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Individual and combined effects of multiple global change drivers on terrestrial phosphorus pools: A meta-analysis

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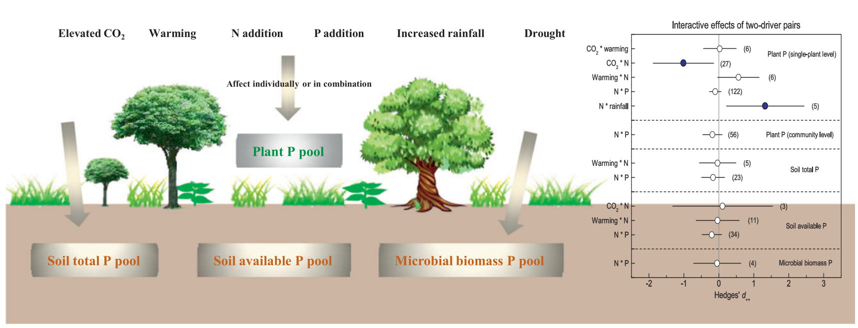
HIGHLIGHTS

- Terrestrial P pools were most sensitive to the individual effects of warming and P addition.
- Terrestrial P pools were consistently stimulated by P addition or N + P addition.
- Individual and combined effects were significantly modulated by environmental and experimental setting factors.
- Interactive effects of multiple drivers on terrestrial P pools were more likely to be additive.

GRAPHICAL ABSTRACT



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ABSTRACT

Human activity-induced global change drivers have dramatically changed terrestrial phosphorus (P) dynamics. However, our understanding of the interactive effects of multiple global change drivers on terrestrial P pools remains elusive, limiting their incorporation into ecological and biogeochemical models. We conducted a meta-analysis using 1751 observations extracted from 283 published articles to evaluate the individual, combined, and interactive effects of elevated CO_2, warming, N addition, P addition, increased rainfall, and drought on P pools of plant (at both single-plant and plant-community levels), soil and microbial biomass. Our results suggested that (1) terrestrial P pools showed the most sensitive responses to the individual effects of warming and P addition; (2) P pools were consistently stimulated by P addition alone or in combination with simultaneous N addition; (3) environmental and experimental setting factors such as ecosystem type, climate, and latitude could significantly influence both the individual and combined effects; and (4) the interactive effects of two-driver pairs across multiple global change drivers are more likely to be additive rather than synergistic or antagonistic. Our findings highlighting the importance of additive interactive effects among multiple global change drivers on terrestrial P pools would be useful for incorporating P as controls on ecological processes such as photosynthesis and plant growth into ecosystem models used to analyze effects of multiple drivers under future global change.

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1. Introduction

Phosphorus (P) is one of the most limiting nutrients for terrestrial biological productivity that usually plays a crucial role in net carbon (C) uptake in terrestrial ecosystems (Filippelli, 2002). Unlike nitrogen (N), which could be fixed by plants such as legumes, the available P for plants and microorganisms is derived mainly from mechanical rock weathering, atmospheric deposition (Newman, 1995) and, to a lesser extent, from organic matter decomposition (Vitousek, 2004). The flux of P is almost unidirectional, moving from on land ecosystems to streams and rivers with minimal input back via spray (Liu et al., 2008). However, global change drivers and human activities such as a rapidly increasing use of synthetic fertilizers could dramatically change the global cycling of P, which further influences the productivity and functioning of ecosystems (Goll et al., 2012; Peñuelas et al., 2013). Thus it is of great importance to assess the effects of global change drivers on terrestrial P dynamics.

Terrestrial biogeochemical models and field manipulative studies have examined the individual effects of several global change drivers on terrestrial P concentration. For example, case studies in field experiments have been conducted to examine the effects of N addition on plant P concentration, but negative (Tessier and Raynal, 2003), positive (Liu et al., 2013) and neutral (Weand et al., 2010) effects were all observed. A recent meta-analysis study suggested that N addition decreased plant P concentration by an average of 8% at the global scale (Deng et al., 2017). In contrast, external P addition is more likely to increase the concentrations of P in both plants and soils (Li et al., 2016). A synthesis study showed that drought stress has significant negative effects on plant P concentration, decreasing which by an average of 9.2% (He and Dijkstra, 2014), but have significant positive effects on the concentration of soil available P (SAP) (Delgado-Baquerizo et al., 2013). Moreover, studies also suggested that the individual effects of one driver can be meditated by another one (Huang et al., 2015), indicating that the combined effects of multiple global drivers may be of greater importance than individual effects. However, despite these explicit assessments on the individual effects of multiple global change drivers on terrestrial P concentration, few global syntheses (but see Deng et al., 2017; Li et al., 2016) have been conducted so far to reveal the individual and combined effects of these drivers on terrestrial P pool. The responses of P pool to global change drivers may significantly differ with P concentration. For example, drought has been found to generally reduce plant P concentration (He and Dijkstra, 2014), but plant P concentration can also increase when plant growth decrease more than plant P uptake in response to drought. In such case, however, plant P pool may decrease even more severely. Thus it is important to individually assess the responses of terrestrial P pool to global change drivers. Moreover, even less available studies have noticed if the interaction of the combined effects (interactive effects) of multiple global change drivers might or might not be additive.

Additive interaction occurs when the combined effect of two or more drivers is equal to or not significantly different from the sum of the individual effect. When the combined effect is greater or weaker than the sum of the individual effects, the net effect could be synergistic or antagonistic, respectively (Crain et al., 2008; Yue et al., 2017a). Because N and P are the most limiting nutrients for plant growth (Elser et al., 2007), their interaction was usually reported to be synergistic (Harpole et al., 2011; Li et al., 2016). However, additive interactive effects of N and P on terrestrial C pool was also reported to be more common at a global scale (Yue et al., 2017b). In addition to the observed common additive interaction of N and P, the interactive effects of two-driver pairs of multiple global change drivers such as elevated CO_2 (eCO_2), warming, increased rainfall and drought on terrestrial C pool (Yue et al., 2017b) and N:P ratio (Yuan and Chen, 2015) were also found to be additive. Despite these interesting findings, both synergistic and antagonistic interactive effects were also observed in previous studies (Dieleman et al., 2012; Mueller et al., 2016; Wu et al., 2011). However, available synthesis studies investigating the interactive effects of global change drivers are mainly focused on N concentration, C pool, or C:N:P ratios (Yue et al., 2017a, 2017b; Yuan and Chen, 2015), no studies have assessed the responses of terrestrial P pools to the interactive effects of multi-drivers. Because the responses of different variables to global change drivers can significantly vary (Zhou et al., 2016), a lack of evaluation on terrestrial P pools will make it difficult to definitively predict whether the interactive effects of multiple global change drivers on terrestrial P pools additive or not, which limits their incorporation into ecological and biogeochemical models under future global change scenarios.

Here, we comprehensively reviewed previously published articles and conducted a meta-analysis to quantitatively evaluate the individual, combined and interactive effects of major global change drivers of eCO_2, warming, N addition, P addition, increased rainfall and drought on different types of terrestrial P pools (i.e. plant, soil and microbial biomass) and the potential influencing factors. The main issues addressed in the present study were (1) how the individual and combined effects of the investigated multiple global change drivers affect different types of P pools; (2) which environmental and experimental setting factors (e.g. latitude, climate, ecosystem type and study length) influence the responses of terrestrial P pools to the individual and combined effects of these drivers; and (3) whether the interactive effects of these drivers additive or not. We hypothesized that (1) both the individual and combined effects of multiple global change drivers can significantly affect terrestrial P pools, but the individual effect of P addition or the combined effects of P addition with other drivers are most manifest; (2) additive interactive effects of the investigated multiple global change drivers on terrestrial P pools will be much more common than synergistic and antagonistic ones; and (3) environmental and experimental setting factors can significantly influence both the individual and combined effects.

2. Materials and methods

2.1. Data collection and extraction

Using *ISI Web of Science*, *PubMed,* and *Google Scholar*, we collected data from peer-reviewed journal articles that reported terrestrial ecosystem P pools in response to key global change drivers of eCO_2, warming, N addition, P addition, increased rainfall, drought, and any combination of these six drivers. We searched articles before July 2017 with no restriction on publication year, and focused on field manipulative studies in both agricultural and natural ecosystems. The following criteria were adopted to minimize publication bias for choosing appropriate studies: (i) field manipulative experiments reported at least one of our concerned global change drivers; (ii) full-factorial design was used to assess the combined effects of multiple drivers; (iii) control plots had the same ecosystem type and environmental conditions as all experimental plots at the beginning of the experiment; (iv) the magnitude of the treatment and the study length were clearly recorded, and measurements of the variables in the experimental and control groups were performed at the same spatial and temporal scales; (v) studies were chosen only when the study length was no less than one growing season; and (vi) means, sample sizes, and standard deviations (SD) or standard errors (SE) of the chosen variables were directly provided or could be estimated from the reported data. The treatment magnitude of increased rainfall or drought was expressed as percentage changes in mean annual precipitation. Plant P pools at both single-plant and plant-community levels were either directly reported in the primary studies or calculated as the product of P concentration and the corresponding biomass of whole plant or compartments. Data for soil P and microbial biomass P (MBP) pools were directly extracted from primary studies or determined with soil bulk density, sampling depth, microbial biomass, and corresponding P concentrations. Because SAP is most important for plant growth and ecosystem productivity, we also discussed SAP (referring to Olsen inorganic P) in this study. For soil total P, SAP and MBP, we only included surface mineral soil samples with a maximum depth of 30 cm to increase sensitivity for detecting small responses of these variables (van Groenigen et al., 2006).

When several measurements were taken at different times for a single primary study, we used values from the last measurement to meet the statistical assumption of independence among observations in the meta-analysis (Hedges et al., 1999). Moreover, we considered each of the observations representing different treatment levels, geographical locations, plant species and/or ecosystem types from a single primary study as independent observations in our analysis. However, strictly speaking, these observations may appear nonindependent, we thus conducted a sensitivity analysis. By comparing the results obtained by analyzing the full database with the reduced database from a randomly selected single effect size per primary study in the case of multiple observations, we found that the mean effect sizes are similar and the 95% confidence intervals (CIs) overlap between the full and the reduced database almost in all cases (Table S1), thus all the data can be confidently included in the analysis (Ferreira et al., 2015; Vilà et al., 2011). Because of the lacking of data assessing the combined effects of three or more drivers, we considered only two-driver pairs in this research. After extraction, a total of 283 published articles representing 1751 observations were included in our database (Fig. S1, Text S1, Table S2).

For the conditions of the control plots across all the data points, ambient CO_2 concentration ranged from approximately 300 to 460 ppm in eCO_2 treatment, temperature from −7.3 to 25.2 °C in warming treatment, N deposition from about 3 to 35 kg N hm^{-2}, and mean annual precipitation from 345 to 1600 mm and 455 to 2900 mm in increased rainfall and drought treatments, respectively. However, data of P deposition in the control plots were seldom reported in the primary studies. As differences in the conditions of control plots may influence P pool responses to each driver, we thus categorized the constructed database into different subgroups according to ecosystem type, because such conditions generally similar for a specific ecosystem type. Moreover, to further assess the influence of moderator variables, which is defined as biotic and abiotic explanatory variables in meta-analysis, we categorized the constructed database into different subgroups according to ecosystem type, plant functional type (PFT), manipulative facility, and fertilizer chemical form. Continuous moderator variables such as latitude, longitude, mean annual temperature (MAT), mean annual precipitation (MAP), treatment magnitude (only for individual effects because of different units in two-driver pairs), study length, and soil depth were also included in our database. When the data in primary studies were presented graphically, the figures were digitized to extract the numerical values using the free software Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA). Moreover, climate factors (i.e., MAT and MAP) included in our database were obtained directly from the primary studies or extracted from the *WorldClim* database (http//:www.worldclim.org) using the location information in case that these data were not reported.

2.2. Calculation and analysis

The individual effect of a global change driver or combined effect of a two-driver pair was defined as the response of a variable (e.g., SAP) in the treatment compared with the control (Crain et al., 2008), which was described by the natural-log response ratio (lnRR) (Hedges et al., 1999):

$$\mathrm{lnRR} = \ln\left(\frac{X_e}{X_c}\right) \tag{1}$$

where X_e and X_c are the mean values for the experimental and control treatments, respectively. The variance (ν_1) and weight (w_1) associated with each lnRR value and the weighted mean lnRR (lnRR_{++}) were also calculated, which were described in detail elsewhere (Yue et al., 2017b). The individual or combined effect was significant if the 95% CI of lnRR_{++} did not overlapped with zero (Rosenberg et al., 2000). We used the equation $(e^{\mathrm{lnRR}_{++}} - 1) \times 100\%$ to calculate the net responses of P pools to the individual or combined effects as mean percentage of changes compared with the control (%), and the effects were considered significant at $P < 0.05$ if the 95% CI did not overlap with zero. The lnRR_{++} and associated 95% CI were calculated using the mixed model included in the meta-analytical software MetaWin 2.1 (Rosenberg et al., 2000). The effect of each categorical moderator variable on lnRR was evaluated by comparing the heterogeneity within (Q_w) and between (Q_b) moderator levels using mixed model (Borenstein et al., 2009). The relationships between continuous moderator variables and lnRR of P pools were assessed by conducting linear regression analyses following Koricheva et al. (2013) that has been widely used in meta-analysis studies (e.g. Deng et al., 2017; Li et al., 2016). Moreover, the publication bias of the overall database for each variable included in this study was evaluated by funnel plots, which are scatter plots of the effect sizes versus the sample sizes of observations, using MetaWin 2.1 (Rosenberg et al., 2000). The funnel plots for all variables were symmetrical, indicating absence of publication bias.

To further assess whether the interaction between individual drivers of a two-driver pair additive or not, we employed established methods according to previous studies (Gurevitch et al., 2000) by calculating Hedges' *d*. We chose Hedges' *d* because it is an estimate of the standardized mean difference not biased by small sample sizes (Gurevitch and Hedges, 2001). The interactive effect size (d_I) between drivers A and B were calculated by Eq. (2):

$$d_I = \frac{(X_{AB} - X_A) - (X_B - X_C)}{s} J(m) \tag{2}$$

where X_C, X_A, X_B, and X_{AB} are means of a variable in the control and treatment groups of A, B, and their combination (AB), respectively; s and $J(m)$ are the pooled SD and correction term for small sample bias, respectively, which were calculated by Eqs. (3) and (4), respectively.

$$s = \sqrt{\frac{(n_c - 1)s_c^2 + (n_A - 1)s_A^2 + (n_B - 1)s_B^2 + (n_{AB} - 1)s_{AB}^2}{n_c + n_A + n_B + n_{AB} - 4}} \tag{3}$$

$$J(m) = 1 - \frac{3}{4m - 1} \tag{4}$$

where n_C, n_A, n_B, and n_{AB} are the sample sizes, and s_C, s_A, s_B, and s_{AB} are the SDs in the control and experimental groups of A, B, and their combination (AB), respectively; m is the degree of freedom ($m = n_c + n_A + n_B + n_{AB} - 4$). The variance of d_I (ν) was estimated by Eq. (5):

$$\nu = \frac{1}{n_c} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{1}{n_{AB}} + \frac{d_I^2}{2(n_c + n_A + n_B + n_{AB})} \tag{5}$$

The weighted mean d_I (d_{++}) was calculated according to Eq. (6):

$$d_{++} = \frac{\sum_{i=1}^{l} \sum_{j=1}^{k} w_{ij} d_{ij}}{\sum_{i=1}^{l} \sum_{j=1}^{k} w_{ij}} \tag{6}$$

where l is the number of groups, k is the number of comparisons in the i^{th} group, and w is weight, which is also the reciprocal of the variances ($1/\nu$). The 95% CI of d_{++} was estimated as $d_{++} \pm C_{\alpha/2} \times s(d_{++})$, in which $C_{\alpha/2}$ is the two-tailed critical value of the standard normal distribution.

Accordingly, the type of interaction between two drivers was classified into additive, synergistic, and antagonistic (Zhou et al., 2016). The interactive effect was considered to be additive if the 95% CI overlapped with zero. If the individual effects of two-driver pairs were either both negative or have opposite directions, the interactions less than zero were synergistic and greater than zero antagonistic. When the individual effects were both positive, the interactions were interpreted in the opposite manner (i.e. greater than zero were synergistic and less than zero antagonistic).

3. Results

3.1. Individual effects of multiple global change drivers on terrestrial P pools

Overall, plant P pool at the single-plant level was significantly decreased by warming with an average of 7%, but significantly increased

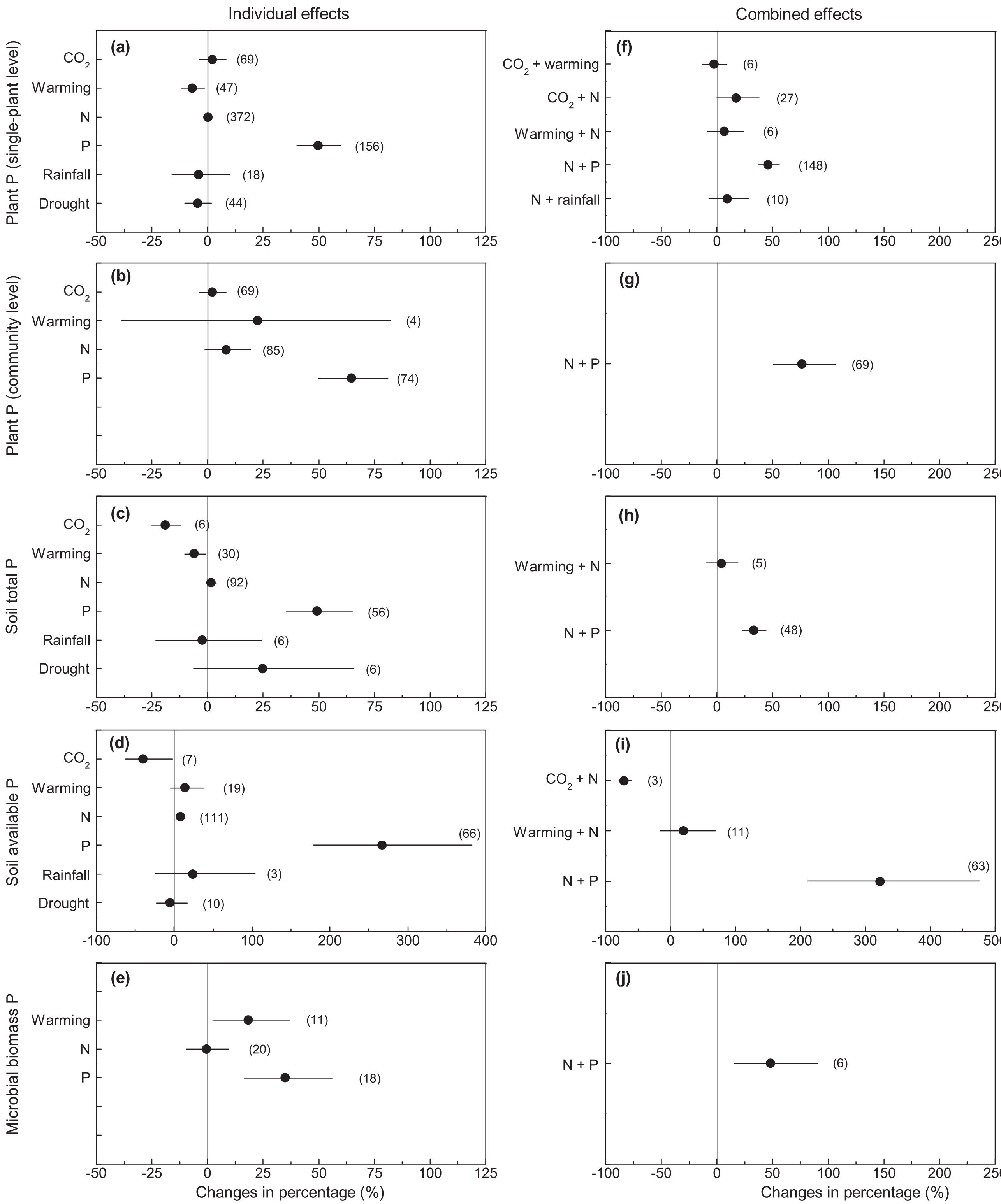

Fig. 1. Individual and combined effects of multiple global change drivers on terrestrial P pools. Results are expressed as the percentage change relative to the control (%). Values indicate the means with 95% confident intervals (CIs) and the numbers of sample size are shown in parentheses. The effects of global change drivers are significant when the 95% CIs does not overlap with zero. CO_2: elevated CO_2; N: nitrogen addition; P: phosphorus addition; Rainfall: increased rainfall.

by P addition with an average of 50% across all observations (Fig. 1a). However, eCO_2, N addition, increased rainfall and drought showed insignificant effects on plant P pool at the single-plant level (Fig. 1a). Similarly, plant P pool at the community level was minimally affected by eCO_2, warming and N addition, but was significantly increased by P addition with an average of 65% (Fig. 1b). Soil total P was significantly decreased by eCO_2 (−19%) and warming (−6%) and stimulated by P addition (+49%), but showed insignificant response to N addition, increased rainfall and drought (Fig. 1c). Likewise, eCO_2 had significant negative effects on SAP pool (−40%), however, warming showed no effects on SAP (Fig. 1d). Both N addition and P addition significantly stimulated SAP pool by 8% and 266%, respectively, while increased rainfall and drought still had no effects (Fig. 1d). As to soil MBP, warming and P addition significantly increased the pools of which by 18% and 35%, respectively, while N addition showed no effects (Fig. 1e).

3.2. Combined and interactive effects of multiple global change drivers on terrestrial P pools

Averaged across all the available observations of two-driver pairs, the combined effects of N addition + P addition showed consistently significant and positive effects on terrestrial P pools, stimulating plant P pool at the single-plant level, plant P pool at the community level, soil total P, SAP, and MBP pools by 46%, 76%, 33%, 72%, and 322%, respectively (Fig. 1f-j). While the combined effects of eCO_2 + N addition only significantly decreased SAP by an average of 72% (Fig. 1i). However, the combined effects of other available two-driver pairs such as warming + N addition and N addition + increased rainfall showed no effects on terrestrial P pools. Across all the individual two-driver pairs, additive interactive effects exhibited a substantial predominance compared with synergistic and antagonistic ones, and only the interactive effects of eCO_2 × N addition and N addition × increased rainfall showed antagonistic interactive effects on plant P pool at the single-plant level (Fig. 2). Despite these overall antagonistic interactions, the frequency distribution suggested that interactions were more likely to be additive among all the individual observations because individual additive interactions accounted for a majority almost in all cases (Fig. 2). Moreover, due to the lack of available data, other potential two-driver pairs (see Table S2) were not discussed in this study.

3.3. Influences of moderator variables

Both the individual and combined effects of multiple global change drivers on terrestrial P pools can be regulated by moderator variables such as ecosystem types, latitude, study length, and climate (i.e. MAT and MAP) (Fig. S2–S14). For example, eCO_2 showed no effects on plant P at the single-plant level across all types of forests, but had significant positive effects (+15%) across subtropical and tropical forests (Fig. S2). Study length was found to be an important moderate variable, showing significant positive influence on the individual effect of P addition on plant P pool at the community level (Fig. S11g). The individual effects of eCO_2 on plant P pool at the single-plant level exhibited significant negative correlations with latitude but significant positive correlations with MAP (Fig. S8). Likewise, the combined effects of N addition + P addition on soil total P showed significant positive correlations with latitude and MAP (Fig. S14).

4. Discussion

Supporting the first hypothesis, our results demonstrated that both the individual and combined effects of multiple global change drivers can significantly affect terrestrial P pools, but varied among different drivers or driver pairs. The individual effects of eCO_2 significantly reduced the pools of soil total P and SAP, which may be attributed to relatively larger plant P uptake from the soil in order to sustain increased growth under eCO_2 (Hoosbeek, 2016). However, our results suggested that eCO_2 showed no effect on plant P pool at both the single-plant and plant community levels, which were inconsistent with the findings of a previous meta-analysis (Deng et al., 2015). The contradictory results may arise from the fact that eCO_2 effects on plant P can vary substantially among different species in both magnitude and direction (Liu et al., 2012), resulting in an overall insignificant effect. Warming

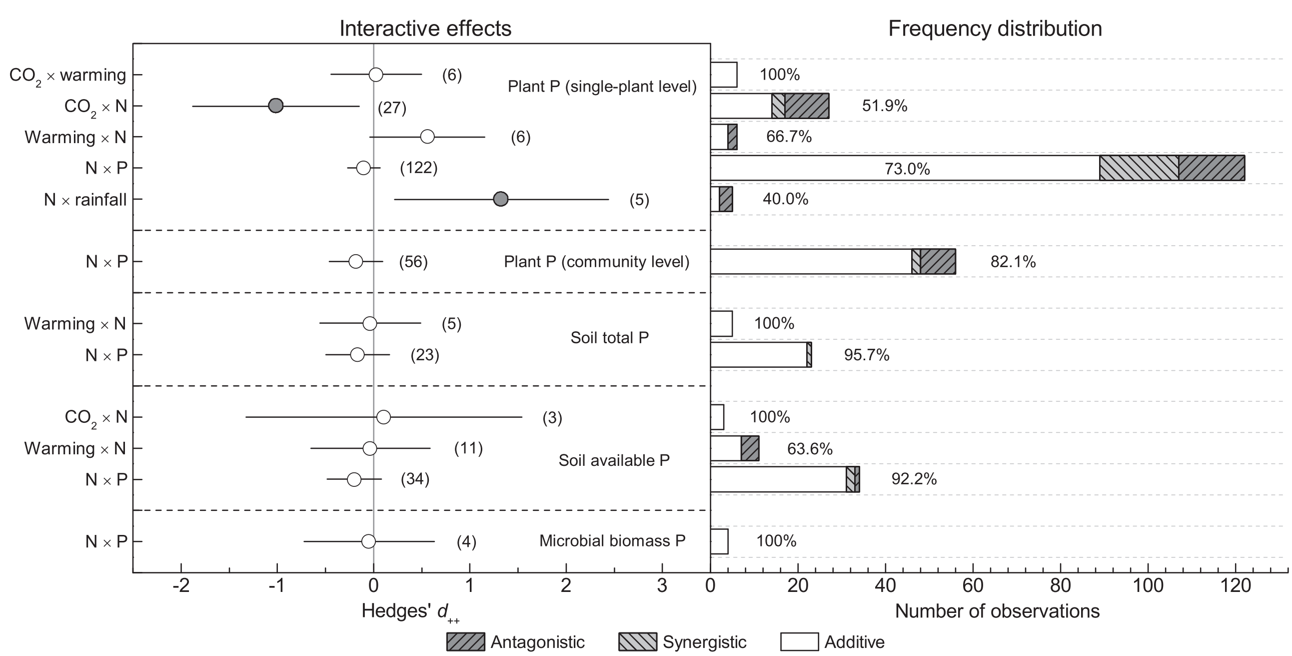

Fig. 2. Interactive effects of multiple global change drivers on terrestrial P pools and the frequency distribution of interaction types among individual observations of two-driver pairs. Values represent means with 95% confident intervals (CIs) and the numbers of sample size are shown in parentheses. If the 95% CI overlapped with zero, the interactive effect was considered to be additive, otherwise the interactive effect was synergistic or antagonistic. Because many studies only reported combined effects, the sample sizes may be smaller than the corresponding ones in Fig. 1. The percentages of individual additive interactions across the overall individual observations are shown. CO_2: elevated CO_2; N: nitrogen addition; P: phosphorus addition; Rainfall: increased rainfall.

significantly decreased plant P pools at the single-plant level and soil total P, but increased MBP. It has been found that warming can stimulate plant growth and P uptake (Vitousek et al., 2010), which results in P transfer from soil to plant. However, we also found that plant P pool at the single-plant level significantly decreased. Such seemingly contradictory results may be attributed to that the response of P pool at the single-plant level failed to depict that of the whole plant community, because different plant species can show varying responses to the effects of warming (Parmesan, 2007). Warming usually tends to increase soil microbial activity and stimulate MBP (Zhou et al., 2012). Our results suggested that drought showed no effects on plant P pool, although a decrease trend was observed. A previous meta-analysis by He and Dijkstra (2014) found that drought can significantly decrease plant P concentration by an average of 9%, but they also suggested that such a decrease trend can be revsersed when the negative effect of drought on plant biomass was higher than on plant P uptake. Thus the response of plant P pool to drought was a mediated by its effects on P conentration and plant growth.

In contrast to the findings of a meta-analysis by Deng et al. (2017) that N addition significantly decreased soil total P but had no effect on SAP and MBP, our results showed that N addition had no effect on plant P pool, soil total P and MBP, but only significantly stimulated SAP pool. The insignificant effect of N addition may be attributed to the fact that the magnitude of P limitation and underlying mechanisms can vary among different ecosystem and soil types, resulting in an overall insignificant effects of N addition. For example, despite the overall insignificant effect on plant P pool, we found that N addition could stimulate plant P pools at both the single-plant and plant-community levels in forest ecosystems (Fig. S4), which may be attributed to a more severe N limitation in forest ecosystems (LeBauer and Treseder, 2008). The increase of soil SAP may be related to the stimulated mineralization of organically bound P as a result of the N addition-induced priming effect on soil (Olander and Vitousek, 2000). The individual effects of P addition on terrestrial P pools were found to be consistently significant and positive in our study, suggesting a similar response pattern with P concentration that was found in a previous meta-analysis (Li et al., 2016). The similar response patterns of P concentration and pool to P addition can be due to the fact that P is generally a major limitation of plant production (Elser et al., 2007; Li et al., 2016). However, ecosystem type showed significant influence on P addition effects on terrestrial P pools. For example, the effects of P addition on plant P pool varied significantly ($Q_b = 25.54$, $P = 0.0006$) among different ecosystem types, and were most manifest in tropical forests. The larger P addition effect in tropical forests may be attributed to the fact that tropical forests are commonly much more limited by P availability (Elser et al., 2007; Vitousek et al., 2010), thus showing a larger sensitivity to additional P input.

Our results further showed that the combined effects of N addition + P addition significantly stimulated the P pools of plants at both the single-plant and community levels, soils and microbial biomass. It has been suggested that terrestrial biomass production is primary limited by N or colimited by N and P (Elser et al., 2007; Li et al., 2016). Plant biomass productivity can be significantly increased with the addition of either nutrient, stimulating the demand for the other one. Thus the simultaneous addition of N and P can promote plant growth and the uptake of nutrients. For example, N addition usually stimulates plant growth and thus induces P limitation (Li et al., 2016) that could even have negative feedback on plant growth. With additional P input, the limitation of P could be compensated and thus facilitate the positive effects of N addition on plant growth and the accompanying nutrient uptake, resulting in increased plant P pool. With the greater uptake of P and subsequent sequestration in biomass and litter under simultaneous N and P additions, soil P pool may decrease because P input are generally low in natural ecosystems (Ilg et al., 2009; Vitousek et al., 2010). However, we found that both soil total P and SAP were significantly stimulated by the combined effects of N addition + P addition. This is probably because that the input of P from plant litter is also stimulated by N and P additions with the increase of P pool in plants, as nutrient addition can stimulate both plant litter production and decomposition (Knorr et al., 2005; Yue et al., 2016). In addition, our study showed that there was no significant relationship between lnRR of terrestrial P pools and N:P ratio of added fertilizer (Fig. S15), indicating that the relative amount of added N and P had no impact on the combined effects of N addition + P addition on terrestrial P pools. Moreover, the addition of P itself can directly increase soil P pools as well. Likewise, soil MBP pool was also significantly increased by the combined effects of N addition + P addition, which may be attributed to the increased SAP, as microbial growth and activity has been found to be positively correlated with SAP (Esberg et al., 2010). Apart from the significant negative combined effects of eCO_2 + N on SAP, the combined effects of other available two-driver pairs on terrestrial P pools were all insignificant, which may be partly attributed to the small sample sizes that have limited the statistical power of analysis (Loladze, 2014).

In line with our second hypothesis, we found that additive interactive effects were likely to be much more common, and only the overall interactive effects of eCO_2 × N addition and N addition × increased rainfall on plant P pool at the single-plant level were antagonistic across all the available two-driver pairs. As discussed above, the eCO_2 effects on plant P pool is dependent on plant species (Liu et al., 2012). When the effects of eCO_2 on plant P pool showed opposite direction with simultaneous N addition, antagonistic interaction occurred. Despite the observed overall non-additive interactive effects, we found that the individual additive interactions exhibited predominance on all types of P pools, suggesting that additive interactions among multiple global change drivers are likely to be common. However, as the observation-weighted approach we used here may overestimate the amount of additive interactions associated with the large variances of some observations (Zhou et al., 2016), we thus tested this potential bias. By conducting statistical analysis, we found that the average weights of the significant (i.e. synergistic and antagonistic) interactions were 4.53, 4.5, 4.79, 4.75, and 4.19 in plant P at the single-plant level, plant-community level, soil total P, SAP and MBP, respectively, which were not significant different from those for the insignificant (i.e. additive) interactions with weights of 4.43, 5.00, 4.05, 4.17, and 4.81, respectively. Therefore the overestimation of additive interactions may not be a problem in this study. Nevertheless, because there is lack of data for many other potential two-driver pairs (see Table S2) and the sample sizes for some of the available two-driver pairs are not large enough, more well-designed primary field studies addressing the interactive effects of multiple global change drivers on terrestrial P pools should thus be carried out to further test other multi-driver pairs and also the found common additive interactive effects here which may be concluded from limited data points.

In accordance with our third hypothesis, we found that moderator variables can significantly influence both the individual and combined effects. The influences of moderator variables on the individual and combined effects of multiple global change drivers have been widely observed in previous studies (Deng et al., 2017; Niu et al., 2016; Yue et al., 2017a). In this study, moderator variables such as latitude, climate and experimental setting factors also showed significant impacts on both the individual and combined effects on terrestrial P pools, but varied among different types of P pools (i.e. plant, soil and microbial biomass). For example, despite the overall null individual effects of eCO_2 on plant P pool at the single-plant level, its effect in subtropical and tropical forests was significant. Tropical forest is usually much more limited by P availability (Vitousek et al., 2010), thus plant P uptake may be much more sensitive to stimulated growth under eCO_2 in tropical forest. The significant negative influence of study length on the individual effects of N addition on soil total P pool may be attributed to the fact that N addition effect tends to be manifest in the early period rather than in the long term (Högberg et al., 2006). Climate (i.e. MAT and MAP) and spatial (i.e. latitude and longitude) factors are also important moderators that regulate both the individual and combined effects of multiple global change drivers on terrestrial P pools. Climate, latitude and longitude can directly influence the responses of terrestrial P pools to global change drivers by regulating temperature and moisture conditions, or indirectly impact the responses by mediating soil organism composition and microbial activity that are closely related to terrestrial P cycling such as plant P uptake, P use efficiency, soil P leaching, and P mineralization rates (Achat et al., 2012; Melillo et al., 2011; Rui et al., 2012).

Overall, through our comprehensive analysis, our results clearly showed that (1) the individual effects of warming and P addition showed the most manifest impacts on terrestrial P pools; (2) P pools were consistently stimulated by P addition alone or in combination with simultaneous N addition; (3) moderator variables of environmental and experimental setting factors such as ecosystem type, climate, and latitude could significantly influence both the individual and combined effects; and (4) the interactive effects of two-driver pairs across multiple global change drivers are more likely to be additive rather than synergistic or antagonistic, suggesting that the combined effects of these drivers are equal to or not significantly different from the sum of the corresponding individual effects. Moreover, as the lack of data for many potential two-driver pairs of the investigated global change drivers, future primary field studies regarding the interactive effects of multi-drivers on terrestrial P pools are therefore necessary to improve our understanding of the dynamics of terrestrial P. Nevertheless, the results of our study would be useful for incorporating P as controls on ecological processes such as photosynthesis and plant growth into ecosystem models used to analyze effects of multiple drivers under future global change.

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Appendix A. Supplementary data

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References

Achat, D.L., Augusto, L., Bakker, M.R., Gallet-Budynek, A., Morel, C., 2012. Microbial processes controlling P availability in forest spodosols as affected by soil depth and soil properties. Soil Biol. Biochem. 44, 39–48.

Borenstein, M., Hedges, L., Higgins, J., Rothstein, H., 2009. Introduction to Meta-analysis. Chichester, John Wiley & Sons Ltd.

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11, 1304–1315.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D., Quero, J.L., et al., 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502, 672–676.

Deng, Q., Hui, D., Dennis, S., Reddy, K.C., 2017. Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: a meta-analysis. Glob. Ecol. Biogeogr. 26, 713–728.

Deng, Q., Hui, D., Luo, Y., Elser, J., Wang, Y.P., Loladze, I., ... Dennis, S., 2015. Down-regulation of tissue N: P ratios in terrestrial plants by elevated CO2. Ecology 96 (12), 3354–3362.

Dieleman, W.I., Vicca, S., Dijkstra, F.A., Hagedorn, F., Hovenden, M.J., Larsen, K.S., et al., 2012. Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature. Glob. Chang. Biol. 18, 2681–2693.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., et al., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10, 1135–1142.

Esberg, C., Du Toit, B., Olsson, R., Ilstedt, U., Giesler, R., 2010. Microbial responses to P addition in six South African forest soils. Plant Soil 329, 209–225.

Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., Graça, M.A., 2015. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biol. Rev. 90, 669–688.

Filippelli, G.M., 2002. The global phosphorus cycle. Rev. Mineral. Geochem. 48, 391–425.

Goll, D.S., Brovkin, V., Parida, B., Reick, C.H., Kattge, J., Reich, P.B., et al., 2012. Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling. Biogeosciences 9, 3547–3569.

van Groenigen, K.-J., Six, J., Hungate, B.A., de Graaff, M.-A., Van Breemen, N., Van Kessel, C., 2006. Element interactions limit soil carbon storage. Proc. Natl. Acad. Sci. 103, 6571–6574.

Gurevitch, J., Hedges, L.V., 2001. Meta-analysis: combining the results of independent experiments. In: Scheiner, S., Gurevitch, J. (Eds.), Design and Analysis of Ecological Experiments. Oxford University Press, New York, USA, pp. 347–369.

Gurevitch, J., Morrison, J.A., Hedges, L.V., 2000. The interaction between competition and predation: a meta-analysis of field experiments. Am. Nat. 155, 435–453.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E., et al., 2011. Nutrient co-limitation of primary producer communities. Ecol. Lett. 14, 852–862.

He, M., Dijkstra, F.A., 2014. Drought effect on plant nitrogen and phosphorus: a meta-analysis. New Phytol. 204, 924–931.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.

Högberg, P., Fan, H., Quist, M., Binkley, D., Tamm, C.O., 2006. Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. Glob. Chang. Biol. 12, 489–499.

Hoosbeek, M.R., 2016. Elevated CO2 increased phosphorous loss from decomposing litter and soil organic matter at two FACE experiments with trees. Biogeochemistry 127, 89–97.

Huang, W., Houlton, B.Z., Marklein, A.R., et al., 2015. Plant stoichiometric responses to elevated CO_2 vary with nitrogen and phosphorus inputs: evidence from a global-scale meta-analysis. Scientific reports 5, 18225.

Ilg, K., Wellbrock, N., Lux, W., 2009. Phosphorus supply and cycling at long-term forest monitoring sites in Germany. Eur. J. For. Res. 128, 483.

Knorr, M., Frey, S., Curtis, P., 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86, 3252–3257.

Koricheva, J., Gurevitch, J., Mengersen, K., 2013. Handbook of Meta-analysis in Ecology and Evolution. Princeton University Press, pp. 95–99.

LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89, 371–379.

Li, Y., Niu, S., Yu, G., 2016. Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. Glob. Chang. Biol. 22, 934–943.

Liu, Y., Villalba, G., Ayres, R.U., Schroder, H., 2008. Global phosphorus flows and environmental impacts from a consumption perspective. J. Ind. Ecol. 12, 229–247.

Liu, J., Zhang, D., Zhou, G., Duan, H., 2012. Changes in leaf nutrient traits and photosynthesis of four tree species: effects of elevated [CO_2], N fertilization and canopy positions. J. Plant Ecol. 5, 376–390.

Liu, J., Huang, W., Zhou, G., Zhang, D., Liu, S., Li, Y., 2013. Nitrogen to phosphorus ratios of tree species in response to elevated carbon dioxide and nitrogen addition in subtropical forests. Glob. Chang. Biol. 19, 208–216.

Loladze, I., 2014. Hidden shift of the ionome of plants exposed to elevated CO2 depletes minerals at the base of human nutrition. elife 3, e02245.

Melillo, J.M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., et al., 2011. Soil warming, carbon–nitrogen interactions, and forest carbon budgets. Proc. Natl. Acad. Sci. 108, 9508–9512.

Mueller, K.E., Blumenthal, D.M., Pendall, E., Carrillo, Y., Dijkstra, F.A., Williams, D.G., et al., 2016. Impacts of warming and elevated CO2 on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. Ecol. Lett. 19, 956–966.

Newman, E.I., 1995. Phosphorus inputs to terrestrial ecosystems. J. Ecol. 83, 713–726.

Niu, S., Classen, A.T., Dukes, J.S., Kardol, P., Liu, L., Luo, Y., et al., 2016. Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle. Ecol. Lett. 19, 697–709.

Olander, L.P., Vitousek, P.M., 2000. Regulation of soil phosphatase and chitinase activity by N and P availability. Biogeochemistry 49, 175–191.

Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob. Chang. Biol. 13, 1860–1872.

Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., Van Der Velde, M., Bopp, L., et al., 2013. Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. Nat. Commun. 4, 2934.

Rosenberg, M.S., Adams, D.C., Gurevitch, J., 2000. MetaWin: Statistical Software for Meta-Analysis, Version 2. Massachusetts, Sinauer Associates Sunderland.

Rui, Y., Wang, Y., Chen, C., Zhou, X., Wang, S., Xu, Z., et al., 2012. Warming and grazing increase mineralization of organic P in an alpine meadow ecosystem of Qinghai-Tibet Plateau, China. Plant Soil 357, 73–87.

Tessier, J.T., Raynal, D.J., 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. J. Appl. Ecol. 40, 523–534.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., et al., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.

Vitousek, P.M., 2004. Nutrient Cycling and Limitation: Hawai'i as a Model System. Princeton University Press.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol. Appl. 20, 5–15.

Weand, M.P., Arthur, M.A., Lovett, G.M., Sikora, F., Weathers, K.C., 2010. The phosphorus status of northern hardwoods differs by species but is unaffected by nitrogen fertilization. Biogeochemistry 97, 159–181.

Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob. Chang. Biol. 17, 927–942.
Yuan, Z., Chen, H.Y., 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. Nat. Clim. Chang. 5, 465–469.
Yue, K., Peng, Y., Peng, C., Yang, W., Peng, X., Wu, F., 2016. Stimulation of terrestrial ecosystem carbon storage by nitrogen addition: a meta-analysis. Sci. Rep. 6, 19895.
Yue, K., Fornara, D.A., Yang, W., Peng, Y., Li, Z., Wu, F., et al., 2017a. Effects of three global change drivers on terrestrial C:N:P stoichiometry: a global synthesis. Glob. Chang. Biol. 23, 2450–2463.
Yue, K., Fornara, D.A., Yang, W., Peng, Y., Peng, C., Liu, Z., et al., 2017b. Influence of multiple global change drivers on terrestrial carbon storage: additive effects are common. Ecol. Lett. 20, 663–672.
Zhou, J., Xue, K., Xie, J., Deng, Y., Wu, L., Cheng, X., et al., 2012. Microbial mediation of carbon-cycle feedbacks to climate warming. Nat. Clim. Chang. 2, 106.
Zhou, L., Zhou, X., Shao, J., Nie, Y., He, Y., Jiang, L., et al., 2016. Interactive effects of global change factors on soil respiration and its components: a meta-analysis. Glob. Chang. Biol. 22, 3157–3169.