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**SYNTHESIS**

# Net plant interactions are highly variable and weakly dependent on climate at the global scale

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**Abstract**

Although plant–plant interactions (i.e. competition and facilitation) have long been recognised as key drivers of plant community composition and dynamics, their global patterns and relationships with climate have remained unclear. Here, we assembled a global database of 10,502 pairs of empirical data from the literature to address the patterns of and climatic effects on the net outcome of plant interactions in natural communities. We found that plant interactions varied among plant performance indicators, interaction types and biomes, yet competition occurred more frequently than facilitation in plant communities worldwide. Unexpectedly, plant interactions showed weak latitudinal pattern and were weakly related to climate. Our study provides a global comprehensive overview of plant interactions, highlighting competition as a fundamental mechanism structuring plant communities worldwide. We suggest that further investigations should focus more on local factors (e.g. microclimate, soil and disturbance) than on macroclimate to identify key environmental determinants of interactions in plant communities.

**KEYWORDS**
biome, climate, competition, facilitation, global patterns, plant performance

## INTRODUCTION

Plants interact with one another negatively and positively in communities, often simultaneously, depending on the species identity, population density, spatial aggregation, seasonality and environmental conditions (Callaway et al., 2002; Callaway & Walker, 1997; Tilman, 1988). Plants can compete for resources, space or mutualists, while they can also simultaneously facilitate one another by accumulating water and nutrients,

decreasing the abiotic stress, providing shelter or protection from herbivores (Brooker et al., 2008). Plant–plant interactions (hereafter abbreviated as plant interactions) play important roles in determining community composition, structure and dynamics (Clements et al., 1929; Grime, 1979; Gross et al., 2009; Kunstler et al., 2016; Losapio et al., 2021), and thereby impact ecosystem functioning and evolutionary trajectories of interacting species (Butterfield & Callaway, 2013; Thorpe et al., 2011). Therefore, research on plant interactions is essential

for providing a predictive understanding of community and ecosystem responses to accelerating environmental change (Gross et al., 2015; He et al., 2013; Tylianakis et al., 2008).

Plant interactions are context dependent across abiotic gradients. First, plant interactions can differ among biomes. Biomes are globally convergent vegetation formations similar in structure and function as a result of similar climatic features, and represent important ecological and evolutionary units (Crisp et al., 2009; Moncrieff et al., 2016). At both ecological and evolutionary time-scales, the functionality of the biome shapes the processes underpinning the plant assembly by selecting for the biota, including plant interactions (Mucina, 2019). For instance, a previous synthesis showed that semi-arid and tropical biomes have more positive neighbour effects than wetlands do (Gómez-Aparicio, 2009). Second, climate can affect plant interactions. Climate has long been recognised as a key driver that increases the effect of competition from the poles to the tropics (e.g. Dobzhansky, 1950; Louthan et al., 2015). An analysis including eight natural biomes and tree plantations distributed in five continents showed that climatic context is one of the main factors determining the sign and magnitude of tree–grass interactions (Mazía et al., 2016). In the Upper Gunnison Basin of the Colorado Rocky Mountains, USA, for instance, plant interactions change from competitive to facilitative over temperature gradients (Lynn et al., 2019). In New England salt marshes, interspecific interactions are linked to climate, but the sensitivity of specific species interactions to climatic variation is highly variable (Bertness & Ewanchuk, 2002). In addition, future climate warming and altered precipitation patterns will mediate plant interactions through increased dominance of certain species or functional groups, as indicated by responses of seminatural grasslands to temperature across a wide climatic gradient (Olsen et al., 2016). Because biome and climate exhibit clear spatial patterns at the global scale, we can expect clear global patterns of plant interactions. The stress-gradient hypothesis (SGH), a long-standing hypothesis that has dominated the scientific debate on plant interactions, proposes that plant interactions should shift from being more facilitative in abiotically harsh environments towards more competitive in benign environments for plant growth (Bertness & Callaway, 1994). Although many empirical studies have found evidence in support of SGH, other studies have not or only partially. After its proposal, the SGH has been revised so as to include that facilitation is predominant in moderately stressful rather than extreme environments (Holmgren & Scheffer, 2010) or even ceases at extremes (Michalet et al., 2014). In addition, resource- and non-resource-based stresses differ in their impacts on plant interactions (Maestre et al., 2009), and plant interactions change with resource availability and growth strategies (Alba et al., 2019). However, despite over a century of research, there is a lack of comprehensive assessments of plant interactions worldwide, notable exceptions being a syntheses of community-level studies from harsh environments (Soliveres & Maestre, 2014) and plant interactions along stress gradients (He et al., 2013). Consequently, spatial patterns of and climatic effects on the outcome of plant interactions at the global scale are still obscure.

Plant interactions can be measured using different performance indicators. Large-scale syntheses have shown that the type of fitness measure affects the outcome of plant interactions (Maestre et al., 2005). For example, a review of field experiments in arid environments showed a significant effect of neighbours on the survival and growth of target plants but not on their density and fecundity (Maestre et al., 2005). An analysis of plant interactions in degraded ecosystems performed worldwide reported that plant interactions are positive for survival because shrubs have large facilitative effects, neutral for growth and negative for density caused by the strong competition by herbs (Gómez-Aparicio, 2009; Verdú et al., 2012). A synthesis of 727 tests across the globe found that plant interactions are often facilitative for survival, but interactions are primarily competitive for growth and reproduction (He et al., 2013). Therefore, large-scale assessments of plant interactions for different performance indicators need to account for potential unique responses of the different measures (including demographic/vital rate) to other species in different environments.

Here, we synthesised a large body of literature to build a global database of plant interactions involving five plant performance indicators (emergence, survival, growth, fecundity and abundance). We used this database to address global patterns of and the effects of climate on the net outcome of plant interactions in natural communities. Specifically, we addressed the following questions: (1) Which type of interactions (competition or facilitation; measured for different performance indicators, neighbour types and study methods) occurs more frequently in plant communities worldwide involving different biomes? (2) Do plant interactions exhibit latitudinal patterns in which the strength of competition being the highest in the tropics but the lowest near the poles? (3) How does climate predict the outcome of plant-plant interactions? Answers to these questions are essential for identifying the contribution of plant interactions to community composition and, thereby, for predicting future dynamics of global biodiversity.

# METHODS

## Plant interaction data

To identify published studies on plant–plant interactions worldwide, we conducted an ISI Web of Science search covering the time period from 1900 onwards using the

following search terms: (facilitat\* OR "positive interaction" OR competit\* OR interference OR mutualis\*) AND (germinat\* OR emergen\* OR surviv\* OR dorman\* OR fecundity OR growth OR abundance) AND (neighb\* plant). We updated the search several times during the last 5 years; and the latest was done in June 2018, which returned 1024 publications. Each publication was individually reviewed, and the reference list was inspected to identify additional relevant publications. Finally, we collected a total of 4379 publications on plant interactions.

To avoid bias in publication selection, only those studies that met all of the following criteria were selected. (1) Experiments were conducted in natural environments, not in glasshouses, and had at least one pair of data (plants growing in isolation vs. neighbouring treatments); (2) Studies were included only when the target species was clearly defined, not the vegetation or species group; (3) Only experiments that examined the presence of live neighbours, rather than the presence of litter or other dead plant matter, or plant extracts or plant organs, were included; (4) Experiments had been carried out at the same temporal and spatial scales in both isolated and neighbour treatments, while those measured plant performance at different time points or plot sizes between the two treatments were excluded; (5) Initial environmental conditions and soil properties in the isolated and neighbour treatments were the same; (6) Only experiments conducted in terrestrial ecosystems were included; (7) Weed/crop experiments were not included given agricultural systems are not natural plant communities and crop species or varieties are usually artificially selected for high productivity. In total, 1220 out of 4379 publications met the above criteria (see Appendix S1 and S2).

For studies that included different levels of natural gradients (e.g. different ecosystems, soil depth, density, plant size, life stage, gender, population or topographic and moisture gradients), data in each gradient level were considered as independent within the study. If multiple environmental conditions were manipulated in a study (e.g. nutrients, warming, $CO_2$, herbivory or mycorrhizal fungi), we only extracted data from the treatment that most closely reflected the situation in the natural condition (e.g. the control treatment in a nutrient addition experiment). Measurements of some studies were conducted at several points in time, and we only used the measurement taken at the end of the experiment to overcome problems of non-independence of data (Gurevitch & Hedges, 1999; Vilà & Weiner, 2004). For single species experiments with different densities, we considered the lowest density (the least interactive, mostly single plant) as isolated and the highest (the most interactive) as neighbour treatment. If a study involved different distances between target and neighbouring plants, we assumed the farthest (the least interactive) to be isolated and the nearest (the most interactive) to be neighbour treatment. We recorded data at the species level. We extracted data of

five components of plant fitness that is seedling emergence, plant growth, survival, fecundity and abundance. If a study involved different performance indicators, we recorded them separately. However, when studies presented different metrics of the same performance indicator (mostly growth and fecundity), we only selected one metric in a hierarchical order. Growth was ordered by above-ground biomass (the most frequent measurement), total biomass, height, root mass, other traits. For fecundity, the order was seed/fruit mass, seed/fruit number, flower mass, flower number, other traits. We excluded synthetic papers and used only studies that reported primary field data. The preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow chart (Moher et al., 2009) for data collection was illustrated in Figure S1. We extracted data from the text, tables, digitised graphs (using the free software Engauge Digitizer 4.1) or supplementary materials.

## Statistical analyses

All statistical analyses were performed with the open-source language R (version 3.6.0, https://cran.r-project.org/). We calculated neighbour-effect intensity index with commutative symmetry ($NInt_C$) defined as follows (Díaz-Sierra et al., 2017):

$$NInt_C = 2 \frac{\Delta P}{P_{sum} + |\Delta P|}$$

where $P_{sum}$ is the sum of the performances of the target species with ($P_{+N}$) and without ($P_{-N}$) neighbours ($P_{sum} = P_{+N} + P_{-N}$) and $\Delta P$ the total impact of neighbours ($\Delta P = P_{+N} - P_{-N}$). $NInt_C$ has values ranging from −1 to 1, with −1 for competitive exclusion and +1 for obligate facilitation and for an infinite increase in performance of the target species with neighbours. This index is recommended when different performance estimators rather than biomass are used, which can span different orders of magnitude (Díaz-Sierra et al., 2017). For studies that reported other interaction indexes (e.g. log response ratio, lnRR; relative interaction intensity, RII; relative neighbour effect, RNE), we transformed them to $NInt_C$. To test whether there was a historical trend in reporting competitive or facilitative cases in our database, we plotted competitive ($NInt_C < 0$), facilitative ($NInt_C > 0$) and neutral cases ($NInt_C = 0$) along publication years and used a linear model to test this statistically.

A four-step procedure was performed to identify which type of interaction (competition or facilitation) was more frequent at the global scale. First, we split data into the five performance indicators. Second, to determine the generality of competitive or facilitative interactions in our dataset, we further split data into different interaction types (intra- vs. interspecific) and neighbour types (mixed vs. non-mixed neighbour). When neighbours were more

than one individual, the neighbour type was considered as mixed neighbour; in contrast, when neighbour was a single individual, it was non-mixed neighbour. Third, we split data into different methods (experimental vs. observational). Finally, we split data of each performance indicators into different biomes according to the location at which the original study was performed. The 14 terrestrial biomes were adapted from Olson et al. (2001). We excluded three biomes (i.e. (sub)tropical coniferous forests, flooded grasslands, and savannas and mangroves) because of low data availability (< 50 data points). At each step, we used linear mixed models (LMMs) whether $NInt_C$ differed among groups (e.g. five performance indicators in the first step). We then used (non-parametric) one-sample Wilcoxon signed rank test to determine whether $NInt_C$ for each performance indicator was significantly different from 0. In parallel with the main tests, we used simple vote-counting methods to compare the numbers for the outcome of plant interactions (competition vs. facilitation).

To test for latitudinal and climatic effects on the outcome of plant interactions, we implemented LMMs for each plant performance indicator using the lme4 package (Bates et al., 2015). The study identity was fitted as random effect in the LMMs to account for the non-independence within study. Because species could account for variance not attributable to the experimental effect across experiments, it was also fitted as a random effect. Latitudinal trends in the outcome of plant interactions were tested by fitting a LMM with $NInt_C$ as dependent variable and absolute latitude as independent variable. Climatic trends were similarly tested by fitting LMMs with $NInt_C$ as dependent variable and different climatic variables as independent variables. Specifically, we used 19 bioclimatic variables extracted from the WorldClim data set (Fick & Hijmans, 2017) and aridity index from Global Aridity Index and Potential Evapo-Transpiration (ET0) Climate Database v2. (Trabucco & Zomer, 2018) according to the location of each study in our database (see Table S1 for detailed information of climatic predictors). These climatic variables have been widely used for analysing plant interactions at large scales (Kikvidze et al., 2011; Soliveres & Maestre, 2014). To reduce multicollinearity in the LMMs, we removed from the analyses variables that were highly correlated with the rest (Spearman rho > |0.7|). The remaining climatic predictors were $\log_{10}$-transformed to improve normality prior to being fitted by LMMs. Marginal coefficients of determination ($R^2m$) were obtained with the r2glmmpackage (Jaeger, 2017).

To test that our results obtained from the analyses using $NInt_C$ are robust to the incorporation of variance across studies, we also calculated the weighted standardised mean effect sizes, Hedges' d, which is the most common (and preferred) metric in ecological meta-analysis (Koricheva et al., 2013):

$$d = \frac{\overline{Y_1} - \overline{Y_2}}{\sqrt{\frac{(n_1-1)s_1^2 + (n_2-1)s_2^2}{n_1 + n_2 - 2}}} J$$

where $J = 1 - \frac{3}{4(n_1 + n_2 - 2) - 1}$ is a correction for small sample size; $\overline{Y_1}$ and $\overline{Y_2}$ are the means in neighbour and control treatments, which are associated with sample sizes $n_1$ and $n_2$ and standard deviations $s_1$ and $s_2$, respectively. Because large proportion of studies (37.1% for emergence, 61.1% for survival, 26.5% for growth, 20.1% for fecundity and 52.9% for abundance) did not report standard deviation (s), we only analysed the subset data from the studies with complete information (Koricheva et al., 2013). To minimise the bias caused by extreme values, the outliers in the data were identified by Rosner's test using EnvStats package (Millard, 2013), and outliers below or above the upper limit were capped with the value of the 5th or 95th percentile, respectively. We then reran all analyses for Hedges' d using the same procedure as for $NInt_C$.

## RESULTS

Our database comprised 10,502 pairs of plant interaction data (see Appendix S2) comparing plants growing in isolation versus neighbouring treatments of five plant performance indicators (979 pairs for emergence; 2250 for survival; 3731 for growth; 728 for fecundity; 2814 for abundance), which were from the natural plant communities across all seven (sub-)continents (Figure 1a). Facilitation was reported as early as competition and the two types of plant interaction data coexisted across the entire study period, indicating that investigators were not biased towards reporting competition in plant interaction studies in certain periods (Figure S2a). Moreover, publication year was not correlated with the ratio of facilitation versus competition (Figure S2b), indicating that there was no investigator bias in reporting competition than facilitation historically.

The five plant performance indicators showed mean $NInt_C$ values significantly lower than zero (Figure 1b). Vote counting also showed that the case of competition was more frequent than facilitation for all five plant performance indicators (see numbers above each boxplot in Figure 1b). Consistently, Hedges' d was significantly negative for all five plant performance indicators, except for abundance, whose 95% CI slightly overlapped 0 (Figure 1c). LMMs showed nonsignificant difference in the mean of $NInt_C$ between intraspecific vs. interspecific neighbours ($t = 1.345$, $p = 0.179$), but significant difference between mixed versus non-mixed neighbours ($t = 3.92$, $p < 0.001$). Vote counting showed that competition was more frequent than facilitation in all cases, except for the outcome for emergence with non-mixed neighbours. Experimental studies yielded significantly lower $NInt_C$ values than observational studies for all the performance indicators except survival. The means of $NInt_C$ from experimental studies were all significantly lower
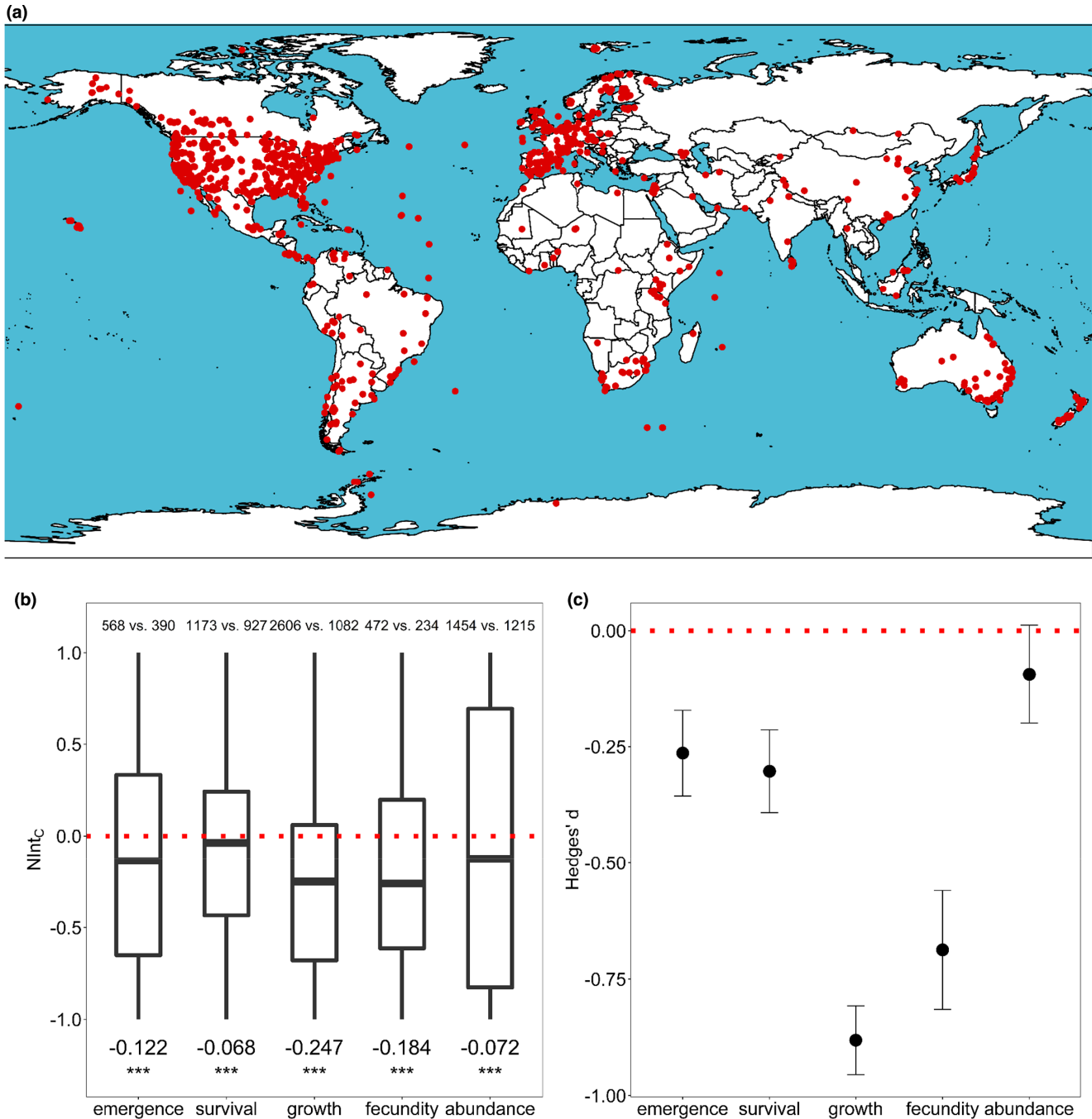
**(a)**



**(b)**



**(c)**



**FIGURE 1** Maps of site locations of studies from which data were collected (a), box plots showing collected $NInt_C$ (neighbour-effect intensity index with commutative symmetry) data (b) and Hedges' d (c) for the five plant performance indicators. In (b), the black horizontal line in the white bars is the median value, the white bar the interquartile range and black line extending from the white bar the upper (max) and lower (min) adjacent values in the data. Vote counting for competition versus facilitation is shown at the top. Mean $NInt_C$, and the significance of each performance indicator departing from zero after one-sample Wilcoxon signed-rank tests are shown at the bottom of each column. ***$p < 0.001$. In (c), black points are the means and bars 95% confidence intervals

than 0 ($p < 0.05$), while those from observational studies did not significantly differ from 0 (Figure 3). $NInt_C$ was highly variable and differed among biomes (Figure 4; LMMs: $p < 0.001$). More outcomes for growth and fecundity were negative (Figure 4c, d), while for emergence, survival and abundance $NInt_C$ got the full range of response (Figure 4a,b,e). Vote counting confirmed that

competition was more frequent than facilitation in all biomes. Analyses using Hedges' d yielded similar results to $NInt_C$ for different interaction types, neighbour types and biomes (Figures S3–S5).

Emergence and survival $NInt_C$ values followed a significant, but extremely weak negative latitudinal pattern (Figure 5a,b, see low $R^2m$ values). Fecundity, growth and

abundance did not show any significant latitudinal pattern (Figure 5c,d,e). Similarly, Hedges' d showed non-significant or extremely weak latitudinal patterns (Figure S6).

After removal of climatic variables that were highly correlated (Figure S7a), six variables were kept for analysing the effect of climate on $NInt_C$ (Figure S7b). LMMs revealed that $NInt_C$ had weak relationships with climate for all five performance indicators (Table 1). Although some climatic variables had significant effects on $NInt_C$, their marginal coefficients of determination were extremely low (all $R^2m < 0.04$). For instance, although LMMs showed that temperature seasonality had significant effect on $NInt_C$ for emergence and growth, the $R^2m$ was lower than 0.01 (Figure 6). Again, similar to $NInt_C$, Hedges' d also showed weak relationships with climate for all five performance indicators (Table S2).

## DISCUSSION

Our global database was derived from in situ experiments and observations in natural plant communities across all biomes and seven (sub-)continents; albeit with much greater data coverage in North America and Europe than elsewhere (Figure 1a). These included a total of 2542 plant species from wide-ranging evolutionary lineages and over a century of research with the oldest publication dating back to 1914 (Pearson, 1914). While our database is not exhaustive of the research on plant interactions, it is the most comprehensive synthesis in this field to date, which allowed us to assess the net outcome of plant interactions at the global scale.

The most important finding of our global assessment is that, although plant interactions are highly variable, competition occurred more frequently than facilitation in the outcome of plant interactions worldwide. First, competition ($NInt_C < 0$) was more frequent than facilitation ($NInt_C > 0$) in the outcome of plant interactions for all five performance indicators (Figure 1b). Second, because the strength of plant interactions may differ among interaction and neighbour types, for example mixed versus non-mixed neighbours and intra- versus interspecific interactions (Adler et al., 2018), we proceeded our analyses for different data types, which showed that the more frequent occurrence of competition held consistently when different interaction and neighbour types were considered (Figure 2a,b). Third, competition was reported more often in experimental studies for all five fitness components (Figure 3). Finally, competition was the more frequent outcome of plant interactions across biomes (Figure 4). Collectively, these findings suggest that competition occurs more frequently than facilitation in plant communities worldwide. Competition is ubiquitous in ecological communities where co-occurring species use the same resources and has been long recognised as one of the most important mechanisms determining plant fitness and community structure (Clements et al., 1929; Keddy, 1989; Tilman, 1988; Whittaker, 1965). Thus, our results confirm this traditional wisdom by showing the more frequent occurrence of competition in plant communities globally.

The five performance indicators used in our study measured major aspects of plant demographical processes, which can provide a more complete assessment of plant interactions. Our analyses showed that the strength of plant interactions differed depending on the performance indicator that was measured (Figure 1b,c), indicating that plants respond differently to neighbours during their life history stages (Le Roux et al., 2013). These results are consistent with the analysis of plant interactions for different performance indicators in degraded ecosystems performed worldwide (Gómez-Aparicio, 2009; Verdú et al., 2012), a removal experiment in natural alpine plant communities of the south-western Alps (Choler et al., 2001), a review of field experiments in arid environments (Maestre et al., 2005) and a synthesis of 727 tests across the globe (He et al., 2013). Therefore, our global analysis affirms the necessity to account for potential unique responses of the different demographical and life history stages to neighbours when assessing plant interactions, especially at large scales.

Our results showed that $NInt_C$ and Hedges' d differed among biomes for all five performance indicators (Figure 4, S5). In addition to several lines of evidence that community assembly and ecosystems responses to environmental forcing are strongly constrained by evolutionary history of biomes (Crisp et al., 2009; Simon et al., 2009), our results demonstrate that plant interactions are also highly constrained by biome conservatism at the global scale. The net outcome of plant interactions is determined by the interacting species and environmental conditions. Biome underlies both determinants: biome conservatism is a major determinant of the global distribution of plant diversity (i.e. similar species groups are more likely found in the same biome; Crisp et al., 2009); furthermore, biomes reflect the differences in climate and geography (i.e. same biome would have similar environmental conditions; Woodward et al., 2004).

Furthermore, our findings for competition-facilitation patterns among biomes are highly variable. Indeed, our results suggest that whether or not plant interactions shift from competitive to more facilitative with increasing environmental severity depends greatly on the fitness parameters and biomes considered. For instance, plant interactions are facilitative for emergence, but are competitive for growth in (sub)tropical moist broadleaf forests (Figure 4), whereas in the stressful tundra biome where facilitative interactions have been widely reported (e.g. Callaway et al., 2002; Cavieres et al., 2014), plant interactions are facilitative only for abundance.

Surprisingly, we did not find strong latitudinal pattern for any of the five performance indicators (Figure 5, S6), which is inconsistent with the results of some regional studies. For instance, latitude is an important predictor
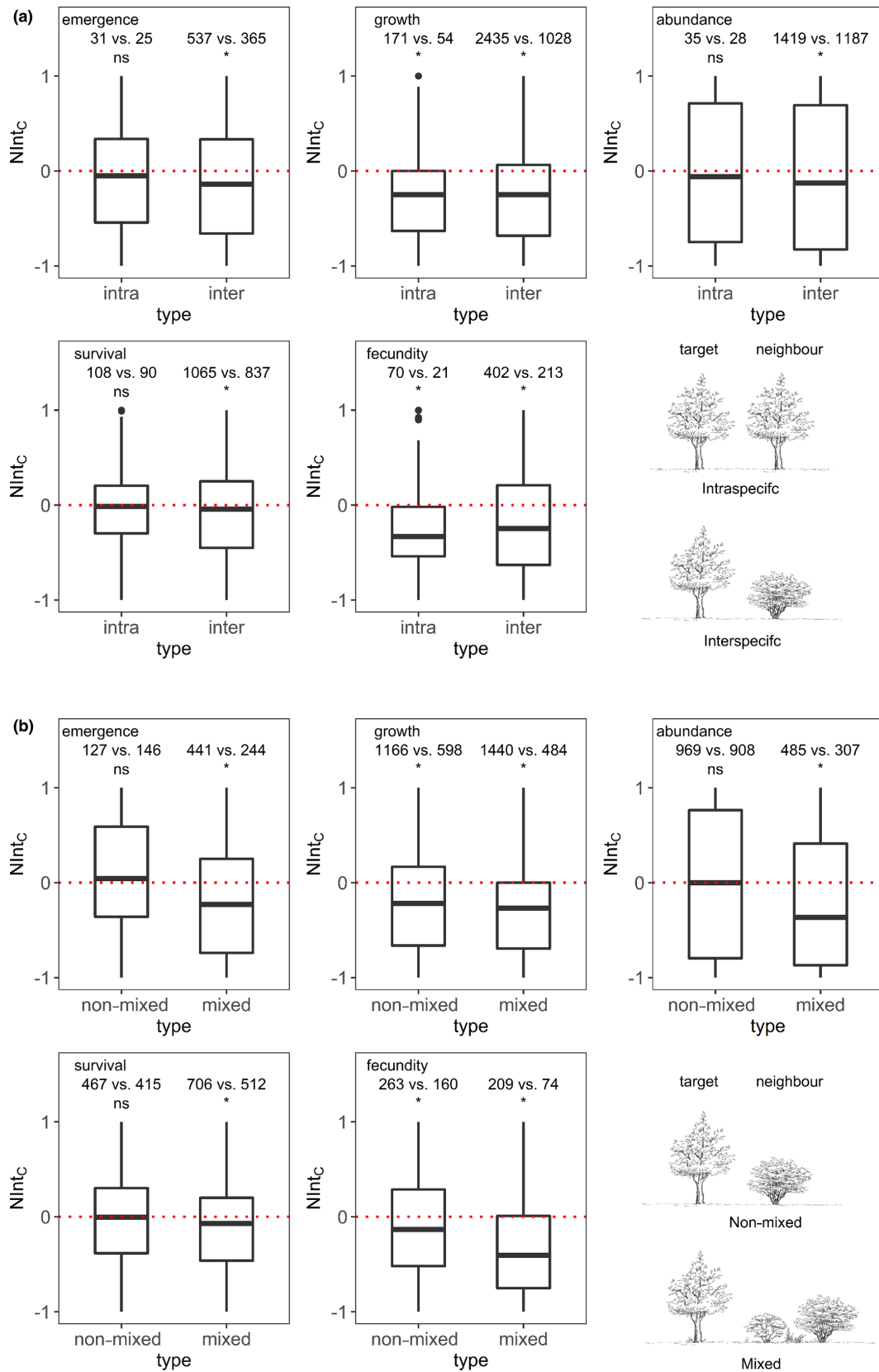
**FIGURE 2** $NInt_C$ (neighbour-effect intensity index with commutative symmetry) in different types of plant interactions for the five plant performance indicators. (a) Intra- and interspecific interactions; (b) mixed and non-mixed neighbours. Vote counting for competition versus facilitation is shown at the top, followed by the significance of each performance indicator departing from zero after one-sample Wilcoxon signed-rank tests. *$p < 0.05$; ns, not significant
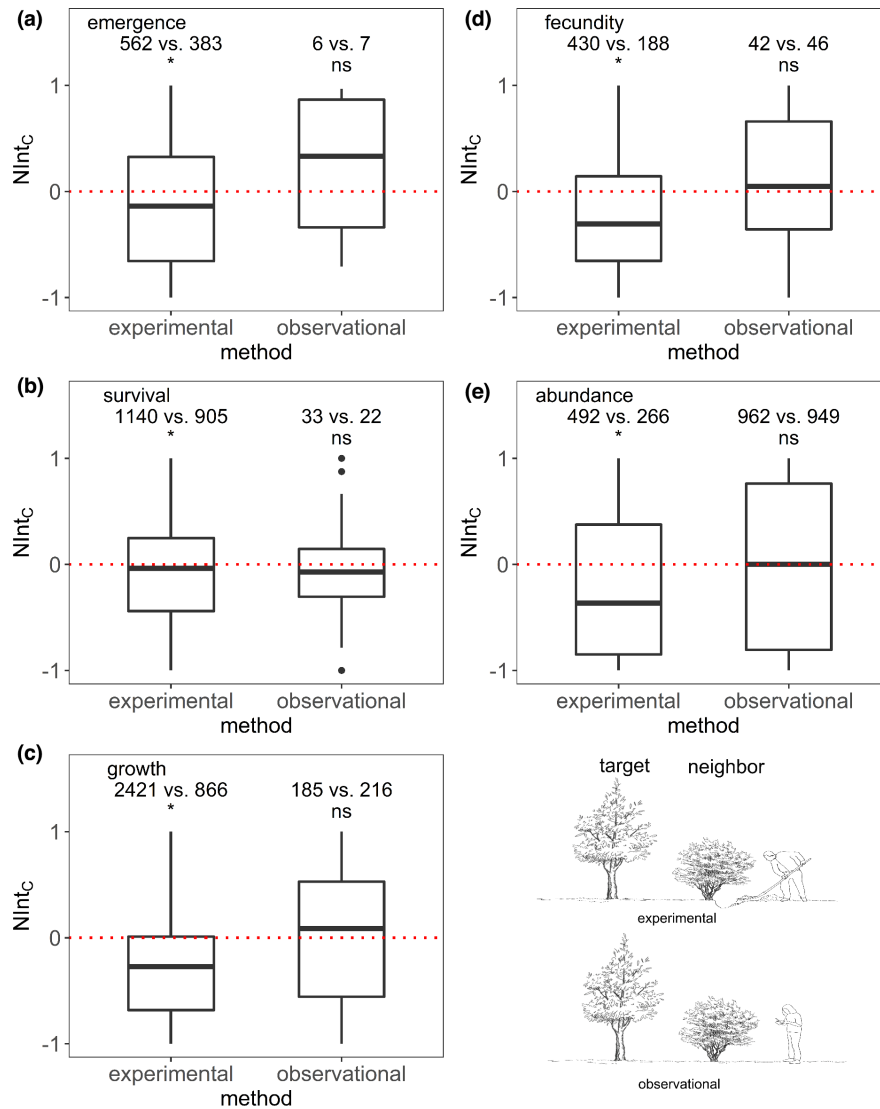
**FIGURE 3** NInt$_C$ (neighbour-effect intensity index with commutative symmetry) measured by different methods for the five plant performance indicators. (a) Seedling emergence; (b) survival; (c) plant growth; (d) fecundity; (e) abundance. Vote counting for competition versus facilitation is shown at the top, followed by the significance of each performance indicator departing from zero after one-sample Wilcoxon signed-rank tests. *$p < 0.05$; ns, not significant

for plant interactions in alpine communities (Kikvidze et al., 2011) as well as for salt marshes plant communities (Bertness & Ewanchuk, 2002). However, our finding of no strong latitudinal pattern is echoed by the weak relationships between plant interactions and climate, although some climatic variables (e.g. temperature seasonality) had significant yet negligible effects on plant interactions for some performance indicators (Table 1, S2; Figure 6).

The weak climatic effects on plant interactions in our study are contrary to the strong effects of climate on tree–grass interactions in a global meta-analysis including eight natural biomes (Mazía et al., 2016) and several studies at more local scales (Bertness & Ewanchuk, 2002; Lynn et al., 2019; Olsen et al., 2016). Given that climate determines the level of resource input into ecosystems and how resources are distributed among co-occurring

species (Alba et al., 2019), our results however indicate that such effects are not necessarily reflected in the outcome of plant interactions. We ascribe this to two possible reasons. On the one hand, mechanisms underlying plant interactions could differ among biomes to cope with climatic conditions wherein. In tundra, for instance, the amelioration of severe stresses (e.g. low temperature and strong wind) by neighbours may favour growth more than competition for resources (Grime, 1979). In global drylands, a shift from facilitation to competition drives species abundances as aridity increases (Berdugo et al., 2019). In mesic savannas, however, strong competition for water, nutrients and light by trees suppresses grass growth (Dohn et al., 2013). On the other hand, the outcome of plant interactions can differ among performance indicators even in the same environment. For
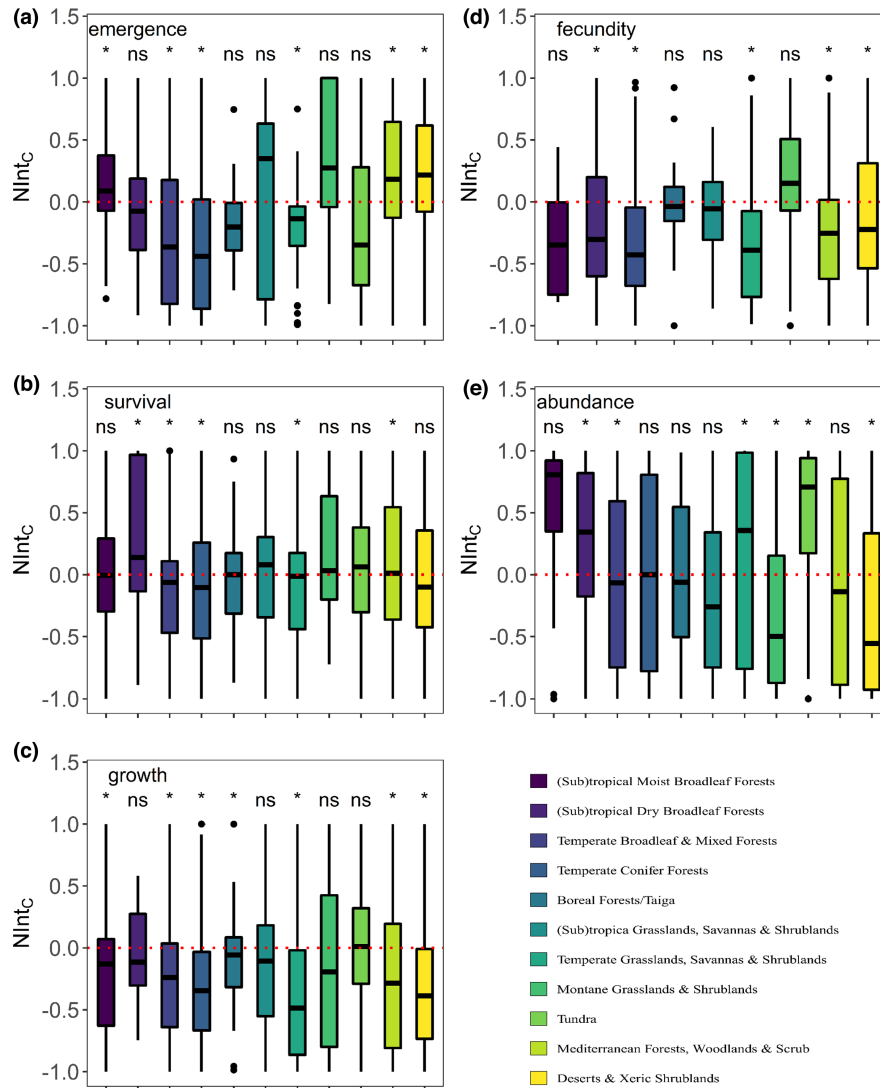
**FIGURE 4** $NInt_C$ (neighbour-effect intensity index with commutative symmetry) for the five plant performance indicators in different biomes. (a) Seedling emergence; (b) survival; (c) plant growth; (d) fecundity; (e) abundance. The significance of each performance indicator departing from zero after one sample Wilcoxon signed-rank tests is shown at the top. *$p < 0.05$; ns, not significant

instance, the outcome for seedling emergence in tropics is competitive due to the inhibitory effect of deep shade in closed forests, while the outcome for growth is facilitative due to a moderate shade (under which the plant still limits access to light) provided by neighbours (Gómez-Aparicio, 2009). Therefore, biome-specific mechanisms underlying plant interactions together with diverse responses among performance indicators may result in a weak effect of climate on the outcome of plant interactions at the global scale.

Our finding of the weak climatic effect calls for further research considering more local variables to identify environmental determinants of plant interactions. First, local soil conditions can affect plant interactions. For instance, soil moisture often is the most limiting and influential resource for plant growth, thereby affecting plant interactions (Brooker et al., 2008). Soil

moisture determines the relationship between fecundity and cover of a dominant shrub ranged from competitive to facilitative in the harsh tundra ecosystems (Mod et al., 2014). In addition, soil texture is an important factor influencing the net outcome of tree–grass interactions in savannas (Dohn et al., 2013). Second, disturbance and resource availability can mediate the outcome of plant interactions, as reported for perennial plants along a resource supply gradient (Brewer, 2011) and for nurse plants along a human-disturbed gradient in the southernmost Chihuahuan Desert (Badano et al., 2016). Third, microclimatic conditions could also affect the outcome of interactions. However, soil conditions, microclimate and disturbance are extremely heterogeneous even at very small scales, and currently we still do not have global soil or disturbance maps with adequate resolutions.
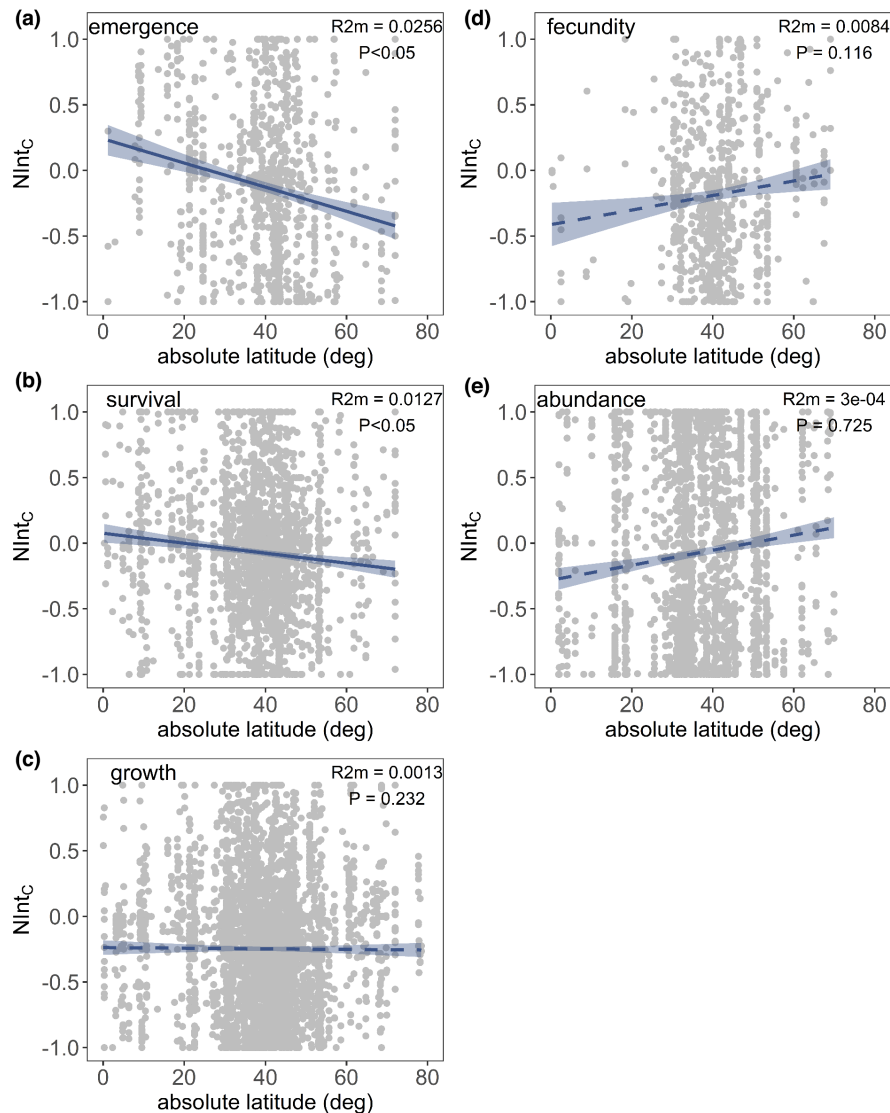
**FIGURE 5** The relationships between absolute latitude and $NInt_C$ (neighbour-effect intensity index with commutative symmetry) for the five plant performance indicators. (a) Seedling emergence; (b) survival; (c) plant growth; (d) fecundity; (e) abundance. The marginal coefficient of determination ($R^2m$) and the $p$-value ($P$) from LMMs are shown. The solid lines indicate significant relationships and dashed lines nonsignificant ones. The shadings are 95% confidence intervals

In addition, species, vegetation and stress type in local communities can determine the outcome of plant interactions. Species differ in their fundamental niches, and the outcomes of plant interactions depend on how neighbours affect the factors that deviate individuals from their niche optima (Liancourt et al., 2005, 2020). Vegetation effects on local limiting resources can also explain the outcomes of plant interactions, as reported in subalpine grasslands (Gross et al., 2010) and freshwater ecosystems (Le Bagousse-Pinguet et al., 2012). Furthermore, the community as a whole can ameliorate the abiotic conditions (community-scale facilitative effect) and thereby facilitate the species from the assembly experiencing stress (Liancourt & Dolezal, 2021). Therefore, the responses of plant interactions across environmental gradients are variable, in which species-specific response,

stress type and the scale of interest (pairwise interactions or community-level response) could play important roles (Soliveres et al., 2015).

Our global synthesis has revealed that competition occurs more frequently than facilitation in plant communities worldwide, which holds consistently for all plant performance indicators, interaction types and biomes, suggesting that competition is a fundamental mechanism structuring plant community at the global scale. Our findings are important for understanding the mechanisms underlying community dynamics and for preserving global biodiversity, since plant interactions are key to structuring plant community and to maintaining biodiversity (Losapio et al., 2021). Surprisingly, plant interactions do not show latitudinal pattern and are weakly related to climate. However,

**TABLE 1**  Results from the linear mixed models (LMMs) analysing the effect of climatic variables on $NInt_C$ (neighbour-effect intensity index with commutative symmetry) for the five plant performance indicators

|  | Estimate | SE | df | *t* value | *p* | $R^2m$ |
|---|---|---|---|---|---|---|
| **Emergence** |  |  |  |  |  |  |
| AMT | 0.299 | 0.171 | 208.33 | 1.749 | 0.082 | 0.0132 |
| TDR | 0.351 | 0.341 | 220.141 | 1.031 | 0.304 | 0.0046 |
| Tseason | −0.104 | 0.112 | 409.43 | −0.926 | 0.355 | 0.0031 |
| TWEQ | −0.172 | 0.104 | 231.144 | −1.648 | 0.101 | 0.0157 |
| AP | −0.102 | 0.143 | 306.181 | −0.711 | 0.478 | 0.002 |
| Pseason | −0.076 | 0.14 | 222.267 | −0.545 | 0.586 | 0.0011 |
| **Survival** |  |  |  |  |  |  |
| AMT | 0.093 | 0.072 | 678.88 | 1.284 | 0.2 | 0.0024 |
| TDR | −0.1 | 0.178 | 511.515 | −0.562 | 0.574 | 0.0005 |
| Tseason | −0.218 | 0.06 | 561.261 | −3.663 | **0.0001** | 0.0184 |
| TWEQ | −0.063 | 0.048 | 423.899 | −1.299 | 0.195 | 0.0026 |
| AP | 0.057 | 0.068 | 487.193 | 0.83 | 0.407 | 0.001 |
| Pseason | 0.175 | 0.067 | 476.729 | 2.616 | **0.009** | 0.0095 |
| **Growth** |  |  |  |  |  |  |
| AMT | 0.071 | 0.05 | 992.395 | 1.413 | 0.158 | 0.0021 |
| TDR | −0.168 | 0.141 | 871.684 | −1.194 | 0.233 | 0.0015 |
| Tseason | −0.107 | 0.052 | 789.669 | −2.064 | **0.039** | 0.0043 |
| TWEQ | 0.009 | 0.045 | 751.397 | 0.197 | 0.844 | 0.0001 |
| AP | −0.023 | 0.056 | 812.529 | −0.411 | 0.681 | 0.0002 |
| Pseason | 0.089 | 0.051 | 902.36 | 1.743 | 0.082 | 0.0031 |
| **Fecundity** |  |  |  |  |  |  |
| AMT | 0.008 | 0.164 | 181.603 | 0.048 | 0.962 | 0.0001 |
| TDR | −0.579 | 0.293 | 188.023 | −1.977 | **0.049** | 0.0169 |
| Tseason | −0.102 | 0.152 | 229.236 | −0.673 | 0.502 | 0.0016 |
| TWEQ | −0.092 | 0.115 | 176.818 | −0.795 | 0.428 | 0.0029 |
| AP | −0.118 | 0.122 | 202.69 | −0.964 | 0.336 | 0.0036 |
| Pseason | −0.135 | 0.11 | 167.179 | −1.232 | 0.22 | 0.0073 |
| **Abundance** |  |  |  |  |  |  |
| AMT | −0.103 | 0.116 | 195.064 | −0.883 | 0.378 | 0.0024 |
| TDR | −0.345 | 0.273 | 231.289 | −1.262 | 0.208 | 0.0053 |
| Tseason | −0.176 | 0.13 | 237.309 | −1.358 | 0.176 | 0.0042 |
| TWEQ | −0.02 | 0.103 | 212.554 | −0.193 | 0.848 | 0.0001 |
| AP | 0.137 | 0.114 | 221.235 | 1.201 | 0.231 | 0.0037 |
| Pseason | 0.074 | 0.105 | 226.414 | 0.705 | 0.481 | 0.0013 |

*Note:* AMT, annual mean temperature; TDR, mean diurnal range (mean of monthly (max temperature - min temperature)); Tseason, temperature seasonality (standard deviation *100); TWEQ, mean temperature of wettest quarter; AP, annual precipitation; Pseason, precipitation seasonality (coefficient of variation). Significant predictors with $p < 0.05$ are shown in bold. $R^2m$, marginal coefficient of determination.

the weak effects of climate reported here do not rule out the potential future effects of climate change on plant interactions, because climate change will modify species composition, local soil environment and disturbance regimes, on which plant interactions may depend (Kunstler et al., 2016; Tylianakis et al., 2008). Further research is now needed to understand how these factors will affect plant interactions from local to global scales, for more accurately predicting the dynamics of plant community and diversity under ongoing global environmental changes.
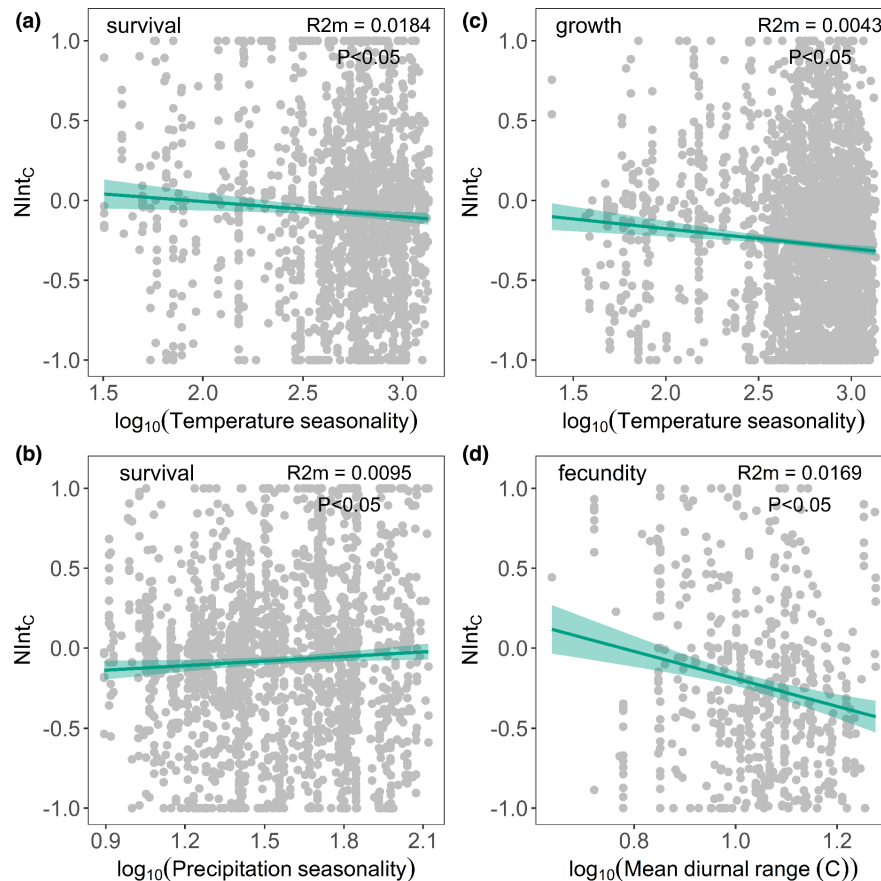
**FIGURE 6** The significant relationships (as revealed by LMMs) between climate predictors and $NInt_C$ (neighbour-effect intensity index with commutative symmetry) for the five plant performance indicators. (a) Temperature seasonality and survival; (b) precipitation seasonality and survival; (c) temperature seasonality and growth; (d) mean diurnal range and fecundity. The marginal coefficient of determination ($R^2m$) and the $p$-value ($P$) from LMMs are shown. The shadings are 95% confidence intervals

## AUTHOR CONTRIBUTION
XY, ZH and JHCC designed the study. XY, ZH, RG, RL and YZ collected the data. XY performed the analyses. The manuscript was drafted by XY, with contributions from LG-A, CJL, MV, LAC, ZH and JHCC.

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