

# The importance of competition and facilitation for global tree diversity

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Although competition and facilitation both influence tree diversity<sup>1–5</sup>, their relative importance and variation with latitude remain poorly understood. Using data from 17 large forest plots, including around 2.7 million trees and over 5,400 species spanning 5° S to 47° N, we quantified the latitudinal trends of the relative importance of negative (competitive) and positive (facilitative) interactions among neighbouring tree species, accounting for three biotic and eight environmental factors. We examined whether the average neighbourhood species diversity around individuals of each focal species was larger or smaller than expected under null models. The results show that negative interspecific interactions prevailed across most plots. Near the equator, the relative proportions of species surrounded by a lower or higher than expected number of neighbours were roughly equal, but at higher latitudes, the proportions of species with a relatively higher number of neighbours declined, and those with fewer neighbours increased significantly. This latitudinal pattern can be attributed in part to reduced abundance of legumes, non-arbuscular mycorrhizal associations, and the weaker canopy nursing effect towards higher latitudes, but it was mediated by mean annual temperature. These findings reveal a previously unrecognized relative decline in facilitative interactions and increase in competitive interactions with latitude and suggest that rising temperatures could enhance facilitative effects and promote tree community diversity at higher latitudes.

The observed decrease in species richness from the tropical to temperate zones is one of the earliest documented patterns in biogeography<sup>6–8</sup>, yet understanding the reasons for this pattern remains a major challenge<sup>9</sup>. Many hypotheses have been proposed to explain the latitudinal diversity gradient, including the passage of evolutionary time<sup>10,11</sup>, stable climate<sup>12</sup>, spatial environmental heterogeneity<sup>13</sup>, geographic constraints on species range distributions<sup>14</sup>, species interactions in

productivity–predation dynamics<sup>15</sup>, specialized natural enemies<sup>16</sup>, and competition<sup>17</sup>. The fact that so many hypotheses have been proposed speaks to the difficulty of explaining the latitudinal diversity gradient and the lack of a theoretical consensus<sup>18,19</sup>.

However, despite the controversy, few would disagree that species diversity in an area is the product of the interplay among local, regional and evolutionary ecological processes<sup>20</sup>. Much evidence has

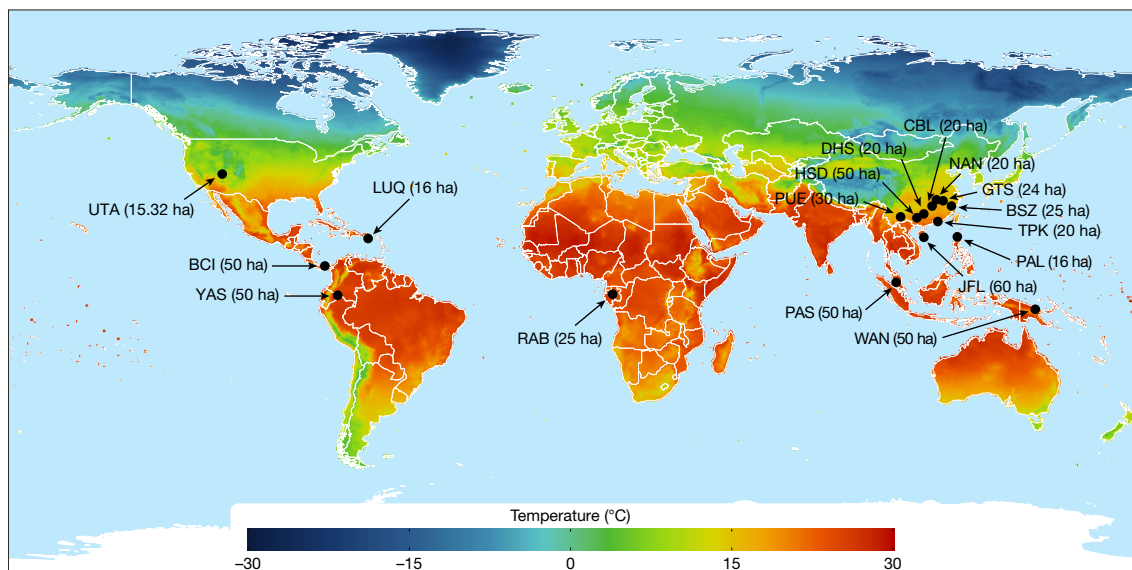
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**Fig. 1 | Locations of the 17 permanent forest plots.** The global thematic map shows MAT. Figure adapted from research by The Nelson Institute Center for Sustainability and the Global Environment, University of Wisconsin–Madison<sup>58</sup>. BCI, Barro Colorado Island; BSZ, Baishanzu; CBL, Chebaling; DHS, Dinghushan;

GTS, Gutianshan; HSD, Heishiding; JFL, Jianfengling; LUQ, Luquillo; NAN, Nanling; PAL, Palanan; PAS, Pasoh; PUE, Puer; RAB, Rabi; TPK, Tai Po Kau; UTA, Utah; WAN, Wanang; YAS, Yasuni.

shown that local processes such as neighbourhood competition or natural-enemy-mediated negative density dependence could play a role equally important to that of evolutionary and regional processes in assembling local communities from the regional species pool<sup>21,22</sup>, but their influence on global diversity patterns remains debated<sup>19,23,24</sup>. Local plant–plant interactions include both negative (competitive) and positive (facilitative) neighbourhood interactions. Negative interactions limit community recruitment, subsequent growth and survival, whereas positive interactions facilitate local establishment of regional species<sup>1</sup>. Most studies reported that competition prevails in more benign habitats and facilitation is often associated with harsh environments<sup>2–5</sup>, although facilitation is also observed in fertile, productive forests with favourable environmental conditions<sup>25–27</sup>.

Many processes can promote plant mutualistic and facilitatory interactions<sup>28,29</sup>. For example, nitrogen-fixing legumes support neighbourhood plant diversity by increasing local soil nitrogen availability<sup>30,31</sup>. The facilitative effect of leguminous species together with the observation that the abundance of nitrogen-fixation trees decreases from the tropics to high-latitude forests<sup>32</sup> suggests that facilitation could contribute to the latitudinal biodiversity gradient. Such a latitudinal gradient might also be maintained by mycorrhizal fungal symbionts that not only help alleviate diffuse competition among plants<sup>33,34</sup> and promote the growth and survival of neighbouring species<sup>35–37</sup>, but also show a latitudinal gradient<sup>38,39</sup>. Still, facilitation could arise from shading protection of canopy or subcanopy species to their own understory shade-tolerant species, which provides a nursing effect on heterospecific seedlings and saplings<sup>26,40</sup>. This facilitative buffering effect—in which canopy or subcanopy trees alleviate the understory microclimatic variation—tends to decrease with increasing latitude and reduced forest complexity<sup>41</sup>. Cold temperatures at high latitudes could also increase the nutrient and energy demands of plants as they must cope with cold stress and strengthen the competitive interactions<sup>42,43</sup>. These examples highlight that facilitation in forests is not a rare phenomenon but is as widespread an ecological process as competition<sup>44–46</sup>.

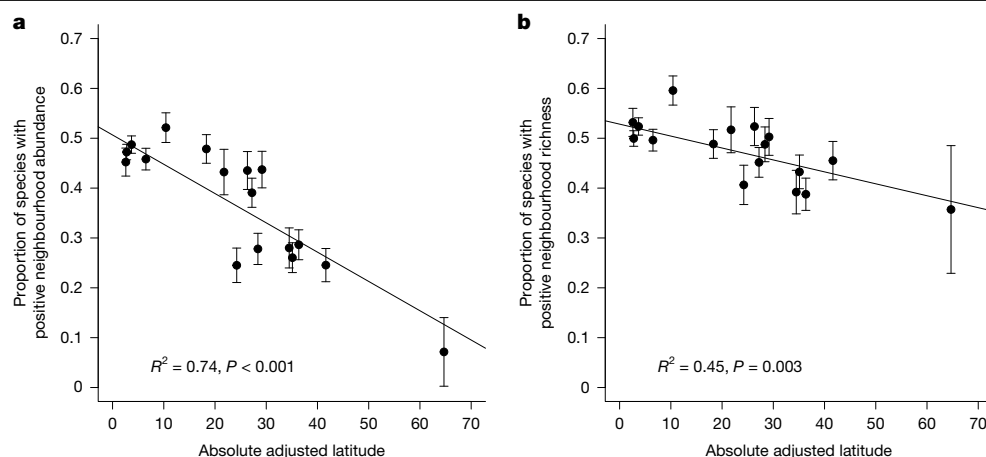
Although the importance of the two contrasting processes—positive and negative neighbourhood interactions—in shaping local species assemblages has been recognized<sup>29,47–50</sup>, how their relative strengths contribute to the global latitudinal forest diversity pattern is an unanswered question. Even less understood is how abiotic factors

may modulate these opposing interactions by either amplifying or weakening their effects.

To start addressing this question, we quantify the relative number of species with positive versus negative neighbourhood interactions using a global set of large, permanent forest plots distributed along latitudes from 5.25° S to 47.20° N (Fig. 1 and Extended Data Table 1). We use point process analysis to quantify whether the number of individuals and species in the neighbourhood of a focal species was larger or smaller than expected by null models. We hypothesize that local tree abundance and local species richness are not only regulated by competitive interactions—as most past studies have demonstrated<sup>44–46</sup>—but are also determined by facilitative interactions. We expected that the relative proportion of positive and negative interactions among species would vary along the latitudinal gradient, reflecting changes in latitude-dependent processes (for example, nutrient-enrichments by leguminous species, mycorrhizal symbioses and microclimate alleviation by forest structural complexity), and modulation by local climate factors.

Seventeen large permanent forest plots from Asia, Africa, Oceania, North America and South America were analysed in this study (Fig. 1 and Extended Data Table 1). Species neighbourhood interactions in each plot were assessed using the individual species–area relationship (ISAR)<sup>51</sup>, which characterizes positive or negative interactions on local diversity in the neighbourhood of a focal tree of a selected species (refer to the ‘Species neighbourhood analysis’ subsection in the Methods). The ISAR is dependent on both neighbourhood species abundance and species richness. A species is considered to have a positive (facilitative) neighbourhood effect when the average local tree abundance or species richness around its individuals exceeds the expected values calculated for the whole plot. Conversely, if a species shows a lower neighbourhood abundance or species richness than expected, it is considered to exert a negative influence, indicative of competitive interactions<sup>30</sup>.

To evaluate whether a focal species exhibits positive or negative effects, and to assess their statistical significance, we applied a local random labelling null model, which involves randomly reassigning the identity of neighbouring heterospecifics to focal individuals from a locally defined pool of trees within the same size class. By doing so, we control for size-related effects and large-scale habitat heterogeneity while preserving the original spatial arrangement of individuals within the plot.



**Fig. 2 | The proportion of facilitative species in each of the 17 forest plots decreases with latitude.** The facilitative relative effect on neighbourhood species was assessed on the basis of abundance (a) and richness (b). The proportion of facilitative species was calculated from circular plots with  $r = 2$  m centred on the focal tree: it is the ratio of the number of positive species over all species (singleton excluded, for a more stringent abundance cutoff see Extended Data Fig. 1). Positive species are those with  $\text{RNA}(r) > 1$  (a) and

$\text{RNS}(r) > 1$  (b), regardless of their significance levels. Data are presented as proportion  $\pm 1$  standard error (calculated using equation (5) with sample size  $n = 282$  (BCI), 167 (BSZ), 183 (CBL), 170 (DHS), 125 (GTS), 205 (HSD), 279 (JFL), 118 (LUQ), 215 (NAN), 303 (PAL), 825 (PAS), 227 (PUE), 314 (RAB), 155 (TPK), 14 (UTA), 526 (WAN), 1,029 (YAS) in each plot, respectively). The latitude was adjusted by altitude (Methods).

We then identified potential underlying mechanisms by sequentially excluding each group of facilitative species—including leguminous species, non-arbuscular mycorrhizal (non-AM) fungi symbioses, and large canopy or subcanopy trees—from the ISAR analysis; we then evaluated whether they reduced the significance of observed latitudinal gradients. If these groups of species contribute to neighbourhood facilitation, we should observe that the strength of positive interactions becomes weakened with the increase in latitude if leguminous species or non-AM fungi symbioses are excluded, respectively. This weakened latitudinal gradient should also be observed if the canopy trees (here defined as trees with the top 5% and 10% of large diameters, respectively) are removed. In addition to these three groups of facilitative species, we also examined eight environmental factors that could influence species neighbourhood interactions and tested their correlation with changes in the relative proportions.

We finally used spatially explicit point pattern simulations to evaluate how variation in species richness across plots might influence our assessment of neighbourhood interactions. In these simulations, individuals dispersed offspring according to a fixed dispersal kernel and engaged in local interactions, which could be either positive or negative. All other parameters were held constant, with only the total number of species changed across simulation runs. This approach allowed us to isolate the effect of species richness and to assess whether richness differences alone could bias the detection of latitudinal gradients in neighbourhood interactions.

Our results show that negative neighbourhood interactions dominated 11 of the 17 plots. The relative proportion of species (all species included except singleton) with higher neighbourhood abundance decreased significantly with increasing latitude adjusted by altitude ( $R^2 = 0.74$ ,  $P < 0.001$ ; Fig. 2a). The relative proportion of species with higher neighbourhood richness showed a similar trend with latitude adjusted by altitude ( $R^2 = 0.45$ ,  $P = 0.003$ ; Fig. 2b). Both patterns show an approximately equal relative proportion of positive and negative interactions near the equator, with the relative proportion of positive interactions decreasing or correspondingly relative proportion of negative interactions increasing significantly towards high latitudes.

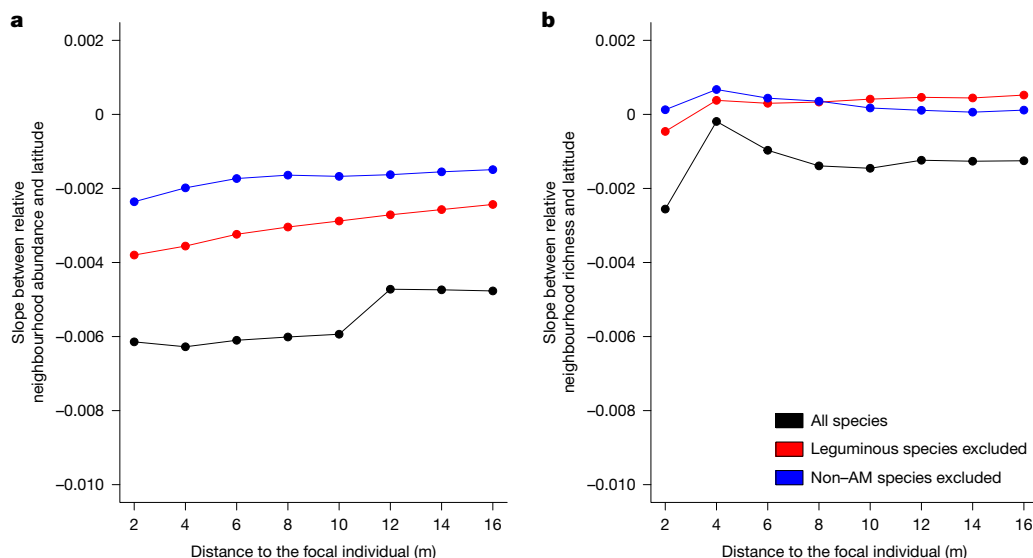
These patterns are also robust to more restrictive species abundance thresholds. For example, after excluding species with fewer than 50 individuals, the latitudinal pattern remains highly significant for both abundance-based neighbourhood interactions ( $R^2 = 0.77$ ,  $P < 0.001$ ;

Extended Data Fig. 1a) and richness-based neighbourhood interactions ( $R^2 = 0.36$ ,  $P = 0.012$ ; Extended Data Fig. 1b).

Using the local random labelling null model, we calculated the proportion of species showing significantly positive neighbourhood effects among those with significant effects (Extended Data Fig. 2). This analysis also supports the latitudinal pattern for neighbourhood abundance ( $R^2 = 0.62$ ,  $P < 0.001$ ; Extended Data Fig. 2a) and for neighbourhood richness ( $R^2 = 0.26$ ,  $P = 0.038$ ; Extended Data Fig. 2b). We also compute the absolute proportions of significantly positive and negative species over all species. After controlling for a higher proportion of significant species at higher latitudes, these patterns show similar trends of increasing facilitation towards tropics (Extended Data Fig. 7a,b) and increasing competition towards high-latitude forests (Extended Data Fig. 7c,d).

Various mechanisms could contribute to the observed latitudinal decrease in the proportion of positive interactions (Fig. 2). These include the decrease in leguminous species and non-AM fungi symbioses from low to high latitude<sup>32,38</sup>. To indirectly test the effect of legumes and non-AM tree species, we excluded leguminous and non-AM species from the neighbourhood interaction calculations, respectively. If these two groups of species contribute to positive neighbourhood interactions, we should observe that the strength of positive interactions becomes weakened with the increase in latitude. The result in Fig. 3 shows that the strength of the latitudinal gradients (that is, the slopes of the gradients in Fig. 2) is consistently weaker after leguminous focal species or non-AM focal species were excluded.

We also tested the possibility of structural effects, such as canopy species facilitating the establishment of shade-tolerant understory species. If this nursing effect is true, we should observe that the removal of canopy trees (here defined as trees with top 5% and 10% large diameter) would weaken the latitudinal trends in neighbourhood interactions. The results show that after 5% largest trees were excluded,  $R^2$  reduced from 0.77 (Extended Data Fig. 1a) to 0.73 ( $P < 0.001$ ; Extended Data Fig. 3a) for neighbourhood abundance, and from 0.36 (Extended Data Fig. 1b) to 0.27 ( $P = 0.033$ ; Extended Data Fig. 3b) for neighbourhood richness. When the largest 10% of trees were excluded,  $R^2$  similarly reduced to 0.71 for neighbourhood abundance ( $P < 0.001$ ; Extended Data Fig. 3c) and to 0.23 for neighbourhood richness ( $P = 0.053$ ; Extended Data Fig. 3d). These results, together with the effects of leguminous and non-AM tree species (Fig. 3), suggest that positive species interactions—facilitated by nitrogen-fixing legumes, non-AM-associated trees and



**Fig. 3 | Slopes between relative neighbourhood interactions and latitude across the 17 forest plots after excluding leguminous or non-AM tree species. a, Abundance-based neighbourhood interactions. b, Richness-based neighbourhood interactions. The neighbourhood interactions were calculated**

for eight circular neighbourhoods with  $r = 2, 4, 6, 8, 10, 12, 14$  and  $16$  m centred on the focal tree, using the proportion of facilitative species over all species (singleton excluded), as in Fig. 2.

canopy nursing effects, or more generally structural effects—might occur more frequently in the tropics than at higher latitudes, thereby promoting the latitudinal gradient in tree diversity.

To test the robustness of our results, we repeated the above analyses by changing the neighbourhood radius from  $r = 2$  m to  $16$  m and also changing the minimum diameter at the breast height (DBH) cutoff to  $\geq 1, 5, 10$  and  $20$  cm, respectively. The results showed that although the latitudinal gradient in neighbourhood interaction measured by species abundance remained qualitatively the same for all radii and DBH classes, it weakened considerably at longer distances. For species richness, the latitudinal pattern was only evident for some radii and DBH classes; for example, significant at  $r = 2$  m at DBH =  $1$  cm and  $5$  cm, and marginally significant or significant for  $r \leq 6$  m at DBH =  $20$  cm (Supplementary Table 1).

The relationships between species abundance and relative neighbourhood abundance or richness were also examined across 17 plots (Fig. 4 and Extended Data Fig. 4). These analyses show that both the ranges of the relative neighbourhood abundance or richness values and the likelihood of statistical significance depended on species abundance, with larger departures being non-significant for species with lower abundances. This pattern is consistent with the wider confidence intervals of rare species and was further illustrated by the z-scores standardized relative neighbourhood abundance and richness (Extended Data Fig. 8). We further conducted spatially explicit simulations to test whether the higher proportion of species exhibiting positive neighbourhood interactions in species-rich forests was due to a sampling effect. The spatial model simulations revealed that the decreasing trend in the relative proportion of species with positive neighbourhood interactions were not biased by the number of species in the plot (Extended Data Fig. 5).

We used multiple regression to model the proportion of species with positive neighbourhood interaction in terms of eight environmental factors. We found that the mean annual temperature (MAT) was the only factor significantly correlated with the relative proportion of species with positive neighbourhood abundance ( $R^2 = 0.72, P < 0.001$ ; Fig. 5a) and positive neighbourhood richness ( $R^2 = 0.38, P = 0.008$ ; Fig. 5b).

## Discussion

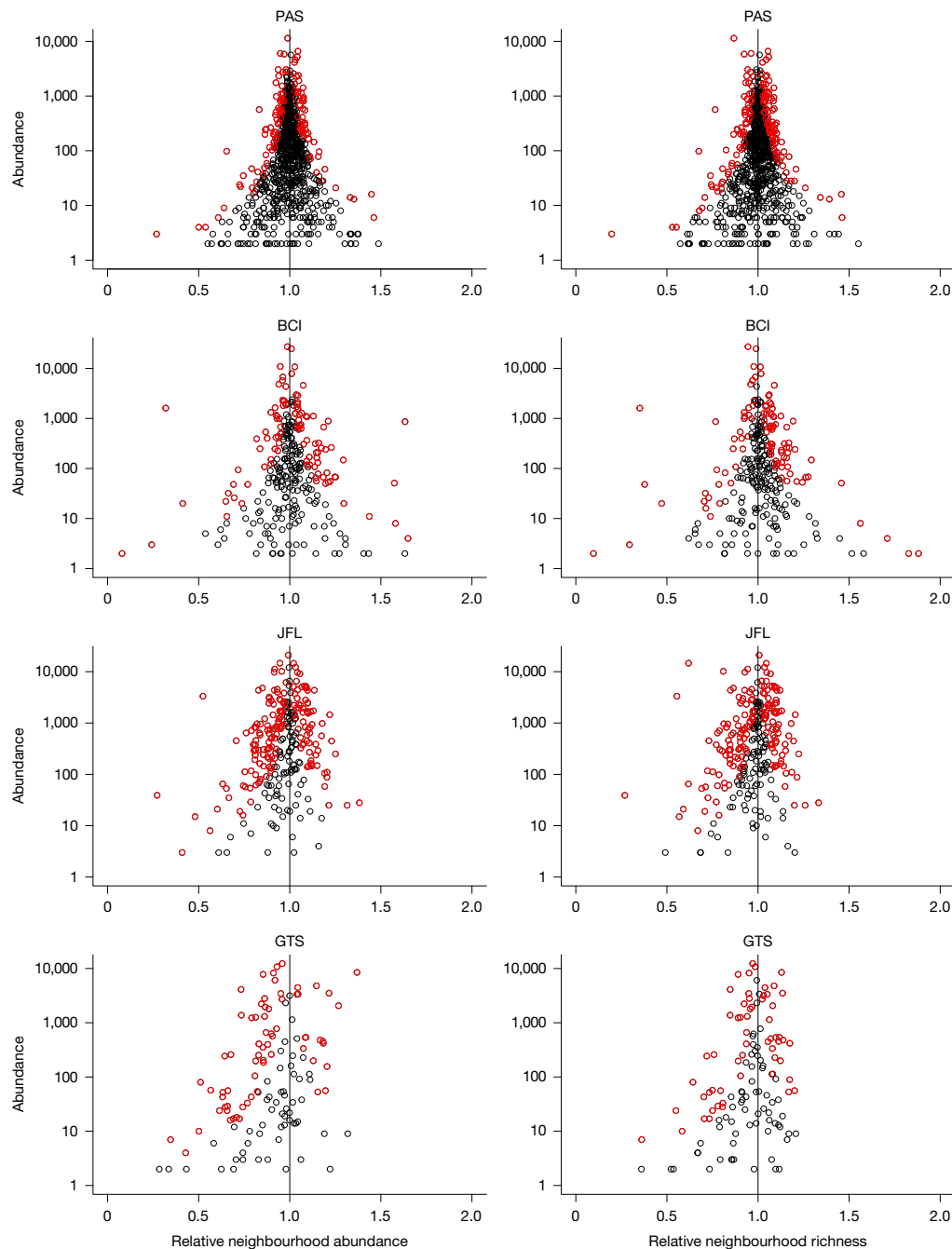
Although species interactions—together with environmental filtering—ultimately determine community assembly<sup>52,53</sup>, there is little

understanding of the relative contributions of positive and negative interactions to the latitudinal pattern of species diversity. Here we show that the proportions of species with a higher-than-expected number of neighbours decrease (Fig. 2), and, correspondingly, those with fewer neighbours increase, from the tropics to higher latitudes, with the relative proportions of species of positive and negative interactions being almost equal near the equator. Our finding that positive (facilitative) interactions decrease or negative (competitive) interactions increase with latitude refines the general belief that facilitation is more prevalent in stressed environments, such as those with increasing cold stress at higher latitudes, than in more benign habitats<sup>2–5</sup>. However, it is consistent with studies showing that facilitation occurs in fertile and productive habitats<sup>25–27</sup> and diminishes under extreme stress<sup>54</sup>.

Although our evidence is indirect, the observed patterns are consistent with possible mechanisms, including a decline in leguminous species, a reduced role of non-AM fungi symbioses (Fig. 3), and a weakening of canopy nursing or other structural effects on understory shade-tolerant species from tropical to high-latitude forests (Extended Data Fig. 3). The decreasing facilitation at high latitudes weakens the strength of complementarity effect, thus reducing productivity and diversity<sup>25,55–57</sup>. These and other possible facilitation mechanisms warrant further investigation.

Our study also reveals a strong positive correlation between MAT and the proportion of species with positive neighbourhood effects (Fig. 5), indicating that temperature may modulate the relative importance of facilitation and competition in community assembly. The decline in positive interactions and increase in negative interactions towards higher latitudes probably reflect reduced facilitative processes and promoted stronger competition. In tropical forests, high productivity, structural complexity and diverse nutrient use strategies can promote facilitation through mechanisms such as nutrient enrichment by nitrogen-fixing or non-AM species symbioses, and microclimatic buffering. Conversely, at higher latitudes, cold temperatures increase the nutrient and energy demands of plants as they must cope with cold stress (for example, developing freezing resistance, increasing non-structural carbohydrate storage)<sup>42,43</sup>. These physiological constraints, combined with shorter growing seasons and lower productivity, reduce facilitation and increase competition among neighbouring species. Thus, temperature limitation constrains positive neighbourhood effects, leading to a higher proportion of competitive interactions at higher latitudes.





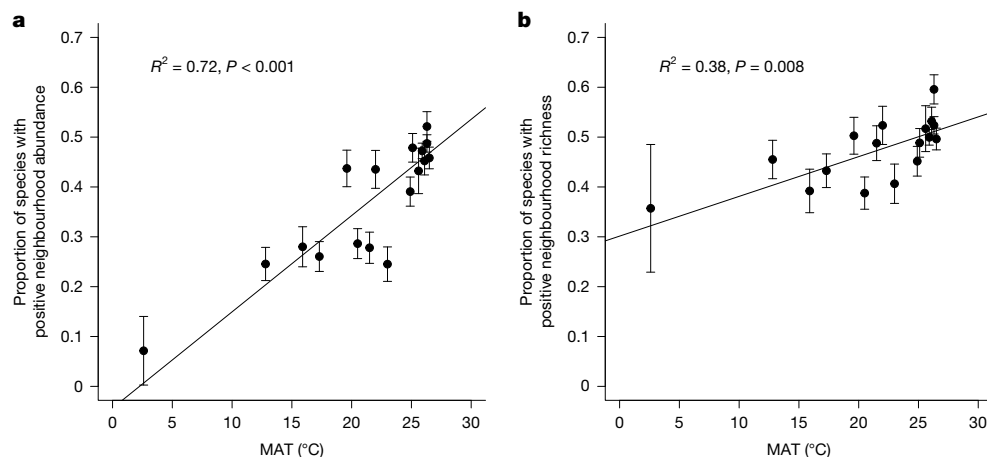
**Fig. 4 | Relationships between species abundance versus relative neighbourhood abundance or richness for four forest plots.** A relative neighbourhood abundance or richness below 1 suggests that species has negative (competitive) interaction with neighbours, and vice versa. Red circles

indicate species with significant neighbourhood interactions ( $P < 0.05$ ; computed from 999 independent randomizations of the local random labelling null model). The relative neighbourhood abundance or richness were calculated from circular plots with  $r = 2$  m centred on the focal tree.

The latitudinal gradients are stronger at small spatial scales and the pattern for neighbourhood abundance is more robust than neighbourhood richness. This probably reflects that the underlying mechanisms are highly localized, operating over distances where plants directly interact through roots, crowns or short-range pathogen and mutualist networks, rather than broader-scale processes. The stronger pattern observed for abundance may arise because individual distributions are often well captured by circular statistics, reflecting predictable small-scale effects driven by dispersal limitation, habitat heterogeneity and canopy gaps, particularly for saplings in tropical forests. By contrast, the spatial distribution of species richness is less predictable, as it depends on a wider range of stochastic and historical

factors that operate beyond the neighbourhood scale. As trees grow, self-thinning further reduces fine-scale clustering and dilutes richness effects, which are therefore strongest among small individuals and at very local scales.

It is important to clarify that our analysis does not estimate the absolute strength of species interactions; it instead assesses the relative contributions of competition and facilitation among forest tree species. This limitation stems from the fact that we evaluated each species' local neighbourhood against a plot-specific null expectation. The observed proportions of facilitative and competitive interactions should therefore be interpreted as relative deviations from the local community baseline, rather than definitive categorizations of interaction type or



**Fig. 5 | Proportions of species with positive neighbourhood species abundance or richness change with MAT for the 17 forest plots.**

**a**, Neighbourhood species abundance. **b**, Neighbourhood species richness. The proportion of facilitative species was calculated from circular plots with  $r = 2$  m centred on the focal tree, as in Fig. 2. Data are presented as proportion

$\pm 1$  standard error (calculated using equation (5) with sample size  $n = 282$  (BCI), 167 (BSZ), 183 (CBL), 170 (DHS), 125 (GTS), 205 (HSD), 279 (JFL), 118 (LUQ), 215 (NAN), 303 (PAL), 825 (PAS), 227 (PUE), 314 (RAB), 155 (TPK), 14 (UTA), 526 (WAN), 1,029 (YAS) in each plot, respectively). The latitude was adjusted by altitude (Methods).

magnitude. However, as shown in the neutral simulations, if all neighbourhood interactions in a plot were uniformly negative (or uniformly positive), our method would still yield a distribution of positive and negative effects due to the comparative nature of the analyses among species. The exception is species-poor forests, where strong conspecific aggregation leads to an apparent excess of positive effects in the simulations. Thus, if anything, such forests should be biased towards positive interactions.

In conclusion, our study provides quantitative evidence on the relative proportion of species with positive or negative neighbourhood interactions along a latitudinal gradient of large, permanent forest plots. The finding that there are similar proportions of species with positive and negative interactions around the equator, but more negative and fewer positive species interactions at higher latitudes suggests that forest diversity in the tropics may be enhanced by the higher number of facilitative interactions. This study reveals the previously unappreciated importance of the relative roles of positive and negative species interactions in shaping global patterns of forest tree diversity.

## Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-026-10349-2>.

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### Data sources

Tree census data were obtained from 17 large, permanent forest dynamics plots distributed in latitudes ranging from 5.25° S to 47.20° N (Extended Data Table 1 and Fig. 1). The plot size varies from 15.32 to 60 ha. Plot census methods followed the ForestGEO network's standard protocol (<https://www.forestgeo.si.edu/>), which includes all stems  $\geq 1$  cm in DBH (1.3 m above the ground). All of the main stems were identified to species, measured and mapped to their relative spatial coordinates within each plot.

Eight environmental factors were compiled for each plot. Five of them—including plot elevation range, MAT, January temperature, July temperature, and mean annual precipitation—were obtained from past work<sup>59</sup>. Soil total nitrogen density ( $\text{g m}^{-3}$ ) was compiled from the Global Gridded Surfaces of Selected Soil Characteristics (IGBP-DIS) database at a resolution of  $5 \times 5$  arc-minutes, and in a soil depth interval 0–100 cm from Oak Ridge National Laboratory Distributed Active Archive Center (<https://daac.ornl.gov>)<sup>60</sup>. We also obtained soil temperature<sup>61</sup> and soil wetness<sup>62</sup>.

The 17 forest plots are located at different elevations, ranging from 28 m to 3,136 m above sea level, which could confound the observed latitudinal gradient in species interactions<sup>63</sup>. Past studies have shown that an elevation increase of approximately 100 m corresponds to a 100-km northward shift in climate conditions<sup>63</sup>. To account for this effect, considering that 1° of latitude equals roughly 111 km, we adjusted the latitude of each plot using the formula:

$$\text{Adjusted latitude} = |\text{latitude}| + \frac{\text{maximum elevation} + \text{minimum elevation}}{2 \times 111}$$

### Species neighbourhood analysis

The analysis of species interactions, particularly the estimation of their magnitude, requires data on population dynamics<sup>64,65</sup>. With only static stem-mapping data, such analyses are often precluded. Here, we do not attempt to estimate the magnitude of species interactions; we instead use the ISAR<sup>51</sup> to evaluate whether a given species had a higher or lower neighbourhood abundance ( $N$ ) or species richness ( $S$ ) than a null expectation. If a species has a higher neighbourhood abundance or richness than some expectation (for example, a null model), we consider the species to have positive neighbourhood interaction. Otherwise, the interaction is negative. Abundance-based statistics capture the quantitative aspect of these interactions, that is, how the number of individuals of a species is affected by the presence of others, whereas richness-based statistics reflect the species composition of a community. Thus, by using both abundance and species richness indices, we capture a fuller picture of community structure and composition.

The individual abundance-area relationship (IAAR<sub>*i*</sub>) and ISAR for focal species  $i$  (ISAR<sub>*i*</sub>) are defined as the average abundance or richness within radius  $r$  from all individuals of the focal species:

$$\text{IAAR}_i(r) = \frac{1}{n_i} \sum_{j=1}^{n_i} N_{ij}(r), \quad (1a)$$

$$\text{ISAR}_i(r) = \frac{1}{n_i} \sum_{j=1}^{n_i} S_{ij}(r), \quad (1b)$$

where  $N_{ij}(r)$  and  $S_{ij}(r)$  are the abundance and richness within radius  $r$  from individual  $j$  of focal species  $i$ , and  $n_i$  is the total number of individuals of the focal species  $i$ . Note that IAAR corresponds to what is commonly referred to as the  $K$ -function in point pattern analysis.

The observed IAAR<sub>*i*</sub> and ISAR<sub>*i*</sub> for each focal species were compared with corresponding IAAR<sub>0,*i*</sub> and ISAR<sub>0,*i*</sub> calculated from non-focal

individuals of similar DBH size classes in a defined spatial area (see equation (3) below). To quantify relative neighbourhood effects, we computed the relative neighbourhood abundance (RNA) and relative neighbourhood richness (RNS) as:

$$\text{RNA}_i(r) = \frac{\text{IAAR}_i(r)}{\text{IAAR}_{0,i}(r)} \quad (2a)$$

$$\text{RNS}_i(r) = \frac{\text{ISAR}_i(r)}{\text{ISAR}_{0,i}(r)} \quad (2b)$$

RNA<sub>*i*</sub>( $r$ ) > 1 or RNS<sub>*i*</sub>( $r$ ) > 1 indicates that an individual of focal species  $i$  has, on average, a higher abundance or richness within radius  $r$  than other species do. This suggests the focal species exerts (directly or indirectly) some positive interaction with its neighbours. Conversely, RNA<sub>*i*</sub>( $r$ ) < 1 or RNS<sub>*i*</sub>( $r$ ) < 1 indicates that the focal species  $i$  has a negative interaction with its neighbours.

IAAR<sub>0,*i*</sub> and ISAR<sub>0,*i*</sub> for each focal species were calculated within a 60-m distance circular neighbourhood centred on each focal tree. The 60-m distance was selected to ensure a sufficient number of non-focal individuals for comparison, while maintaining a relatively homogeneous habitat environment<sup>30</sup>. To ensure comparability between focal and non-focal individuals, the values of IAAR<sub>0,*i*</sub> and ISAR<sub>0,*i*</sub> were computed only for non-focal trees falling within the same DBH class as the focal tree; DBH was categorized into 20 logarithmically spaced size classes to account for variation in tree diameter in each plot. The IAAR<sub>0,*i*</sub> and ISAR<sub>0,*i*</sub> of non-focal trees were calculated as follows:

$$\text{IAAR}_{0,i}(r) = \frac{1}{n_i} \sum_j \frac{1}{m_{ij}} \sum_{k \neq j} \sum_l I_{ijkl} N_{kl}(r) \quad (3a)$$

$$\text{ISAR}_{0,i}(r) = \frac{1}{n_i} \sum_j \frac{1}{m_{ij}} \sum_{k \neq j} \sum_l I_{ijkl} S_{kl}(r) \quad (3b)$$

where  $I_{ijkl}(r)$  is an indicator function that is one if the tree  $l$  of non-focal species  $k$  is within 60 m circular neighbourhood and in the same DBH class of tree  $j$  of focal species  $i$ , and zero otherwise;  $m_{ij}$  is the number of the non-focal trees in the same DBH class and within 60 m from tree  $j$  of focal species  $i$  (that is,  $m_{ij} = \sum_{k \neq j} \sum_l I_{ijkl}$ ).

### Test differences in neighbourhood diversity by a local random labelling null model

A local random LRL was proposed to evaluate whether a focal species had statistically significant positive or negative effects compared with the null model expectation. For each focal individual  $j$ , we randomly reassigned the identity of neighbouring heterospecific individuals to focal individuals within a 60 m distance and within the same DBH size class. This implementation represents a focal-centred and locally constrained form of random labelling, rather than a global permutation of species identities across the plot. This procedure was repeated 999 times for all individuals of each species  $i$ , from which simulation envelopes for IAAR<sub>0,*i*</sub>( $r$ ) and ISAR<sub>0,*i*</sub>( $r$ ) were constructed for each species. Observed values of IAAR<sub>*i*</sub>( $r$ ) and ISAR<sub>*i*</sub>( $r$ ) were considered significant if they fell outside the 95% confidence envelopes of the null distribution (Extended Data Fig. 2).

The local random labelling null model removes: (1) local habitat heterogeneity effects of the focal species (by restraining the simulation within a 60-m radius); (2) collective effects of environmental variation that cause heterogeneity in the local density of (heterospecific) trees; and (3) effects of the size of the trees (by restraining the simulation to the same size class).

### The latitudinal pattern of species neighbourhood interactions

To examine whether patterns for the relative role of positive and negative interactions changed with latitude, we computed the proportion



(RNA( $r$ ) > 1 and RNS( $r$ ) > 1) in each plot along the absolute adjusted latitudinal gradient, and fitted the gradient using a weighted linear function. The proportions were measured by relative proportion (Fig. 2, and Extended Data Figs. 1 and 2), absolute proportion (Extended Data Fig. 6) and standardized absolute proportion (Extended Data Fig. 7) as described below.

For each plot, the relative positive proportions of neighbourhood abundance and richness were computed as follows:

$$p_N = \frac{1}{S} \sum_i \text{RNA}_i(r) > 1 \quad (4a)$$

$$p_S = \frac{1}{S} \sum_i \text{RNS}_i(r) > 1 \quad (4b)$$

where  $S$  is the total number of species examined. The relative negative proportions of neighbourhood abundance and richness were equal to  $1 - p_N$  or  $1 - p_S$ , respectively.

The standard error for the estimated proportion  $\hat{p}$  is:

$$\text{SE} = \sqrt{\frac{\hat{p}(1 - \hat{p})}{S}} \quad (5)$$

The standard errors were plotted as error bars in the figures. The inverse of the squared standard error was also used as weights for the linear regression between  $p$  (that is,  $p_N$  or  $p_S$ ) and latitude. In Fig. 2 we used all species (except for singletons); however, in Extended Data Fig. 1, species with fewer than 50 individuals were excluded.

The same analysis was repeated for significant species according to the local random labelling null model (Extended Data Fig. 2). The relative proportion of significant facilitative species for neighbourhood abundance was computed as follows:

$$p_N = \frac{\sum_i \text{RNA}_i(r) > h_i^+}{\sum_i \text{RNA}_i(r) < h_i^- \mid \text{RNA}_i(r) > h_i^+} \quad (6)$$

where  $h_i^-$  and  $h_i^+$  are the lower and upper 95% confidence intervals obtained from the local random labelling null model.

We also computed the absolute proportions relative to all species for neighbourhood abundance as follows:

$$p_N^+ = \frac{1}{S} \sum_i \text{RNA}_i(r) > h_i^+ \quad (7a)$$

$$p_N^- = \frac{1}{S} \sum_i \text{RNA}_i(r) < h_i^- \quad (7b)$$

Analogous expressions to equations (6) and (7a,b) were also derived for neighbourhood richness; however, we note that the absolute proportion of species with significant effects (either positive or negative) increases with latitude (Extended Data Fig. 6), because tropical forests include many rare species that seldom pass the significance test. This is demonstrated by a strong relationship between the proportion of significant species as a function of the mean species abundance of each plot ( $R^2 = 0.79$  for significant neighbourhood abundance and  $R^2 = 0.81$  for significant neighbourhood richness).

This confounding effect acts differently for negative and positive interactions. For negative interactions, both the confounding effect and the ecological pattern (fewer negative interactions in the tropics) push the trend in the same direction, leading to a strong apparent gradient towards high-latitude sites. For positive interactions, by contrast, the confounding effect acts in the opposite direction of the ecological signal (more positive interactions in the low latitude tropics), thereby weakening or even reversing the pattern (Extended Data Fig. 6 and Supplementary Table 2).

To account for the abundance bias effect, we standardized the absolute proportion to a common reference abundance across all plots. Specifically, we fit a logistic regression between the probability of being a significant positive (or negative) species as a function of species log abundance as:

$$\text{logit}(y_i) = \alpha + \beta \log(n_i) + \varepsilon_i \quad (8)$$

where  $y_i$  is 1 if species  $i$  is significantly positive (or negative) and is 0 otherwise.

We then predicted the corresponding value at an arbitrarily given  $n = 1,000$  (so that to standardize the effect of species abundance). Results shown in Extended Data Fig. 7 and Supplementary Table 2 are consistent with the relative proportion analysis in Fig. 2 and Extended Data Figs. 1 and 2, showing a decreasing absolute proportion of positive species and an increasing absolute proportion of negative species towards higher latitudes. Other reference abundance values at  $n > 1,000$  or  $n < 1,000$  produced qualitatively similar results.

### Species neighbourhood interactions varied with the radius from the focal individuals and DBH thresholds

The RNA( $r$ ) and RNS( $r$ ) models allow us to define species associations as positive (or facilitative) or negative (or competitive). IAAR and ISAR were computed at eight radii from  $r = 2$  m to  $r = 16$  m at 2 m intervals. The results at  $r = 2$  m are reported in the main text, with other radii included in Supplementary Table 1.

All trees with DBH  $\geq 1$  cm were used in the above analysis; however, trees with different DBH sizes could have different (asymmetric) effects on neighbours. To test this effect, we performed an analysis that only included trees larger than a minimum DBH cutoff. We exercised the analyses with three minimum DBH cutoffs of  $\geq 5$ , 10 and 20 cm, with results reported in Supplementary Table 1.

### Testing the effect of facilitation on neighbourhood interactions

Niche partitioning, or complementarity, could result either from reduced competition among species or from facilitative interactions, whereby individuals positively influence one another (for example, the canopy trees provide nursing effect on shade-tolerant seedlings)<sup>55,56</sup>. It has long been hypothesized and empirically tested that species competition reduces from the tropics to the high latitudes<sup>10,65</sup>. In this context, our result of reduced facilitative interactions along the latitudinal gradient (Fig. 2) suggests that facilitation does not simply track reductions in competition. Here we further showed that the reduced neighbourhood facilitative interaction could also result from a reduced prevalence of facilitative species along the latitudinal gradient.

In this analysis we considered three possible types of facilitation. We hypothesized that the facilitative effects of legumes, non-AM fungi associated trees, and canopy or subcanopy trees decrease with the increase of latitude. To test their effects, we identified leguminous species, non-AM fungal symbioses and counted their abundances in each of the 17 plots. We defined large DBH canopy or subcanopy trees as those individuals with the top 5% and 10% of DBH in each plot. We calculated and compared the neighbourhood facilitative interactions with and without the inclusion of leguminous species, non-AM fungal symbioses, or large DBH canopy or subcanopy trees. If leguminous species, non-AM trees, and large DBH canopy or subcanopy trees provided facilitative effects, we would expect the latitudinal gradients of neighbourhood interactions to become weakened after these potential facilitators were excluded. The results are shown in Fig. 3 and Extended Data Fig. 3.

### Species abundance effects on the neighbourhood abundance and richness

Species varied from rare to common in all 17 plots. The species population size in the whole plot may affect neighbourhood

species abundance or richness<sup>64,66</sup>, possibly producing unexpected biases in the latitudinal patterns. To test this effect, we plotted the relationship between species abundance and RNA(*r*) or RNS(*r*) for each plot. The results of four plots at different latitudes are shown in Fig. 4 as examples; the results for all 17 plots are reported in Extended Data Fig. 4.

We further estimated z-scores (standardized effect sizes of relative neighbourhood abundance) as  $(\text{IAAR}(r) - \text{IAAR}_0(r))/\sigma$ , where  $\sigma$  is the standard deviation derived from the 999 permutations of the null model. Analogous z-scores were computed for ISAR. Thresholds of -1.96 and 1.96 were used for visual interpretation, with red circles indicating significant values and black circles indicating non-significant values across species of differing abundance. Results from all 17 plots are shown in Extended Data Fig. 8.

## Spatial model simulation to assess a potential bias for the latitudinal neighbourhood interaction pattern

To explore whether the reported latitudinal patterns were somehow affected by the total number of species in a plot, by creating undesirable and unpredictable bias in detecting the proportion of species with positive or negative interactions across forests with different richness, we used spatially explicit simulations of point pattern processes. We considered a local community having *N* individuals and ecologically equivalent species randomly chosen from a pool of *S* species (the metacommunity). Parents disperse offspring according to a dispersal kernel, and individual survival is a negative function of local density, as described below. Immigration is allowed with rate *v* from the metacommunity. In the metacommunity, the abundances of the *S* species follow a log-series distribution, and a species with higher abundance has a higher probability of immigration into the local community.

We simulate these cases as point processes with *N* individuals on an area of  $L \times L$ , with periodic boundary conditions considered to minimize edge effects. Initially, all *N* individuals are placed at random with identity randomly assigned from species in the metacommunity. Every birth event is paired with a death event such that the total number of individuals is constant (zero-sum game). For every death event, an individual is chosen to die with a probability that depends on the density of its neighbours. Specifically, for each individual *i* time to death is drawn from an exponential distribution with rate:

$$\mu_i = 1 + \alpha \sum_{j \neq i} K(d_{ij}) \quad (9)$$

where *K* is a quadratic kernel with finite range  $L_k$ ,  $\alpha$  is the strength of local interactions and  $d_{ij}$  is the distance between the focal individual *i* and neighbour *j*. The individual with the shortest death time is removed. For birth, the new individual can be an immigrant or an offspring of an individual in the local community with probability *v*. If it is an immigrant, it is placed at a random spatial location, and its species identity is chosen from the species in the metacommunity according to their abundance distribution. If it is not an immigrant, a parent is chosen at random from the local community and disperses an offspring at a distance *r* according to a fat-tail kernel:

$$D(r) \sim \left(1 + \frac{r^2}{L_D^2}\right)^{-2} \quad (10)$$

where  $L_D$  is a species-specific dispersal parameter. A total of *N* deaths and *N* births or immigrations constitute one generation time. We performed two sets of 17 simulations with *N* = 30,000 and varying *S* from 20 to 600 to generate local communities with different richness comparable with the plot data (equivalent to an area of 5–7 ha). The first set simulates negative interactions ( $\alpha > 0$ ), whereas the second set simulates positive interactions ( $\alpha < 0$ ). Each simulation was conducted for 20 generations (600,000-time steps). The code to simulate the point pattern is available in Extended Data 5.

In the simulations, all species are considered ecologically equivalent, and individuals interact independent of species identity, therefore we did not expect to find significant relationships between the proportion of species with positive interactions and forest diversity. Thus, any pattern that might emerge from the simulations can be attributed to sampling artefacts or biological effects common to all communities, such as conspecific aggregation that causes more abundant species to generate more negative density dependent effects. If the pattern obtained from the real data has, qualitatively, the same trend as the pattern obtained by the simulations, it is likely that sampling issues have contributed to the empirical pattern. Conversely, if the pattern has a different trend (Extended Data Fig. 5), we can rule out sampling bias as a mechanism for the observed latitudinal pattern seen in Fig. 2.

The simulations showed that low-richness plots have a higher proportion of facilitating species, opposite to the observed trend. This pattern arises because dispersal limitation promotes spatial aggregation, and the degree of clustering differs among species depending on their abundance<sup>67</sup>. Abundant species tend to form denser clusters that suppress local diversity, thereby increasing the relative diversity of other species. In contrast, in species-rich plots in which no single species is dominant and abundances are more evenly distributed, this effect becomes negligible. For this reason, a complete spatial randomness process (that is, a Poisson process) would not produce any plot species richness effect, as, by definition, complete spatial randomness lacks spatial structure—each individual, regardless of species identity, is surrounded by a random number of neighbours and species.

## Abiotic factors responsible for latitudinal differences in the type of species interactions

Latitude per se is a proxy, not a mechanism; we therefore analysed the specific abiotic factors that co-vary with it. In addition to the three groups of species facilitators described above, environmental factors could also affect species neighbourhood interactions. To test which of the eight environmental variables (see the second paragraph in the ‘Data Sources’ subsection of Methods) might explain the relative number and type of neighbour interactions among species across the forest plots, we used a multiple regression to model the relationship between the proportion of species with positive RNA(*r*) or RNS(*r*) and all the eight environmental factors for each forest plot. The stepwise approach was used for model selection. The best model retained the MAT as the only factor for both RNA(*r*) and RNS(*r*). The proportion of species that had higher neighbourhood abundance RNA(*r*) or richness RNS(*r*) than expected was plotted against the MAT and is presented in Fig. 5.

## Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

Data from 17 plots can be requested from the ForestGEO plot network via <https://www.forestgeo.si.edu/>. Chebaling plot data can be requested from the principal investigators of Heishiding plot in the ForestGEO plot network; Nanling and Puer plots’ data can be requested from the principal investigators of Jianfengling plot in the ForestGEO plot network. Plot elevation range, MAT, January temperature, July temperature and mean annual precipitation, were obtained from a past work<sup>59</sup>. Soil total nitrogen density ( $\text{g m}^{-3}$ ) was compiled from the IGBP-DIS database at a resolution of  $5 \times 5$  arc-minutes, and in a soil depth interval 0–100 cm from Oak Ridge National Laboratory Distributed Active Archive Center (<https://daac.ornl.gov/>)<sup>60</sup>. Soil temperature was obtained from <https://zenodo.org/record/4558663#.ZFRV46BBztU> (ref. 61) and soil wetness was obtained from <https://climate.esa.int/en/projects/soil-moisture/> (ref. 62). We also stored the running results of 17 plots to Github via <https://github.com/mdetto/Positive-Interactions> (ref. 68).

## Code availability

Extended Data 1–4 are stored on Github at <https://github.com/mdetto/Positive-Interactions> (ref. 68), whereas Extended Data 5 was uploaded to Code Ocean at <https://codeocean.com/capsule/4844196/tree> (ref. 69). Extended Data 1: R script for computing the number of individuals ( $N$ ) and number of species richness ( $S$ ) around all stems, 'ISAR'. Extended Data 2: R script for calculating the relative neighbourhood abundance and richness for trees within 60 m circular neighbourhood of focal species and falling within the same DBH class as the focal tree, 'RNA.RNS'. Extended Data 3: R script for local random labelling null model test, 'LocalRLNullModel'. Extended Data 4: R script for large tree exclusion analysis, 'LargeTreeExclusion'. Extended Data 5: Matlab script for running spatial model simulation to assess the potential biases for the latitudinal neighbourhood interaction pattern, 'SpatialBirthDeathSim'.

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**Author contributions** H.X., M.D., S.F. and F.H. conceived the study. H.X. and M.D. analysed data. H.X., M.D., S.F. and F.H. led the writing. J.A.H., A.A., J.D.B., P.B., C.C., S.J.D., G.A.F., B.C.H.H., D.K., B.L., J.L., M.L., W.L., Y.L., Z.L., J.A.L., H.R.M., X.M., V.N., H.R., J.S., J.T., M.U., R.V., T.L.Y., S.L.Y., Y.Z., J.K.Z., G.D.W., Y.L. provided constructive suggestions or substantively revised the paper. M.D. and F.H. derived the analytical models. H.X., M.D., J.A.H., A.A., J.D.B., P.B., C.C., S.J.D., G.A.F., B.C.H.H., D.K., B.L., J.L., M.L., W.L., Y.L., Z.L., J.A.L., H.R.M., X.M., V.N., H.R., J.S., J.T., M.U., R.V., T.L.Y., S.L.Y., Y.Z., J.K.Z., G.D.W., Y.L., S.F. and F.H. contributed to the data collection of the 17 forest plots.

**Competing interests** The authors declare no competing interests.

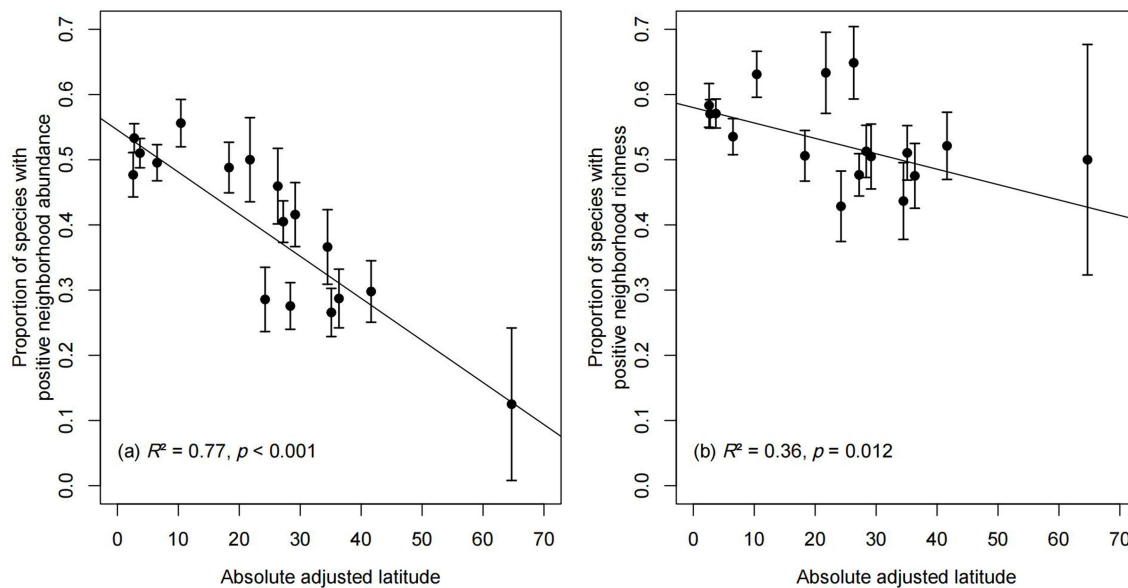
### Additional information

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41586-026-10349-2>.

**Correspondence and requests for materials** should be addressed to Han Xu or Suqin Fang.

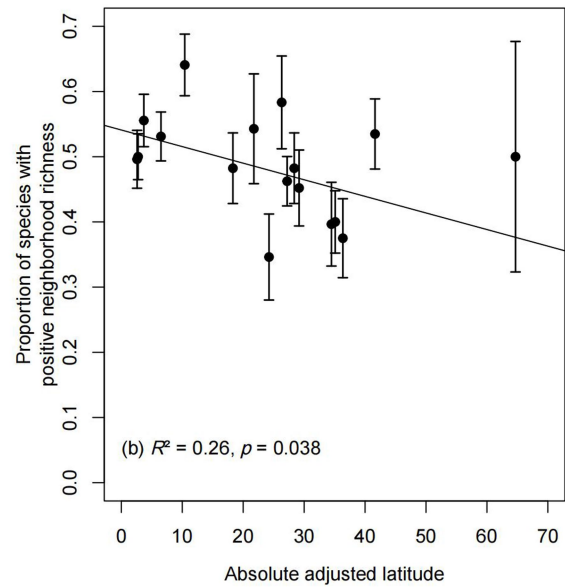
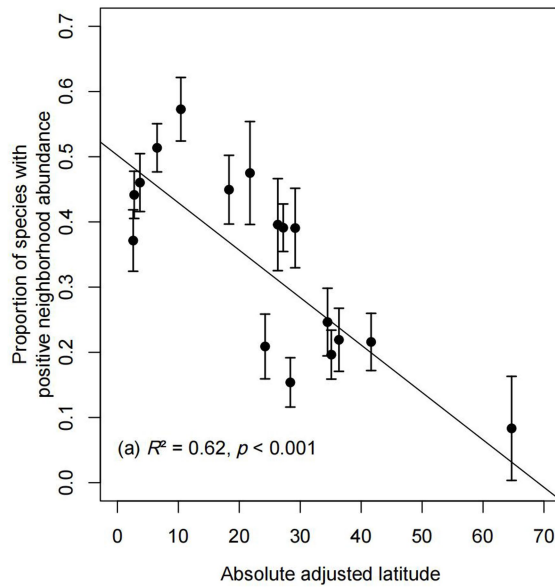
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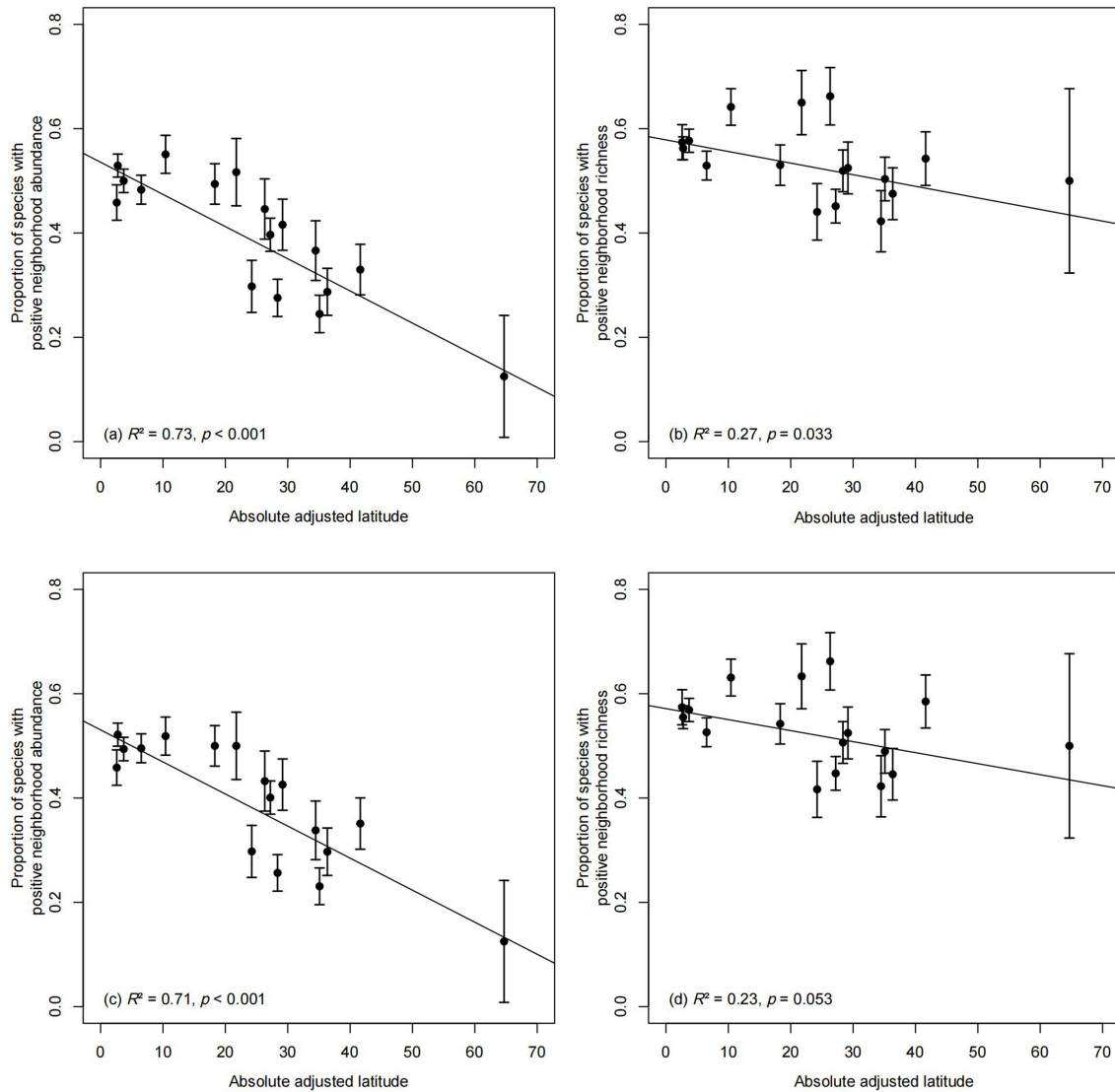
**Extended Data Fig. 1 | The proportion of facilitative species in each of the 17 forest plots decreases with latitude.** The relative facilitative effect on neighbourhood species was assessed based on abundance (a) and richness (b). The proportion of facilitative species was calculated from circular plots with  $r = 2$  m centred on the focal tree. It is the ratio of the number of positive species over all species with at least 50 individuals. Positive species are those species

with  $RNA(r) > 1$  (a) and  $RNS(r) > 1$  (b), regardless of their significance levels (equation (2) in Methods). Data are presented as proportion  $\pm 1$  standard error (calculated using equation (5) with sample size  $n = 187$  (BCI), 94 (BSZ), 101 (CBL), 74 (DHS), 71 (GTS), 156 (HSD), 237 (JFL), 60 (LUQ), 143 (NAN), 166 (PAL), 494 (PAS), 101 (PUE), 216 (RAB), 84 (TPK), 8 (UTA), 325 (WAN), 512 (YAS) in each plot, respectively). The latitude was adjusted by altitude (Methods).



**Extended Data Fig. 2 | The proportions of significantly facilitative species across the 17 forest plots decrease with latitude, as tested by the local random labelling null model.** The proportion of facilitative species was assessed based on abundance (a) and on richness (b) and calculated from circular plots with  $r = 2$  m centred on the focal tree, as in Fig. 2, but restricted to species with significantly facilitative effects. The significant effect was assessed

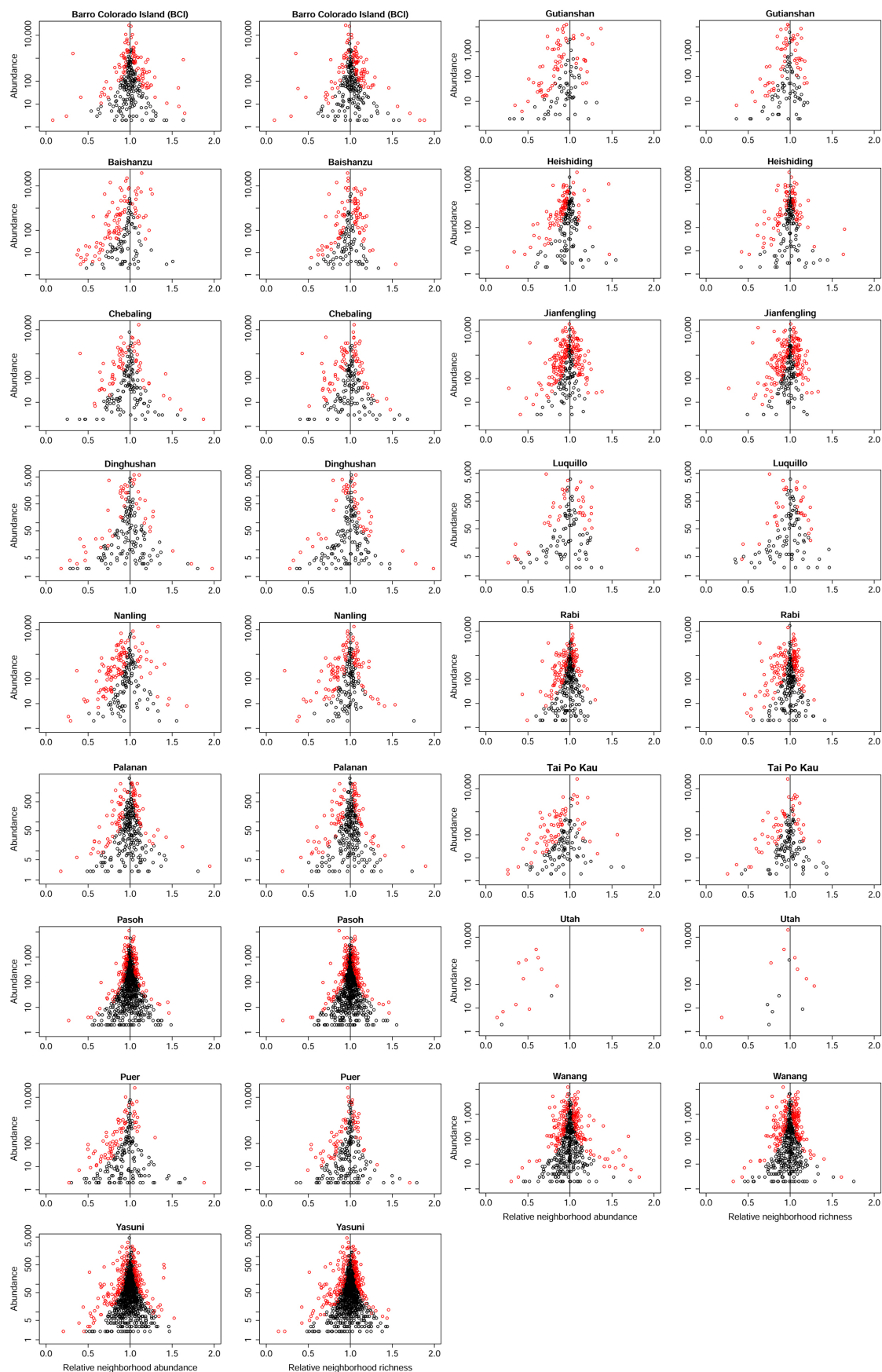
based on 95% confidence intervals computed from 999 randomizations of the local random labelling null model. Data are presented as proportion  $\pm 1$  standard error (calculated using equation (5) with sample size  $n = 103$  (BCI), 86 (BSZ), 73 (CBL), 48 (DHS), 58 (GTS), 85 (HSD), 173 (JFL), 35 (LUQ), 105 (NAN), 85 (PAL), 153 (PAS), 64 (PUE), 127 (RAB), 52 (TPK), 8 (UTA), 177 (WAN), 202 (YAS) in each plot, respectively). The latitude was adjusted by altitude (Methods).



**Extended Data Fig. 3 | Relationship between the proportions of facilitative species in each of the 17 forest plots and latitude after 5% and 10% largest trees excluded.** The proportions of positive species interactions were calculated for neighbourhood species abundance (**a, c**) and species richness (**b, d**), respectively. (**a, b**) 5% largest trees were excluded; (**c, d**) 10% largest trees were excluded. The proportions of facilitative species were calculated as the ratio of the number of positive species over all species with at least 50 individuals, for neighbourhood of 2 m radius. Positive species are those species

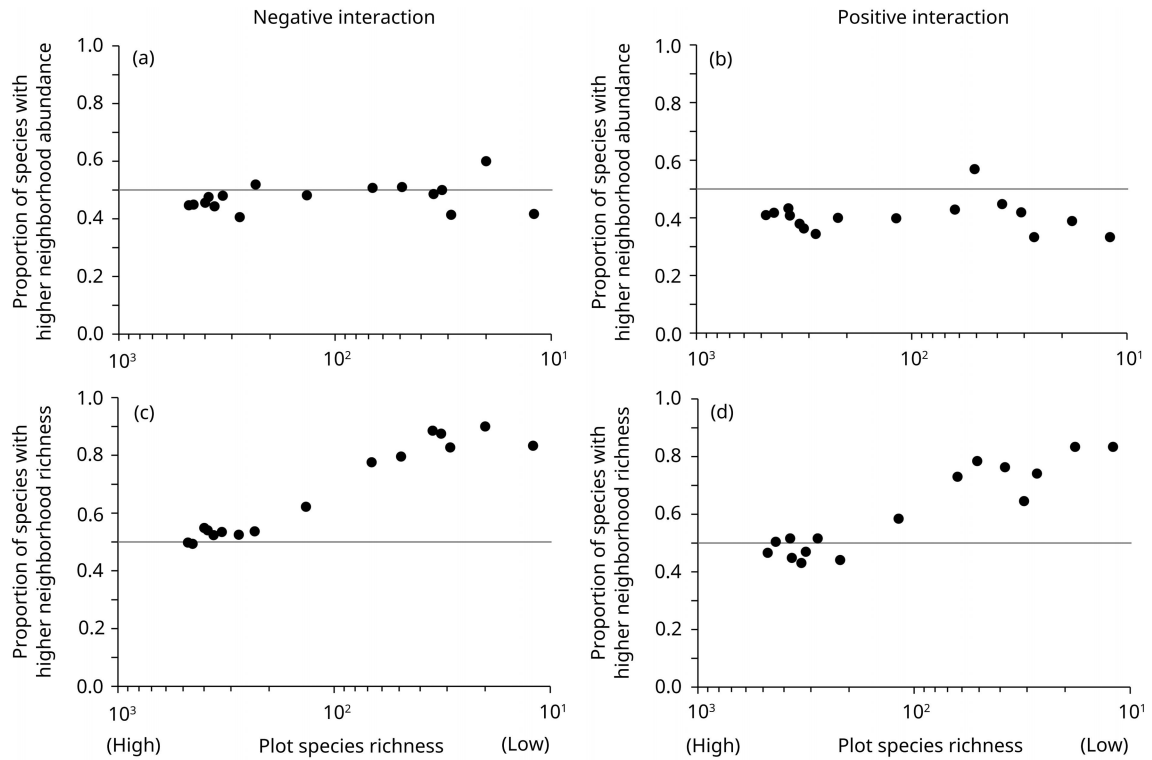
with  $RNA(r) > 1$  (**a, c**) and  $RNS(r) > 1$  (**b, d**), regardless of their significance levels (equation (2) in Methods). Data are presented as proportion  $\pm 1$  standard error (calculated using equation (5) with sample size  $n = 187$  (BCI), 94 (BSZ), 101 (CBL), 74 (DHS), 71 (GTS), 156 (HSD), 237 (JFL), 60 (LUQ), 143 (NAN), 166 (PAL), 494 (PAS), 101 (PUE), 216 (RAB), 84 (TPK), 8 (UTA), 325 (WAN), 512 (YAS) for 5% largest trees excluded and 510 (YAS) for 10% largest trees excluded in each plot, respectively). The latitude was adjusted by altitude (Methods).





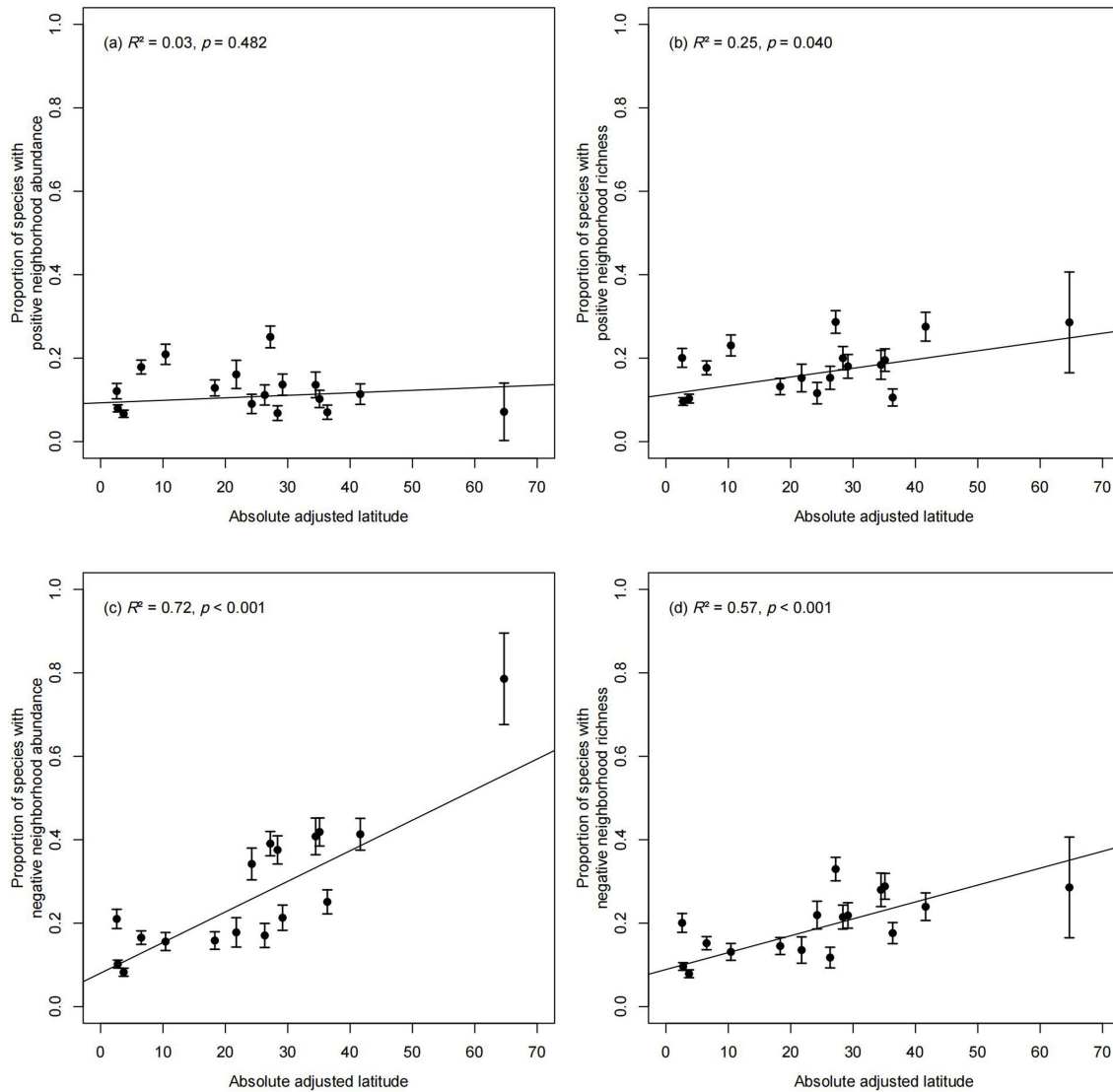
**Extended Data Fig. 4** | See next page for caption.

**Extended Data Fig. 4 | Relationship between relative neighbourhood abundance and relative neighbourhood richness and species abundance in all 17 forest plots.** Relative neighbourhood abundance or richness below 1 suggests that species has negative (competitive) interaction with neighbours, and vice versa. Red circles indicate species has either significantly negative or positive neighbourhood interactions ( $P < 0.05$ ; computed from 999 independent randomizations of the local random labelling null model). The relative neighbourhood abundance or richness were calculated from circular plots with  $r = 2$  m.



**Extended Data Fig. 5 | Proportions of positive species interactions versus species richness for the 17 plots simulated from a spatially explicit neutral model.** A birth-death point process with limited dispersal and immigration, allows individuals to interact locally through either (a, c) negative interactions or (b, d) positive interactions. The results show that, contrary to what was

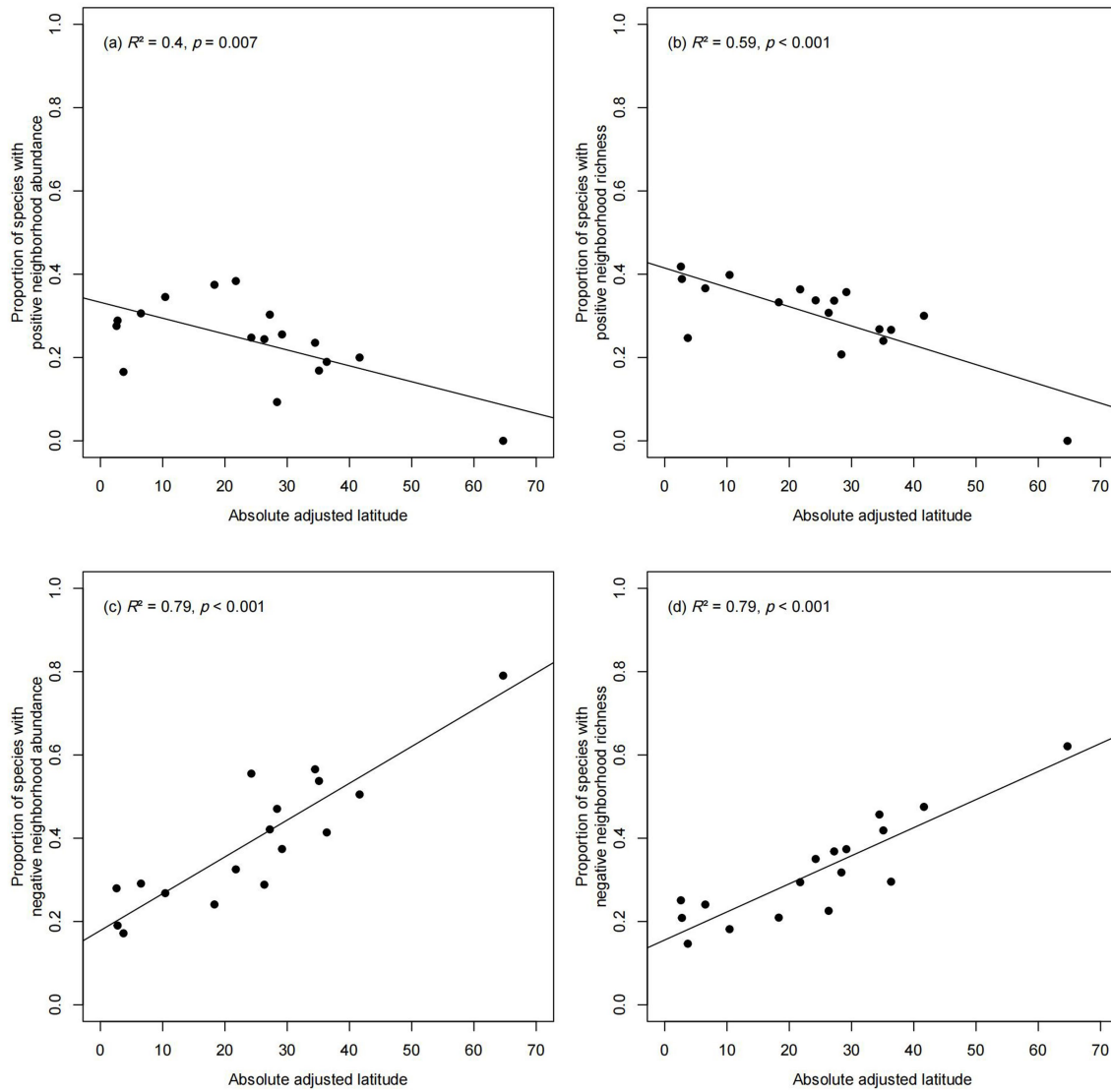
observed in the 17 plots in Fig. 2, the proportion of species with higher neighbourhood abundance or richness decreases as overall plot richness shows no change (a, b) or increases (c, d), suggesting that the higher neighbourhood diversity in species-rich plots is not driven by a simple sampling effect.



**Extended Data Fig. 6 | Absolute proportions of significant facilitative (a, b) and competitive (c, d) species as a function of the absolute adjusted latitude in all 17 forest plots using the local random labelling null model.**

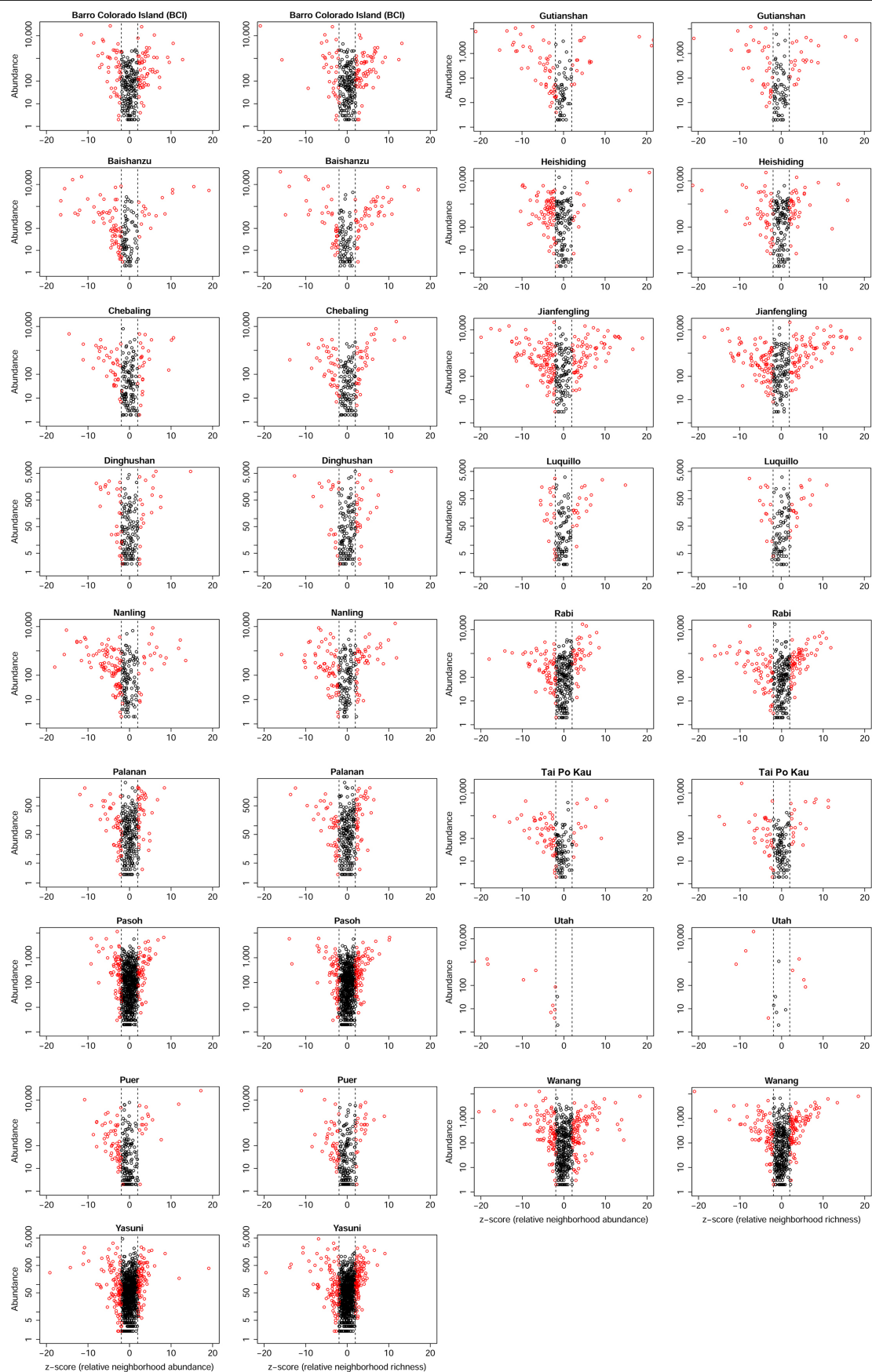
The absolute proportion (significantly positive or significantly negative species over all species) was calculated from circular plots with  $r = 2$  m centred on the focal tree. Significance was estimated from the local random labelling

null model. Data are presented as proportion  $\pm 1$  standard error (calculated using equation (5) with sample size  $n = 282$  (BCI), 167 (BSZ), 183 (CBL), 170 (DHS), 125 (GTS), 205 (HSD), 279 (JFL), 118 (LUQ), 215 (NAN), 303 (PAL), 825 (PAS), 227 (PUE), 314 (RAB), 155 (TPK), 14 (UTA), 526 (WAN), 1029 (YAS) in each plot, respectively). The latitude was adjusted by altitude (Methods).



**Extended Data Fig. 7 | Absolute proportions of significant facilitative (a, b) and competitive (c, d) species standardized at reference abundance  $N=1000$  as a function of the absolute adjusted latitude in all 17 forest plots.** The absolute proportion (significantly positive or significantly negative

species over all species) was calculated for circular plots with  $r = 2$  m. Significance was estimated from the local random labelling null model. Standardization at  $N=1000$  was estimated by generalized linear regression (Methods). The latitude was adjusted by altitude (Methods).



**Extended Data Fig. 8** | See next page for caption.

**Extended Data Fig. 8 | Relationship between relative neighbourhood abundance and relative neighbourhood richness standardized by z-scores and species abundance in all 17 forest plots.** Red circles indicate species with either significantly negative or positive neighbourhood interactions

( $P < 0.05$ ; computed from 999 independent randomizations of the local random labelling null model). The relative neighbourhood abundance or richness were calculated from circular plots with  $r = 2$  m. Vertical lines at  $\pm 1.96$  are shown for reference.



Extended Data Table 1 | Location, forest and environmental information of all 17 permanent forest plots

| Plot name and country                     | Adjusted latitude by altitude | Latitude | Longitude | Plot area (ha) | Total number of all species | Total live individuals of all species | Soil total N concentration (g m <sup>-3</sup> ) | Elevation range m | Mean annual temperature (°C) | January temperature (°C) | July temperature (°C) | Mean annual precipitation (mm) | Soil temperature (°C) | Soil wetness (%) |
|-------------------------------------------|-------------------------------|----------|-----------|----------------|-----------------------------|---------------------------------------|-------------------------------------------------|-------------------|------------------------------|--------------------------|-----------------------|--------------------------------|-----------------------|------------------|
| Utah, USA (UTA)                           | 64.6870                       | 37.66    | -112.85   | 15.32          | 16                          | 27458                                 | 1181.1                                          | 136               | 2.6                          | -6.2                     | 13.8                  | 864                            | 17.7                  | 61.0             |
| Gutianshan, China (GTS)                   | 34.4797                       | 29.25    | 118.117   | 24             | 134                         | 118673                                | 680.2                                           | 269               | 15.9                         | 4                        | 26.8                  | 1430                           | 20.6                  | 119.6            |
| Baishanzu, China (BSZ)                    | 41.6342                       | 27.68    | 119.0667  | 25             | 177                         | 210959                                | 588.2                                           | 223               | 12.8                         | 4.3                      | 21.4                  | 2342                           | 15.3                  | 99.8             |
| Nanling, China (NAN)                      | 35.1059                       | 24.9167  | 113.0167  | 20             | 229                         | 132740                                | 588.2                                           | 246               | 17.3                         | 3.3                      | 25.2                  | 2022                           | 17.1                  | 107.0            |
| Chebaling, China (CBL)                    | 29.1729                       | 24.7167  | 114.2500  | 20             | 206                         | 97201                                 | 588.2                                           | 131               | 19.6                         | 7.6                      | 22.8                  | 1468                           | 23.3                  | 110.3            |
| Heishiding, China (HSD)                   | 28.3736                       | 23.27    | 111.53    | 50             | 213                         | 213954                                | 734.0                                           | 263               | 21.5                         | 12.6                     | 28.4                  | 1719                           | 26.3                  | 95.3             |
| Dinghushan, China (DHS)                   | 26.3227                       | 23.1695  | 112.511   | 20             | 195                         | 71461                                 | 1164.3                                          | 240               | 22                           | 13.4                     | 28.8                  | 1870                           | 25.1                  | 121.0            |
| Puer, China (PUE)                         | 36.3544                       | 22.5976  | 101.1435  | 30             | 270                         | 130915                                | 877.1                                           | 120               | 20.5                         | 15.4                     | 22.5                  | 1528                           | 16.8                  | 91.8             |
| Tai Po Kau, China (TPK)                   | 24.2371                       | 22.4263  | 114.181   | 20             | 172                         | 81021                                 | 734.0                                           | 112               | 23                           | 15.7                     | 28.6                  | 2334                           | 24.8                  | 112.6            |
| Jianfengling, China (JFL)                 | 27.2128                       | 18.7308  | 108.905   | 60             | 290                         | 391686                                | 877.1                                           | 151               | 24.9                         | 19.7                     | 28.5                  | 2102                           | 19.4                  | 110.5            |
| Luquillo, Puerto Rico (LUQ)               | 21.7541                       | 18.3262  | -65.816   | 16             | 135                         | 36655                                 | 1234.4                                          | 95                | 25.6                         | 23.4                     | 27                    | 2363                           | 23.5                  | 80.7             |
| Palanan, Philippines (PAL)                | 18.3141                       | 17.4402  | 122.388   | 16             | 321                         | 68173                                 | 1102.3                                          | 50                | 25.1                         | 22.5                     | 26.6                  | 2724                           | 26.7                  | 109.9            |
| Barro Colorado Island (BCI), Panama (BCI) | 10.4156                       | 9.1543   | -79.8461  | 50             | 301                         | 203732                                | 1510.5                                          | 40                | 26.3                         | 25.7                     | 26.9                  | 3025                           | 23.7                  | 81.8             |
| Pasoh, Malaysia (PAS)                     | 3.7027                        | 2.982    | 102.313   | 50             | 911                         | 262167                                | 958.9                                           | 20                | 26.3                         | 25.7                     | 26.4                  | 1896                           | 24.8                  | 101.8            |
| Yasuni, Ecuador (YAS)                     | -2.7351                       | -0.663   | -76.397   | 50             | 1070                        | 145823                                | 1345.8                                          | 30                | 25.9                         | 26.3                     | 24.8                  | 3270                           | 22.5                  | 98.6             |
| Rabi, Gabon (RAB)                         | -2.5922                       | -2.2228  | 9.88004   | 25             | 346                         | 175661                                | 845.3                                           | 26                | 26.1                         | 27.3                     | 23.6                  | 1943                           | 24.0                  | 79.9             |
| Wanang, Papua New Guinea (WAN)            | -6.5113                       | -5.25    | 145.267   | 50             | 581                         | 253530                                | 1745.8                                          | 100               | 26.5                         | 26.8                     | 25.8                  | 3366                           | 24.0                  | 111.8            |

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|                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
|-----------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Data collection | Data collection was described in the first paragraph of the method part and as below. No software was used for data collection.                                                                                                                                                                                                                                                                                                                                                                                                          |
| Data analysis   | We used R 4.3.2 and Matlab to write the codes to analyze the data. How data were statistically analyzed are illustrated in detail in the method part. Related codes have been archived in Github and Code Ocean. Extended Data R codes 1-4 were stored in Github, " <a href="http://github.com/mdetto/Positive/Interactions">http://github.com/mdetto/Positive/Interactions</a> ". While Matlab code 5 was uploaded to Code Ocean, <a href="https://codeocean.com/capsule/4844196/tree">https://codeocean.com/capsule/4844196/tree</a> . |

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Data from 17 plots can be requested from the ForestGEO plot network (<https://www.forestgeo.si.edu/>). Of them, data of Chebaling plot can be requested from the Pls of Heishiding plot in the ForestGEO plot network. Nanling and Puer plots can be requested from the Pls of Jianfengling plot in the ForestGEO plot network. Eight environmental factors were compiled for each plot. Five of them, including plot elevation range, mean annual temperature (MAT), January temperature, July temperature and mean annual precipitation (MAP), were obtained from Anderon-Teixeira et al. (2015). Soil total N density (g m<sup>-3</sup>) was compiled from the Global Gridded Surfaces of Selected Soil Characteristics (IGBP-DIS) database at a resolution of 5×5 arc-minutes, and in a soil depth interval 0-100 cm from Oak Ridge National Laboratory Distributed Active Archive Center (<https://daac.ornl.gov>). We also obtained soil temperature from <https://zenodo.org/record/4558663#.ZFRV46BBztU> and soil wetness from <https://climate.esa.int/en/projects/soil-moisture/>. We also stored the running results of 17 plots to Github, "<https://github.com/mdetto/Positive Interactions>".

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| Population characteristics                                         | This paper does not involved with any human participants, human data or biological material. |
| Recruitment                                                        | This paper does not involved with any human participants, human data or biological material. |
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## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

|                   |                                                                                                                                                                     |
|-------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Study description | Tree census data were obtained from 17 large, permanent forest dynamics plots distributed in latitude ranging from 5°S to 47°N. These 17 plots are natural forests. |
|-------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------|

|                          |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
|--------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Research sample          | <p>The plot size varies from 15.32 to 60 ha.</p> <p>Plot census methods followed the standard ForestGEO protocol to include all stems <math>\geq 1</math> cm in diameter at the breast height (DBH <math>\geq 1</math> cm). All stems were identified to species, measured and mapped to their relative spatial coordinates within each forest plot.</p> <p>Eight environmental factors were compiled for each plot in this study. Five of them, including plot elevation range, mean annual temperature (MAT), January temperature, July temperature and mean annual precipitation, were obtained from Anderon-Teixeira et al. (2015). Soil total N density (g m<sup>-3</sup>) was compiled from the Global Gridded Surfaces of Selected Soil Characteristics (IGBP-DIS) database at a resolution of 5×5 arc-minutes, and in a soil depth interval 0–100 cm from Oak Ridge National Laboratory Distributed Active Archive Center (<a href="https://daac.ornl.gov">https://daac.ornl.gov</a>).</p> <p>We also obtained soil temperature from <a href="https://zenodo.org/record/4558663#.ZFRV46BBztU">https://zenodo.org/record/4558663#.ZFRV46BBztU</a> and soil wetness from <a href="https://climate.esa.int/en/projects/soil-moisture/">https://climate.esa.int/en/projects/soil-moisture/</a>.</p> |
| Sampling strategy        | A set of 17 large forest plots from Asia, Africa, Oceania, North America and South America, consisting of >2.7 million trees from >5400 species, distributed in latitude ranging from 5°S to 47°N and varied from 15.32 to 60 ha plot sizes were used. The sample sizes are sufficient to study the latitudinal pattern of species diversity.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| Data collection          | Many individuals, institutions and funding agencies supported the establishment of 17 dynamic plots across used in this study. They are listed in the Acknowledgments in the Supplementary Information.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Timing and spatial scale | A set of 17 large forest plots from Asia, Africa, Oceania, North America and South America, distributed in latitude ranging from 5°S to 47°N were used. Only the census data for one time is used.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Data exclusions          | We described different data exclusion method in detail in the legends of each figures and methods part.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
| Reproducibility          | The statistical analysis is reproducible. Anyone can use the same 17 plots data and codes to repeat the results.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Randomization            | <p>We used spatial model simulation to assess a potential sampling effect for the latitudinal neighborhood interaction pattern in the method part.</p> <p>We also described in detail how randomization were applied and codes were stored in Github and Code Ocean.</p> <p>We also developed a null model to test the observed latitudinal gradient.</p>                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Blinding                 | Blinding was not applicable because we used the real field tree investigation data.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |

Did the study involve field work? ☐ Yes ☒ No

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|                       |                                |
|-----------------------|--------------------------------|
| Plants                |                                |
| Seed stocks           | No seed stocks used.           |
| Novel plant genotypes | No novel plant genotypes used. |
| Authentication        | Not applicable.                |