies, response ratios associated with warming cables tended to be stronger than those combined with other aboveground warming methods (Fig. S2).

Fine-root dynamics and physiology Compared with the control, warming increased fine-root production by 30.4% (12.2–48.6%, $P = 0.006$, $n = 86$; Table S3), belowground net primary production by 42.5% (19.7–65.4%, $P < 0.001$, $n = 74$), and specific root respiration by 19.5% (10.1–28.9%, $P = 0.011$, $n = 29$; Fig. 2). Warming did not affect fine-root mortality ($n = 64$), life span ($n = 7$) and turnover ($n = 7$) ($P > 0.05$; Fig. 2).

The response ratios of fine-root production showed no significant relationships with either fine-root biomass or length (Fig. S3a,b). However, there was a significant and positive relationship between response ratios of fine-root production and mortality ($P < 0.001$; Fig. S3c). The response ratios of fine-root respiration did not correlate with response ratios of fine-root biomass, root N or root nonstructural carbohydrates (Fig. S3d–f).

Responses of fine-root functional traits to warming magnitude and duration

With increasing magnitude of warming, the effect size for fine-root biomass decreased significantly ($P < 0.001$; Fig. 3a; Table S3), especially in short-term experiments (magnitude × duration, $P = 0.022$; Fig. 4a). By contrast, the effect size for fine-root N increased ($P = 0.035$; Fig. 3a; Table S3) while that for fine-root C : N ratio decreased with increasing magnitude of warming ($P = 0.011$; Fig. 3a; Table S3). Further, the effect size for fine-root N did not vary with warming duration, while the negative effects of warming on fine-root C : N ratio as well as for nonstructural carbohydrates increased with increasing warming duration ($P = 0.002$ and $P = 0.031$, respectively; Fig. 3b; Table

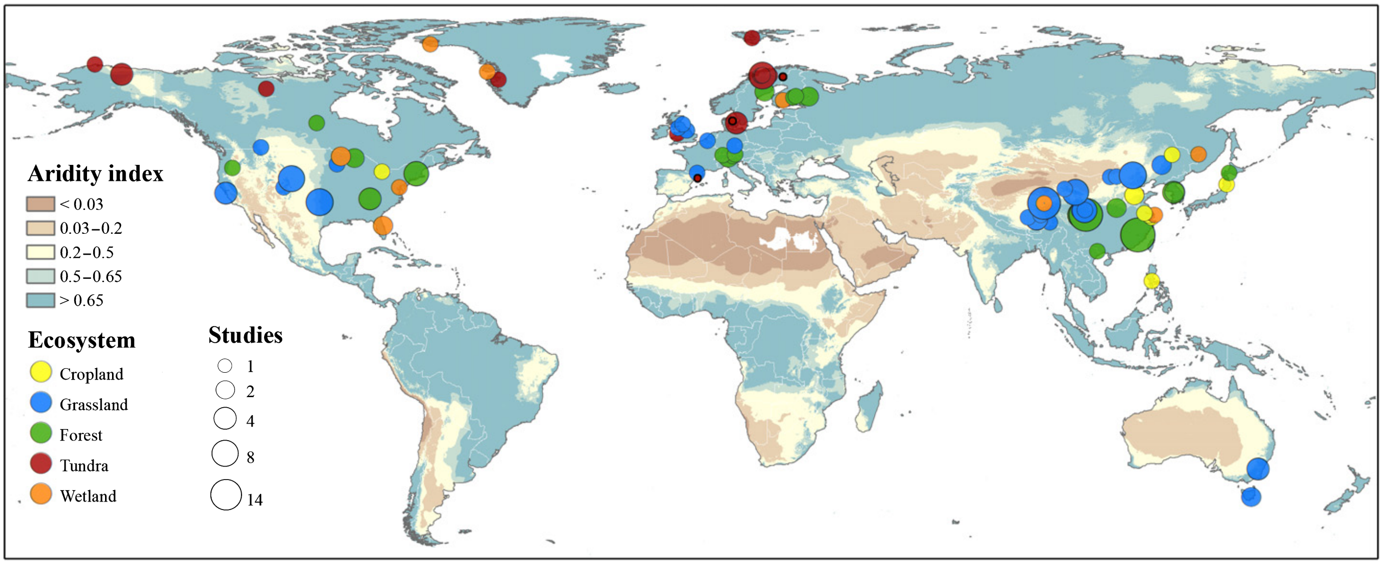

Fig. 1 Geographical distribution of the studies included in this meta-analysis. The terrestrial ecosystems were classified in five groups: cropland, grassland, forest, tundra and wetland.

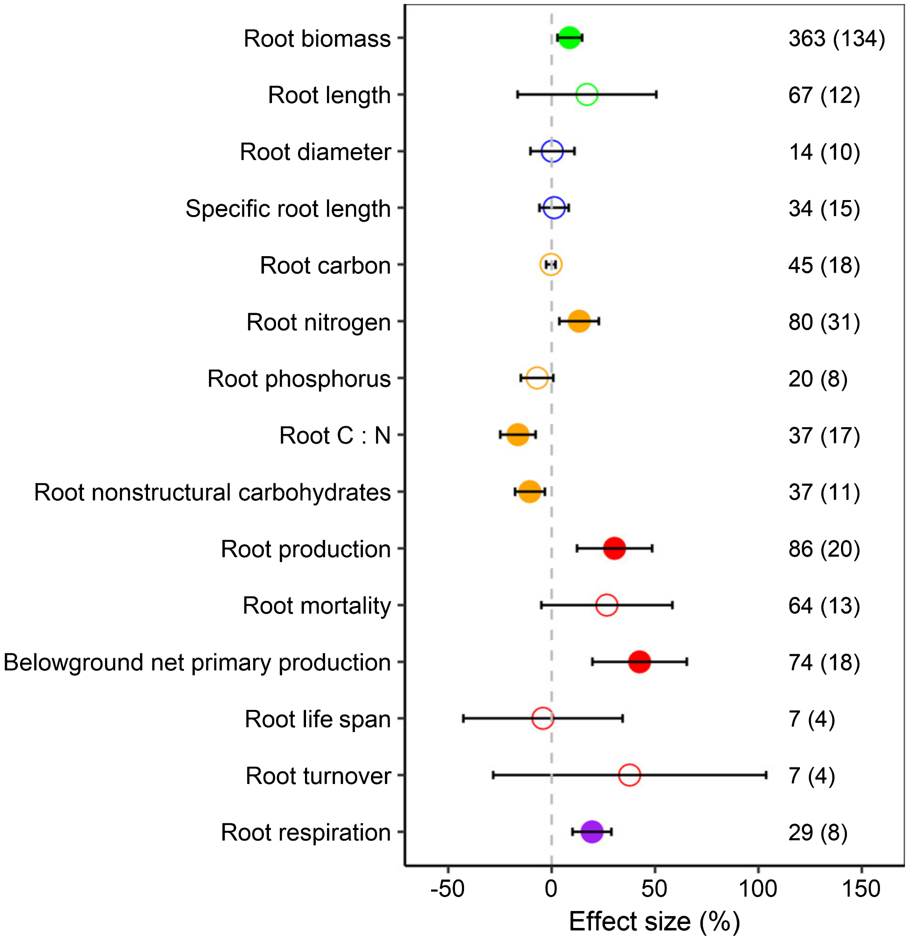

Fig. 2 Effect of warming on fine-root traits (%). Coefficients are bootstrapped mean and their 95% confidence intervals. The coefficient illustrates the strength of the effect of warming on fine-root traits compared with the controls. Numbers represent the number of observations and studies (in brackets). Fine-root carbon : nitrogen (C : N) is the ratio of fine-root C concentration to N concentration. Traits of root system, morphology, chemistry, dynamics and physiology are colored in green, blue, orange, red and purple, respectively. Closed circles represent significant warming effects and open circles indicate insignificant warming effects.

S3). The effect size for belowground net primary production significantly increased with both warming magnitude ($P = 0.041$; Fig. 3a; Table S3) and warming duration ($P = 0.008$; Fig. 3b; Table S3). We also found a larger increase in the effect size with warming magnitude for belowground net primary production in long-term experiments (magnitude × duration, $P = 0.011$; Fig. 4b; Table S3).

Abiotic and biotic factors regulating warming effects

The effects of warming on all fine-root traits did not differ significantly among ecosystem types except for fine-root N (Table S4), which was increased by elevated temperature in forests only (Fig. S4f). The positive effect of warming on fine-root biomass decreased with MAT and in wetter sites (i.e. higher AI) (Fig. 5a, b; Table S6). The warming effect on fine-root N varied with MAT, and the effect sizes for fine-root C : N ratio and nonstructural carbohydrate both changed with MAT and AI (Table S6). We found that the warming effect on fine-root biomass was more pronounced in deeper soil horizons (Fig. 5c). The responses of fine-root dynamics and physiological traits did not change with MAT, AI or soil depth (Table S6).

Discussion

The present meta-analysis provides evidence that experimental warming affects fine-root biomass, chemistry, dynamics and physiology at the global scale. Our findings offer a solid foundation to reconcile the seemingly contrasting responses of these fine-root functional traits to global warming. First, we found that fine-root biomass, N concentration, production and respiration increase with warming while root C : N ratio and nonstructural carbohydrates decrease. Second, we showed that the size of the warming effect on fine-root biomass decreases with increasing magnitude of warming, especially with short-term experiments. By contrast, the effect size of belowground net primary production (i.e. the annual productivity of the whole root system) increased with warming magnitude, particularly among longer-running experiments. Third, our meta-analysis revealed that warming effects were contingent upon environmental conditions.

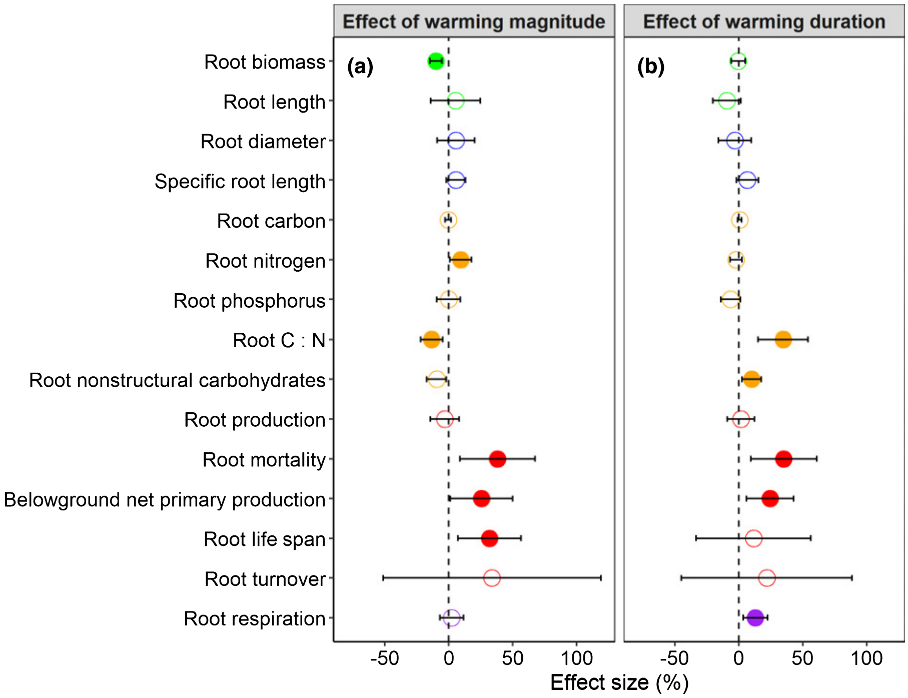

Fig. 3 The effect of warming on fine-root traits (%) in relation to warming magnitude (a) and warming duration (b). The estimated β_1 and β_2 in Eqn 3 are bootstrapped mean coefficients of warming magnitude and duration, respectively (mean ± 95% confidence intervals). Fine-root carbon : nitrogen (C : N) represents the ratio of fine-root C concentration to N concentration. Traits of root system, morphology, chemistry, dynamics and physiology are colored in green, blue, orange, red and purple, respectively. Closed circles represent significant warming effects and open circles indicate insignificant warming effects.

In particular, we found that the positive effect of warming on fine-root biomass was stronger in colder and drier climates and in deeper soil horizons.

Warming induces variable responses of fine-root traits

We found that experimental warming was associated with increases in fine-root biomass and N concentration and decreases in fine-root C : N and nonstructural carbohydrates, but had no significant effects on total root length and morphological traits. As expected, warming increased fine-root biomass across a wide range of terrestrial ecosystems, which is consistent with Lin *et al.* (2010), who showed that warming increases total root biomass by 13%. This may be attributable to a significant increase in fine-root production coupled with limited or variable changes in fine-root mortality (Wan *et al.*, 2004). It is also notable that the stimulation of photosynthesis and extension of growing season under elevated temperature could also benefit root growth (Malhotra *et al.*, 2020).

In contrast to biomass, total root length was not significantly increased by warming in our meta-analysis. Logically it is impossible to change biomass without concomitant changes in total root length or compensatory changes in root morphology (e.g. increases in diameter or decreases in SRL associated with increased tissue density). However, there was wide variation reported among different studies, many of which indicated that warming increased total fine-root length (Yin *et al.*, 2013; Mueller *et al.*, 2018). In some cases, the warming-induced increase in soil N availability may reduce relative C allocation to fine roots compared with above ground, leading to limited changes or even decreases in standing root length (Arndal *et al.*, 2018). The differences reported between biomass and total length may also be as a result of differences in measurement approach, with bulk soil collections (e.g. soil cores) comprising the majority of biomass data and minirhizotron observations representing a higher proportion of root length observations. Meanwhile, insignificant responses of root diameter and SRL to warming could have largely been a result of the limited sample size (14 and 34 observations, respectively) compared with that of biomass (363 observations). Thus, further study with concurrent measurements of root size and root biomass is warranted to verify their independent responses to warming.

Fine-root N concentration increased while C concentration showed no significant response, which led to a decrease in fine-root C : N ratio under warming. Warming stimulates net N mineralization and soil N availability, which may be associated with simultaneous increase in root N content (Bai *et al.*, 2013; Salazar *et al.*, 2020). A low C : N ratio is usually an indicator of high root litter quality, which may accelerate root decomposition (See *et al.*, 2019). Fine-root nonstructural carbohydrates also decreased with warming, suggesting that more C is likely allocated to compensatory growth, as proposed by McDowell (2011). Moreover, the warming-induced water stress may reduce the nonstructural carbohydrates as a result of metabolic needs for osmotic adjustment (Hartmann & Trumbore, 2016).

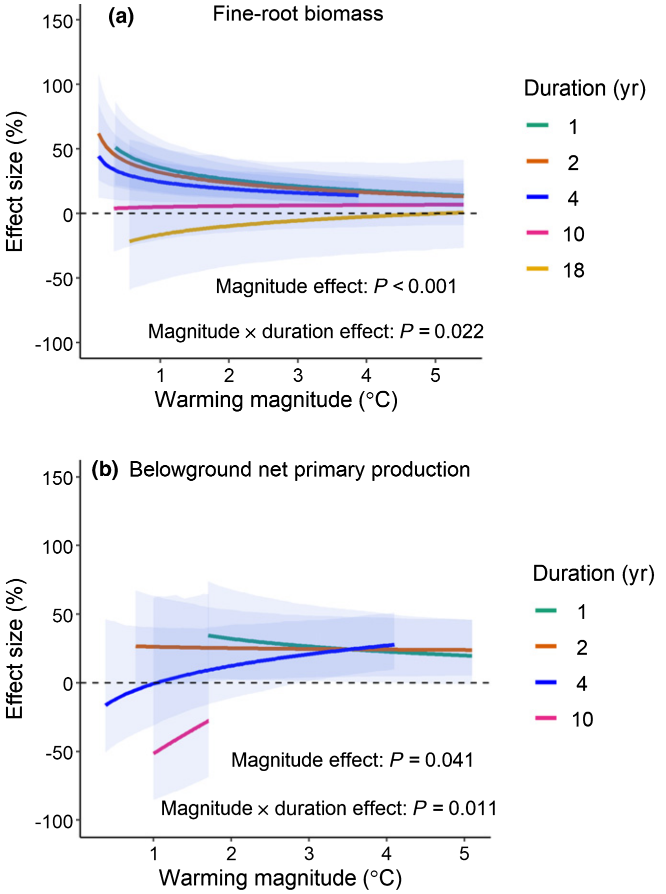

Fig. 4 Interactive effects of warming magnitude and duration on fine-root biomass (a) and belowground net primary production (b). Lines are fitted from duration-specific regressions with bootstrapped 95% confidence intervals (blue shading). Colored lines represent warming duration at 1, 2, 4, 10, 18 yr, respectively. For fine-root biomass, the numbers of observations are 90, 106, 86, 58 and 23 for green, orange, blue, pink and yellow lines, respectively. For belowground net primary production, the numbers of observations are 11, 20, 19 and 21 for green, orange, blue and pink lines, respectively.

Fine-root production was higher in warming treatments than in the controls. This could be explained by faster plant growth as a result of higher photosynthetic rates induced by warming (Liang *et al*., 2013) or by the increases in soil N net mineralization and availability associated with higher microbial activity, which may also be caused by warming (Bai *et al*., 2013). Moreover, as a response to soil drying after warming, more C is allocated to root growth in order to increase water uptake (Xiong *et al*., 2018). We similarly found that belowground net primary production – the annual productivity of the whole root system – increased with warming. This is in agreement with Wu *et al.* (2011) who found that warming stimulated plant growth and increased belowground net primary production by *c.* 52% across diverse ecosystems. Root mortality, unlike production, was not responsive to warming. However, it should be noted that while not significant, there was an apparent trend towards increased mortality as reflected in many previous studies (Xiong *et al*., 2018; Liese *et al*., 2019). The nonsignificant change of root mortality could be a result of variable estimation of mortality on a minirhizotron window, where it can sometimes be difficult to assess root death, or a lag effect where mortality takes longer to display a measurable response to experimental warming well after production effects become apparent. In either case, we suggest that further study is needed to confirm or amend our current observation for limited changes of root mortality with warming.

As expected, fine-root respiration increased under warming conditions, probably because of increased root activity and C used for maintaining root function (Pregitzer *et al*., 2000). However, fine-root turnover and life span were unresponsive, despite the enhanced root respiration that has been suggested to cause faster turnover rate and shorter life span (Eissenstat & Yanai, 1997; Roumet *et al*., 2016; M. Zhou *et al*., 2018). Turnover is generally defined as annual production divided by standing biomass (McCormack *et al.* 2014). In our study, increases in production were partly balanced by increases in standing biomass, which may have led to the lack of change in turnover. It is also important to note that the lack of significant responses in turnover and life span could be ascribed to their low sample numbers compared with most other measured traits.

Warming effects depend on warming magnitude and duration

Our results suggest that warming magnitude may interact with duration to affect fine-root traits. This interactive effect has not been fully considered in previous manipulative experiments or global syntheses. The decrease in the effect size of fine-root biomass at higher temperatures (*c.* > 2°C) could have been a result of increased root mortality with increasing magnitude of warming. This threshold of warming magnitude for fine-root biomass has implications for soil organic C sequestration in the context of future global warming. The warming effect on fine-root biomass switched from positive to negative with longer warming duration (*c.* > 10 yr), which is probably a consequence of higher root mortality with warming time. Conversely, the increasing effect size for belowground net primary production with warming magnitude could be explained by a stimulation of overall plant growth at higher temperatures, leading to increasing transport of carbohydrate from the leaves to fine roots (Wu *et al*., 2011). The interactive effect of warming magnitude and duration on belowground net primary production suggests a lasting effect of warming on root-derived C inputs into soils with time. Long-term observations are therefore needed to improve our forecasting of the long-term effects of warming on soil C cycling and storage.

At the species or ecosystem level, the effect of warming on root respiration might be transient, as plants may acclimate to warmer temperature over time (Luo *et al*., 2001; Jarvi & Burton, 2013; Melillo *et al*., 2017). However, we found that warming continued to increase fine-root respiration with increasing treatment duration. This provides no clear evidence of acclimation of fine-root respiration to warming across a wide range of experimental durations. Sustained increases in fine-root respiration could in turn lead to the release of a large amount of C to the atmosphere. This is particularly true in grasslands and tundra where plant

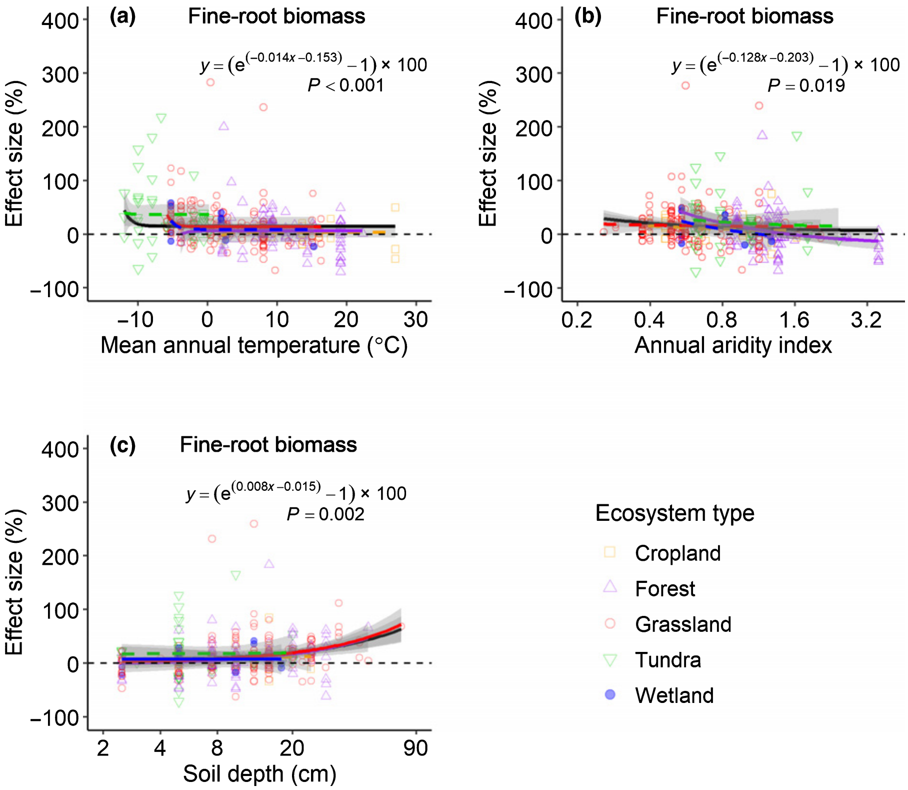

Fig. 5 Effect size (%) of warming on fine-root biomass in relation to mean annual temperature (a), annual aridity index (b) and soil depth (c). The sizes of the circles represent the relative weights of the corresponding observations. Lines are fitted from ecosystem-specific regressions with bootstrapped 95% confidence intervals (gray shading). Colored and black lines represent each ecosystem type and the average across all observations. Significant and nonsignificant responses are showed with solid and dashed lines, respectively. The fitted equation is the average response across all the ecosystem types. The numbers of observations for cropland, grassland, forest, tundra and wetland are 24, 151, 111, 66 and 11, respectively.

biomass is mainly located below ground (Schenk & Jackson, 2002; Iversen *et al.*, 2015).

Warming effects are modulated by environmental conditions

Our analysis detected that the responses of fine-root traits to warming were consistent across global terrestrial biomes with the exception of fine-root N, which increased in forests only. The strongest response of fine-root N to warming in forests may be ascribed to the higher soil net N mineralization in forests compared with other ecosystems (e.g. grassland and tundra) at the global scale (Bai *et al.*, 2013). But even here, results are equivocal. Lim *et al.* (2019) reported that soil warming did not increase soil N mineralization in a boreal forest across an 18 yr experiment. Thus, we should be cautious about the conclusions we draw, as many studies represent relatively short-term experiments, which may overestimate warming-induced changes in fine-root traits.

While root trait responses were largely consistent among global biomes, we also found that warming effects were affected by specific environmental conditions. The positive effect of warming on fine-root biomass decreased with mean annual temperature, suggesting a stronger response of fine-root biomass in colder environments where plant growth is generally limited by temperature (Chapin *et al.*, 1995). Consistent with our findings, Salazar *et al.* (2020) showed that warming increased belowground root biomass in high-latitude tundra and grassland ecosystems at the global scale. Furthermore, the effect size of fine-root biomass increased with increasing aridity, indicating that plants growing in dry sites tend to prioritize fine-root growth, possibly because warming exacerbates water stress. Similarly, a recent study reported that warming effect on plant root : shoot biomass ratio ($\log_e$RR) switched from positive in dry areas, indicating greater investment in roots, to negative in wet areas, indicating greater investment in shoots (Song *et al.*, 2019).

Our analysis also revealed a stronger warming response of fine-root biomass in deeper soil layers. This is probably because roots increase foraging in deeper soil layers under water stress induced by warming (Keuper *et al.*, 2017; Wang *et al.*, 2017; Liu *et al.*, 2018). Warming enhances the accumulation of root biomass in deeper soil horizons. This has the potential to increase root-derived C inputs (including root litter and exudates) at depth and to favor subsoil C sequestration (Ding *et al.*, 2017; Jackson *et al.*, 2017; Jia *et al.*, 2019).

Limitations and implications

The present study indicates that experimental warming induces variable responses of fine-root traits. The warming effects on fine-root traits are also modulated by warming magnitude and duration as well as environmental conditions. It is also important to note that different warming methods can impact the detection of a warming effect on fine-root traits. Therefore, the mechanisms underlying specific fine-root trait responses deserve further exploration in future field studies, with emphasis placed on maintaining trials over long timescales while considering the potential impacts of variable methodologies.

Root life span and turnover are critical parameters in C cycle models for the evaluation of plant C allocation and soil C storage (McCormack *et al.*, 2015b; Wang *et al.*, 2019). Unfortunately, the limited data available on root dynamics hamper the exploration of the tradeoffs between these traits and other root traits. Thus, further examination of these critical traits in response to climate warming should be a priority of future studies. The nonsignificant results when testing warming responses within ecosystem types may be the result of under-representation of croplands, wetlands and tundra in warming studies. This hampers our ability to identify the significant differences among ecosystems more broadly.

To the best of our knowledge, our study is one of the first global syntheses investigating an array of fine-root traits in response to experimental warming. Our findings have important implications for ecosystem modeling and future manipulative experiments. First, the differential responses of fine-root traits to warming can help inform which ecosystem process are likely to change in the face of future warming scenarios. Second, the representation of fine-root traits in Earth system models is too simplistic, which is a serious shortcoming for simulating global biogeochemical cycling (Iversen, 2010; Warren *et al.*, 2015). In this context, our findings could be valuable to help parameterize, constrain or benchmark models. Third, our study detects that the responses of fine-root traits to warming vary with time and environmental conditions, highlighting the importance of longer-timescale observations. The responses of fine-root traits to other global change factors, such as N deposition (Li *et al.*, 2015), precipitation change (G. Zhou *et al.*, 2018; Wang *et al.*, 2020) and CO_2 enrichment (Nie *et al.*, 2013), have been investigated at the global scale. Yet, the interactive effects of warming with these global change drivers are still uncertain, highlighting the need to conduct multifactorial experiments (Rillig *et al.*, 2019; Rineau *et al.*, 2019; Hanson & Walker, 2020).

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Author contributions

JW and SN conceived the ideas and designed methodology; JW and LY collected the data; JW and SN analyzed the data; JW, CD, MLM and SN drafted the manuscript; DT, YL, EH, TY, ZL, WB and YC commented on the manuscript. All authors gave final approval for publication.

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Data availability

Data can be found in Supporting Information Dataset S1.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Detailed data used in this meta-analysis.

Fig. S1 Five typical techniques for field warming manipulation experiments.

Fig. S2 Effects of warming method on natural log response ratios of fine-root biomass, fine-root length and fine-root nitrogen.

Fig. S3 Relationships between natural log response ratios of fine-root functional traits.

Fig. S4 Comparison of fine-root trait responses to warming magnitude among five ecosystem types.

Table S1 Summary of site characteristics, warming magnitude and duration in the dataset.

Table S2 Summary of site characteristics, warming magnitude and duration in five ecosystem types.

Table S3 Akaike information criterion (AIC) values for the full model and the most parsimonious model.

Table S4 Effect of ecosystem type on natural log response ratios of fine-root traits.

Table S5 Akaike information criterion (AIC) values for the linear and log-linear warming magnitude and warming duration models.

Table S6 Effects of soil sampling depth, mean annual temperature and annual aridity index on natural log response ratios of fine-root traits.

Table S7 Effect of warming method on natural log response ratios of fine-root traits.

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