

Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity

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The tropical forests of Borneo and Amazonia may each contain more tree species diversity in half a square kilometre than do all the temperate forests of Europe, North America, and Asia combined¹. Biologists have long been fascinated by this disparity, using it to investigate potential drivers of biodiversity². Latitudinal variation in many of these drivers is expected to create geographic differences in ecological^{2–4} and evolutionary processes^{4,5}, and evidence increasingly shows that tropical ecosystems have higher rates of diversification, clade origination, and clade dispersal^{5,6}. However, there is currently no evidence to link gradients in ecological processes within communities at a local scale directly to the geographic gradient in biodiversity. Here, we show geographic variation in the storage effect, an ecological mechanism that reduces the potential for competitive exclusion more strongly in the tropics than it does in temperate and boreal zones, decreasing the ratio of interspecific-to-intraspecific competition by 0.25% for each degree of latitude that an ecosystem is located closer to the Equator. Additionally, we find evidence that latitudinal variation in climate underpins these differences; longer growing seasons in the tropics reduce constraints on the seasonal timing of reproduction, permitting lower recruitment synchrony between species and thereby enhancing niche partitioning through the storage effect. Our results demonstrate that the strength of the storage effect, and therefore its impact on diversity within communities, varies latitudinally in association with climate. This finding highlights the importance of biotic interactions in shaping geographic diversity patterns, and emphasizes the need to understand the mechanisms underpinning ecological processes in greater detail than has previously been appreciated.

Tree species diversity at the hectare scale increases by an order of magnitude from boreal to temperate forests, and again from temperate to tropical forests, despite the fact that basic resources, such as soil nutrients and sunlight, act similarly in their role as limiting resources across latitudes¹. Even with higher speciation rates, maintaining these high levels of tropical diversity over geological time scales is likely to require coexistence mechanisms that can reduce the potential for extinction as a result of competitive exclusion between species⁷. Numerous processes have been identified in tropical forests that could prevent competitive exclusion and allow a high degree of coexistence⁸, including selective predation by specialist herbivores and pathogens^{9–11}, resource competition¹², trade-offs between competitive and colonization abilities^{13–15}, adoption of different adult growth forms¹⁶, and species-specific responses to variation among germination sites¹⁷. Ecological coexistence theory states that any of these mechanisms could

promote coexistence by making interspecific competition consistently weaker than intraspecific competition¹⁸. However, these coexistence conditions are rarely quantified, and there is little evidence that any of these processes vary in strength across latitudes in a manner consistent with geographic biodiversity patterns^{19–21}.

Here, we investigate geographic variation in potential coexistence, resulting from reduced interspecific synchrony of tree recruitment. Reducing synchrony among recruitment periods can lead to interactions with conspecific individuals clustering in periods favourable for reproduction; if adults are sufficiently long-lived to buffer populations through unfavourable periods, this can ultimately decrease interspecific competition relative to intraspecific competition through the storage effect¹⁸. For tree communities, inter-annual variation in recruitment into the understory contributes to the concentration of intraspecific, relative to interspecific, seedling interactions^{1,22}. Crucially, interspecific annual asynchrony derives from species-specific responses to environmental fluctuations over the course of the year, during reproduction, germination, and post-germination periods²³. The seasonal timing of reproduction is important because it determines the conditions to which species are exposed during germination and post-germination processes^{23,24}.

Annual climate variation is a major driver of inter-annual fluctuations in both biotic and abiotic conditions, but is often not distributed evenly throughout the year. This is a well-established relationship in tropical forests for which El Niño and La Niña events are the major source of inter-annual variation; these events hit more strongly in particular months (for example, El Niño can exacerbate dry conditions in the January–April dry season of many Caribbean forests) and therefore have larger effects on the seed production of species that reproduce at these times^{23,24}. As a consequence, species reproducing at different times in a season will experience different amounts of variation in their recruitment in a given year; reduced seasonal synchrony may reduce inter-annual synchrony by increasing the likelihood that species experience climate conditions differently in the same year. Following on from this hypothesis, the longer and more stable growing seasons in the tropics should permit greater differentiation between species in the seasonal timing of their reproduction⁵, and therefore a latitudinal gradient in the storage effect should emerge as a result of an underlying gradient in seasonality^{25,26}.

We hypothesized that the storage effect promotes coexistence more strongly in tropical forests than in temperate or boreal forests (premise 1), because longer growing seasons at lower latitudes correspond to a reduction in between-year synchrony in species' reproduction (premise 2), and tested these two premises separately. We assembled

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seed production and seedling recruitment data from ten forests distributed from 0° 41' S to 64° 51' N, including three tropical forests (Yasuni, Pasoh, and Barro Colorado Island), three subtropical forests (Luquillo, Kenting, and Fushan), three temperate forests (Coweeta, Ogawa, and Changbaishan), and one boreal forest (Bonanza Creek) (Extended Data Table 1). We partitioned seed production into monthly and annual counts for nine forests (Coweeta lacked sub-annual data), and seedling production into annual counts, following previous work²².

To evaluate geographic variation in coexistence by the storage effect (premise 1), we used a mathematical model of forest dynamics, parameterized by our recruitment data. This allowed us to quantify the degree to which among-year fluctuations in recruitment promote coexistence by reducing interspecific (relative to intraspecific) competition between pairs of species²². We measured the potential for coexistence on the basis of observed annual seedling recruitment rates, in a pairwise fashion, using competition coefficients A_{ij} (defined as the proportional reduction in interspecific competition relative to intraspecific competition, caused by reducing recruitment synchrony²²): A_{ij} is analogous to the competition coefficients α_{ij} in Lotka–Volterra models of resource competition. Values of A_{ij} of less than 1 indicate that interspecific competition is low enough, relative to intraspecific competition, to permit coexistence between pairs, with lower values indicating a stronger potential for the storage effect to promote coexistence. The overall ease of coexistence for species pairs depends on both A_{ij} and A_{ji} , summarized by $A_{ij}A_{ji}$ (ref. 22). We generated distributions of $A_{ij}A_{ji}$ for each forest site (Extended Data Fig. 1) by calculating all pairwise $A_{ij}A_{ji}$ for species with sufficiently detailed records (Extended Data Table 1). Community-wide values of $A_{ij}A_{ji}$ will tend to be lower where recruitment fluctuations promote coexistence more strongly; we therefore expected lower median values of $A_{ij}A_{ji}$ in less seasonal forests.

We found that coexistence in tropical and subtropical forests generally benefits more from asynchrony than does coexistence in either temperate or boreal forests (Fig. 1). Our $A_{ij}A_{ji}$ calculations showed that, for more than half of the species in almost all of the tropical and subtropical forests, a decrease in synchrony reduces pairwise interspecific competition to less than 40% of intraspecific competition: this means that, in head-to-head competition, one species would have to produce only 40% of the recruits of the other species to avoid competitive exclusion. In comparison, the benefit to the more northerly sub-tropical forests, temperate forests, and boreal forests is weaker, with median reductions in interspecific, relative to intraspecific, competition of 42% (Kenting), 45% (Fushan), 45% (Coweeta), 48% (Ogawa), 46% (Changbaishan), and 52% (Bonanza Creek). These results were consistent even after accounting for differences between sites in terms of the numbers of species recorded and time series length (Extended Data Fig. 2, see Methods), and when a growing season metric based on monthly variation in insolation, precipitation, and temperature (Extended Data Table 2, see Methods) replaced latitude as the predictor variable (Extended Data Fig. 3). This demonstrates that the strength of the storage effect is greater in the tropics, producing a 0.25% decrease in average pairwise interspecific, relative to intraspecific, competition per degree decrease in latitude ($P < 0.001$). Our choice of linear fit in Fig. 1 ignores the potential for any nonlinearity in this trend, showing only the general pattern: as more datasets are accumulated, it will be possible to assess whether change is more rapid in key regions, such as the transition from tropical to temperate forests (at around 23° of latitude).

To evaluate whether seasonality underlies latitudinal differences in recruitment synchrony (premise 2), we examined the correlation between growing season length and interspecific synchrony in seed and seedling production across latitudes. We quantified interspecific synchrony as pairwise correlations, calculating these at a monthly time scale for within-year synchrony of seed production and at an annual time scale for among-year synchrony of seed and seedling production. We quantified growing season length based

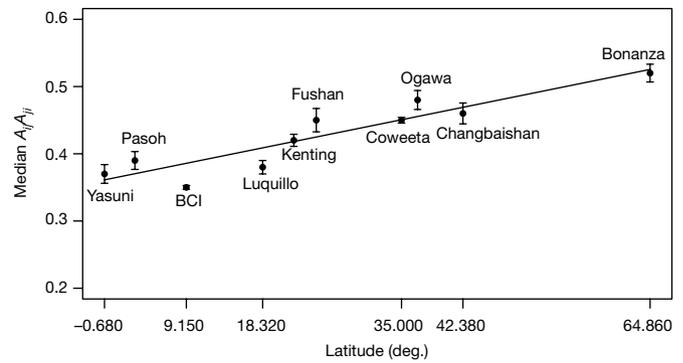


Figure 1 | The median values of pairwise competition coefficients $A_{ij}A_{ji}$ are correlated with latitude. The slope of the best-fit line for ten forests (slope = 0.0025, $R^2 = 0.83$, $P < 0.001$) indicates a median reduction in interspecific competition relative to intraspecific competition of 0.25% per degree decrease in latitude. Here, the $A_{ij}A_{ji}$ have been calculated with standard error bars by repeated jack-knifing of six-year subsets of the full forest community in order to match the shortest time series. BCI; Barro Colorado Island. See Extended Data Table 1 for sample sizes.

on the combination of monthly solar insolation, precipitation, and minimum and maximum temperatures, selecting climate-based variables that have often been cited as influencing the latitudinal diversity gradient directly or as being associated with factors that have direct effects on physiology related to survival and reproduction (such as potential evapotranspiration^{5,27}). To differentiate seasonality between the forests, we used the summed coefficients of variation for each climate variable; shorter growing seasons produce higher total coefficients of variation as a result of more marked seasonal fluctuations (see Methods).

We found that reproduction and recruitment were generally less synchronous in tropical forests (Fig. 2). Between species, within-year synchrony in reproductive timing was, on average, lower at lower latitudes (Fig. 2a); among-year synchrony between species in the magnitude of their reproduction and recruitment was, on average, also lower in lower latitude forests (Fig. 2b). Synchrony at both timescales is inversely related to growing season length. As species pairs with lower within-year correlations also tended to have lower among-year correlations (Fig. 2c, Extended Data Fig. 4), within-year synchrony may contribute to among-year synchrony. The greater seasonal differences in the timing of reproduction made possible by longer growing seasons in the tropics could, therefore, permit lower synchrony in the within-year timing of reproduction (Fig. 2a), leading ultimately to a reduction in interspecific among-year synchrony in reproduction and recruitment (Fig. 2b).

Our results complement evolutionary studies that find support for latitudinal climatic variation as an underlying factor in geographic biodiversity variation^{5,27}; however, they contrast with previous ecological studies that have found no evidence for latitudinal differences in ecological processes^{20–22}. The storage effect mechanism investigated here arises as a consequence of differences in species-specific responses to varying environmental conditions, and can thus account for the effects of seasonally driven reproductive patterns on biodiversity: mechanisms of this type cannot be detected without paying attention to variable ecological processes. It is, therefore, important that the storage effect and other variation-driven mechanisms be considered in future work on geographic patterns in biodiversity, a finding strengthened by the increasing number of studies that emphasize the role that environmental variation can play in maintaining biodiversity^{18,22,28}.

Although we found support for latitudinal differences in climate seasonality (Fig. 2) as a factor underlying geographic variation in coexistence (Fig. 1), it is likely that geographical gradients in other features also contribute to the phenological separation of species. For example, a host of biotic factors such as pollination, disease,

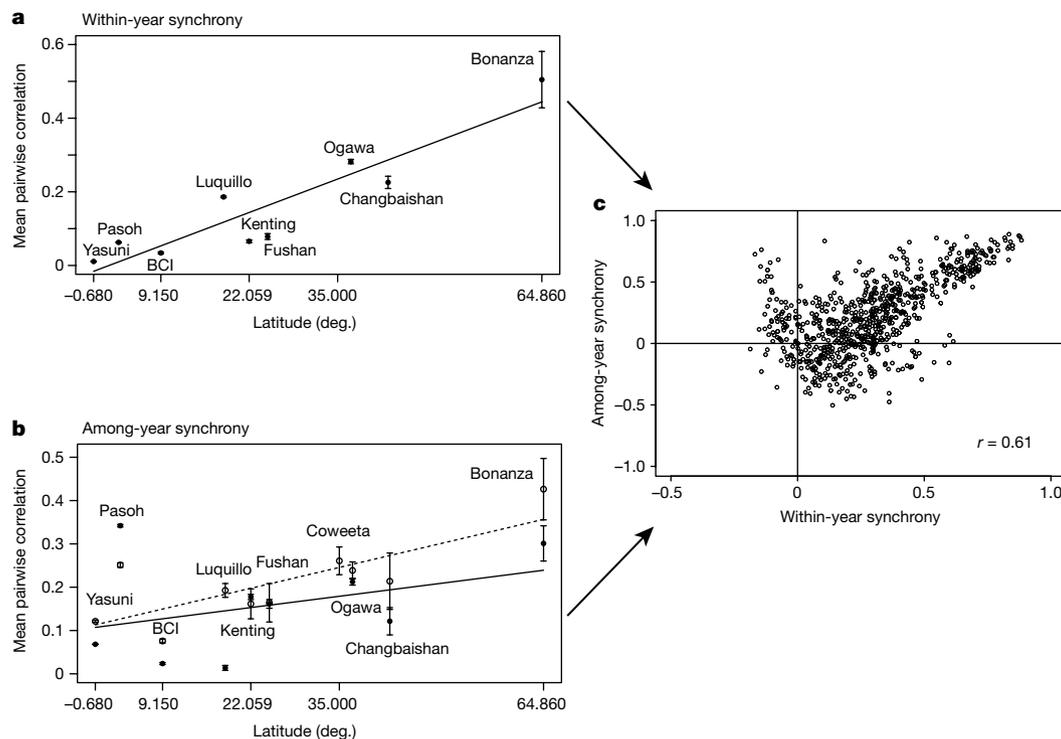


Figure 2 | Relationship between within-year and among-year synchrony and latitude. The synchrony of within-year reproduction (**a**) is linked to among-year reproduction (**b**), and varies across a latitudinal gradient. The two timescales are linked because species pairs with lower within-year synchrony also tend to have lower among-year synchrony (**c**), where synchrony is measured as the Pearson's correlation between species pairs. Longer growing seasons at lower latitudes permit species to be less synchronous in their within-year timing of reproduction (**a**). This in turn leads to lower synchrony among years (**b**), because species that reproduce at different times of year at lower latitudes will tend to experience the environmental conditions of the same year differently (**c**). Average forest-wide synchrony decreased with latitude for within-year

and herbivory can also influence seasonal patterns of recruitment¹. Additionally, some evidence suggests that all of these interactions are stronger and more frequent in the tropics⁵; the importance of climatic seasonality as a sole driver of phenological separation in tropical forests may itself decrease relative to biotic factors, in comparison with temperate and boreal ecosystems. Finally, we note that seasonality may contribute further to a latitudinal gradient in coexistence by allowing greater within-year phenological separation of seedling cohorts. In order to establish the relative importance of seasonality, studies focusing on additional ecological mechanisms are required to identify the processes that translate within-year reproductive asynchrony to among-year recruitment asynchrony.

Reduced recruitment synchrony can contribute substantially to coexistence in forests, but the full range of diversity is also supported by other mechanisms. Though we cannot currently compare the relative contributions of different mechanisms to the overall gradient in diversity, several of our observations suggest directions for future studies. Our study includes one tropical forest (Pasoh) in which recruitment synchrony is strongly determined by whether species are annual flowering or general flowering types. Within-year synchrony tends to be low between these two groups (Fig. 2a), reducing the community-wide distribution of $A_{ij}A_{ji}$ consistent with other aseasonal equatorial forests (Fig. 1). However, within-year synchrony is unusually high between the hundreds of sympatric general flowering species that reproduce at irregular intervals²⁹ (Fig. 2b), generating a high community-wide mean of $A_{ij}A_{ji}$ relative to other tropical forests. Additional mechanisms clearly contribute to diversity in this forest, especially among general

seed production (**a**, 0.007 decrease in the average Pearson's correlation per degree latitude, $P < 0.001$), among-year seed production (**b**, solid line, 0.002 decrease in the average Pearson's correlation per degree latitude, not significant; however, removing Pasoh makes it significant at $P = 0.015$ with slope 0.004), and among-year seedling recruitment (**b**, dashed line, 0.004 decrease in the average Pearson's correlation per degree latitude, $P = 0.013$). The correlation between these two scales of synchrony was calculated as the Pearson's correlation ($r = 0.61$ in **c**); the median correlation across all forests was 0.28, and ranged from 0.05 (BCI) to 0.80 (Bonanza Creek). See Extended Data Table 1 for sample sizes, and Methods for details of calculations of correlations.

flowering species, a situation which may be echoed in other forests (albeit for different reasons).

We have demonstrated that stable within-year climates in the tropics can remove abiotic restrictions on the timing of species' reproduction, thereby temporally partitioning competitive interactions in a manner that permits greater potential for coexistence. Recent syntheses of evolutionary processes also find that favourable, stable climate conditions in the tropics may support higher speciation rates by removing the abiotic limits on selection imposed by harsher higher-latitude environments; instead, tropical conditions allow biotic interactions to dominate, creating a greater potential for reciprocal selection and coevolution⁶. Despite the fact that evolutionary and ecological processes are often treated separately, this suggests that biogeographical biodiversity patterns are driven by a combination of latitudinal variation in climate and in biotic interactions^{3–5,27}. Through further studies of ecological mechanisms, it may become possible to produce a common framework that links together the multiple biological processes that support variation in geographic biodiversity.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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METHODS

Unless otherwise indicated, no statistical methods were used to predetermine sample size and the experiments were not randomized. The investigators were not blinded to allocation during experiments and outcome assessment.

Forest data. We used data on seed production from ten forests spanning a latitudinal gradient: Yasuní (0° 41' S), Pasoh (2° 58' N), BCI (9° 9' N), Luquillo (18° 19' N), Kenting (20° 57' N), Fushan (24° 45' N), Coweeta (35° 00' N), Ogawa (36° 56' N), Changbaishan (42° 23' N), and Bonanza Creek (64° 51' N). Seed collection protocols are similar across sites, although they were established independently in many cases and differ in certain details. Yasuní, Pasoh, BCI, Luquillo, Kenting, Fushan, and Changbaishan follow Forest Dynamics Plots protocols, first established for BCI³⁰. Protocols at Ogawa are similar but were established independently³¹. Coweeta and Bonanza Creek are long term ecological research sites with unique protocols. Seed collection occurs weekly at BCI, Pasoh, and Fushan, and every two weeks at Luquillo, Kenting, Ogawa, Changbaishan, and Yasuní: monthly seed production could, therefore, be determined directly for six sites. Monthly counts were aggregated into annual counts using an established approach³². For Bonanza Creek, published observations of phenology for the six species in the final dataset were used to extrapolate monthly counts from annual totals³³; annual totals were distributed across three months according to a normal distribution centred on the first month of peak seed release. The final annual time series varied in length from 6 to 23 years, as summarized in Extended Data Table 1.

Annual seedling censuses were conducted at all sites except for Bonanza Creek; protocols are similar across sites, and details are described elsewhere^{30,31}. For Bonanza Creek, the results of annual germination viability tests were used to convert annual seed counts to approximate annual seedling counts; these final counts for Bonanza Creek are likely to be an overestimation of annual seedling germination and survival in the first several months, as these do not typically exceed 20% under ideal conditions and are more often on the order of 5%³³. The final standardization of recruitment data before calculation of $A_{ij}A_{ji}$ (discussed below) greatly reduced the potential for this to influence results.

Both seed and seedling counts were filtered to consider only species that were well-sampled over the duration of data collection. Yearly seed counts were used only for species with more than 50 records of seeds occurring in 3 separate years, and with adults occurring in the experimental plot. Seedling counts were used only for species with at least 25 records of recruitment occurring in 3 separate years, and with adults occurring within the experimental plot. In all forests, more species were retained in the seed datasets than in the seedling datasets. Final numbers are summarized in Extended Data Table 1.

The correlation in seed production between species i and j is partitioned as $\text{cor}(R_i, R_j) = \text{cor}(R_{m,i} - \bar{R}_{m,i}, R_{m,j} - \bar{R}_{m,j}) + 12\text{cor}(\bar{R}_{y,i} - \bar{R}_i, \bar{R}_{y,j} - \bar{R}_j)$, where $R_{m,i}$ is total monthly seed production, $\bar{R}_{y,i}$ is the mean seed production of species i within year y , and \bar{R}_i is the overall mean for each species. Thus, within-year synchrony is measured by $\text{cor}(R_{m,i} - \bar{R}_{m,i}, R_{m,j} - \bar{R}_{m,j})$, and among-year synchrony by $12\text{cor}(\bar{R}_{y,i} - \bar{R}_i, \bar{R}_{y,j} - \bar{R}_j)$.

Growing season metrics. To summarize differences in forest growing seasons, we calculated the log of the sum of the coefficients of variation in four climate metrics: monthly average solar insolation (I), which indicates fluctuations in irradiation; monthly average precipitation (P); monthly average maximum temperature (X); and monthly average minimum temperature (N). This summary metric has a clear biological rationale: the growing season for extra-tropical forests is largely limited by cold temperatures in winter, and though growth is possible year-round in most tropical forests, the seasonality of cloud cover, solar irradiance, and rainfall causes substantial variation in primary production⁴.

We found in preliminary analyses that the log of the sum of the coefficients of variation was the best predictor of species pairwise synchrony, both within-year and among-year, and of trends in $A_{ij}A_{ji}$ (Extended Data Table 2). Summing the coefficients of variation for all four variables provided a consistent metric for growing season that also distinguished tropical forests, with a year-round growing season that is overlain by the seasonality of precipitation and light, from those found elsewhere. Additional statistical analyses using each coefficient of variation as a predictor variable (CV) for site-average within-year pairwise correlations, site-average among-year pairwise correlations, and $A_{ij}A_{ji}$ revealed that each variable is a significant predictor individually, but that summing the variables generally provided the highest R^2 and almost always produced the lowest Akaike information criterion (AIC) (Extended Data Table 2). Precipitation and temperature data are from published records for the Forest Dynamic Plots sites³⁰, from historical records from the National Oceanic and Atmospheric Administration (NOAA) for both of the long term ecological research sites, and from historical records from the Japan Meteorological Agency for the Ogawa site. Insolation data originate from the NASA (National Aeronautics and Space Administration) CERES satellite, available

online (<https://ceres.larc.nasa.gov/>). The results of these calculations are given in Extended Data Table 1.

Forest dynamics model. The forest dynamics model that we use in this study has been previously published²²: we repeat the essential elements here. The model assumes that tree populations of a given species can be divided into seedlings, saplings, and adults. Tree-fall gaps are essential for the establishment of reproductive adults, and the likelihood of a tree of a particular species filling a gap is based on its proportion in the sapling bank (lottery competition). Adults produce seedlings directly, and thus the intermediate processes of flowering, seed production, and germination are not modelled explicitly. Seedlings must survive intense competition with their annual cohorts before being recruited into the understory sapling bank. The forest dynamics model represents all of these processes as a stage-structured model with only two stages, allowing analytical solutions for the storage effect.

The first stage links seedling production, competition, and establishment with sapling survival into a sapling dynamics equation, in which time is discrete (to capture the dynamics of distinct reproductive and recruitment events). Although it does not inherently assume any units for time steps, the model is appropriately interpreted as an annual one, as a result of both the annual timescale of the seedling recruitment data and the biological significance of annual seedling cohorts (explained below, and in more depth in previous studies^{22,32}). The sapling density, $s_i(t+1)$, of species i ($i = 1, \dots, n$) in year $t+1$ is given by:

$$s_i(t+1) = f_i s_i(t) + \frac{R_i(t)x_i(t)}{1 + \sum_{j=1}^n \alpha_{ij}x_j(t)R_j(t)} \quad (1)$$

Saplings survive from the previous year at a density-independent rate (f_i). Although there is evidence for density-dependent reductions in survival from conspecific saplings and adults⁹, we do not include this process in the model, because it introduces additional coexistence mechanisms (for example, classic resource partitioning among saplings), and our purpose here is to isolate the impact of the storage effect.

Recruitment into the sapling population (s_i) is a function of the abundance of species i adults, $x_i(t)$, multiplied by the species-specific per capita seedling production rate, $R_i(t)$, which gives the number of seedlings of species i produced per year. equation (1) incorporates annually fluctuating seedling recruitment because the $R_i(t)$ values represent random variables drawn from distributions defined by species-specific means (μ_i) and variances (σ_i^2) of observed annual seedling counts. The $R_i(t)$ for all n species at a site are treated jointly as $\mathbf{R}(t)$, an n -dimensional random variable that accounts for correlations (ρ_{ij}) in annual seedling production between every species pair as calculated from the data.

The number of seedlings of species i that survive the first year depends on the density of competitors^{8,22}, which reduce survival according to a modified Leslie-Gower competition model. The coefficients α_{ij} measure the per capita effect of species j seedlings on the seedling production rates of species i . Empirical evidence suggests that density dependence is mostly the result of interactions with conspecifics⁸; however, we chose to model competition with all species' seedlings, and removed the possibility of resource partitioning in this stage by setting all $\alpha_{ii} = \alpha_{ij} = 1$. This large value for interspecific competition was chosen to reflect the substantial impact of seedling density dependence on understory proportions; a lower value of these coefficients has the ultimate effect of increasing the strength of the storage effect, and our choice of $\alpha_{ii} = \alpha_{ij} = 1$ should therefore be seen as a lower-bound or worst-case scenario. By representing the seedling-to-sapling transition as a yearly event, our model is consistent with previous studies that show a strong filter of density-dependent mortality that reduces survival to less than 10% in the first year or two, but which largely abates in subsequent years; even young seedlings have a survival advantage of as much as 60% over new seedlings, making them demographically equivalent to saplings^{9,23,30,32}.

The second stage of the model encompasses gap-recruitment processes and adult survival. Gaps are created randomly and filled by assuming lottery-style competition from the understory bank given in equation (1). The low mortality rate of saplings makes the likelihood of a gap being filled by a member of a given species approximately proportional to its sapling population. The recruitment of seedlings into the adult stage is given by:

$$x_i(t+1) = \delta_i x_i(t) + \left(1 - \sum_{j=1}^n \delta_j x_j(t)\right) \frac{s_i(t)}{\sum_{j=1}^n s_j(t)} \quad (2)$$

The probability of adult survival is given by δ_i , and all other terms are as previously defined. The population of adults is measured relative to the total number of

individuals across all species (the sum across all species equals 1). equation (2) therefore states that the adult density of species i is the proportion of adults surviving from the previous year plus lottery recruitment into gaps created by tree deaths; it is very similar in structure to the lottery model first presented by Chesson and Warner³⁴. Although it is possible to allow factors such as initial heights of saplings or species-specific growth responses to gaps to influence gap capture probability, we treat species as equivalent to highlight the contribution of recruitment asynchrony to coexistence.

Analysis of competition, $A_{ij}A_{ji}$. We analysed the model using invasibility analysis⁸, treating each species as an invader against an established resident and assessing whether a species experiences a population growth rate advantage when it is rare. Mathematically, this entailed assessing the stability of the point at which one species is established at equilibrium, and the second species is at zero population, under a small perturbation. If invasion is successful, the slope of population growth near this invasion limit serves as a proxy for the strength of interspecific, relative to intraspecific, competition; the analytical approach measures the growth rate at this invasion limit. Following our previous work²², we used the invasibility criterion to define the pairwise competition coefficient A_{ij} :

$$A_{ji} = E \left[\frac{\sum_{\tau=1}^t f_i^{\tau} \frac{R_i(t-\tau-1)}{1+R_j(t-\tau-1)}}{\sum_{\tau=1}^t f_j^{\tau} \frac{R_j(t-\tau-1)}{1+R_i(t-\tau-1)}} \right]^{-1} \quad (3)$$

By defining population-level competition coefficients with this invasion growth rate approach, the values of A_{ij} are consistent with interaction coefficients in classical models of coexistence: coexistence requires $A_{ij}A_{ji} < 1$, with A_{ij} analogous to population-level alpha competition coefficients (α_{ij}). A_{ij} quantifies the degree to which a particular mechanism (here, recruitment fluctuations) can reduce interspecific competition, relative to intraspecific competition. For this interpretation the $R(t)$ must also be standardized so that the log-mean and log-variances of recruitment are symmetrical for all species; this allows the invasion growth rate and A_{ij} to be determined only by the strength of the storage effect arising from reduced seedling recruitment synchrony, and not fitness differences ($r_i = 0$ in equation 9 of ref. 18). Therefore, we standardize $R(t)$ so that the log-means = 0 and log-variances = 1.

Although this approach best preserves our interpretation of A_{ij} as a measure of potential coexistence arising from reduced seedling recruitment synchrony, we also considered the degree to which species-specific variances in $R(t)$ may contribute to or detract from coexistence. As the variances in $R(t)$ contribute to fitness differences, and to the storage effect, it is important to precisely quantify the per capita value of $R(t)$ by incorporating information regarding reproductive adults of each species. These data are not available for all forests, and we were able to perform this additional calculation of $A_{ij}A_{ji}$ only for BCI, Ogawa, and Bonanza Creek. We assessed whether the resulting values of $A_{ij}A_{ji}$ were similar to the variance-standardized results (column 1 of Extended Data Figure 1) by performing a linear fit of one set of calculations on to the other and assessing whether most points fell close

to the one-to-one line (slope = 1). We found an approximate slope of 0.9 ($P < 0.001$, $R^2 = 0.43$) indicating that the standardized variances are not substantially changed by the inclusion of this additional information relating to adult density, and that our qualitative results would therefore be unlikely to change.

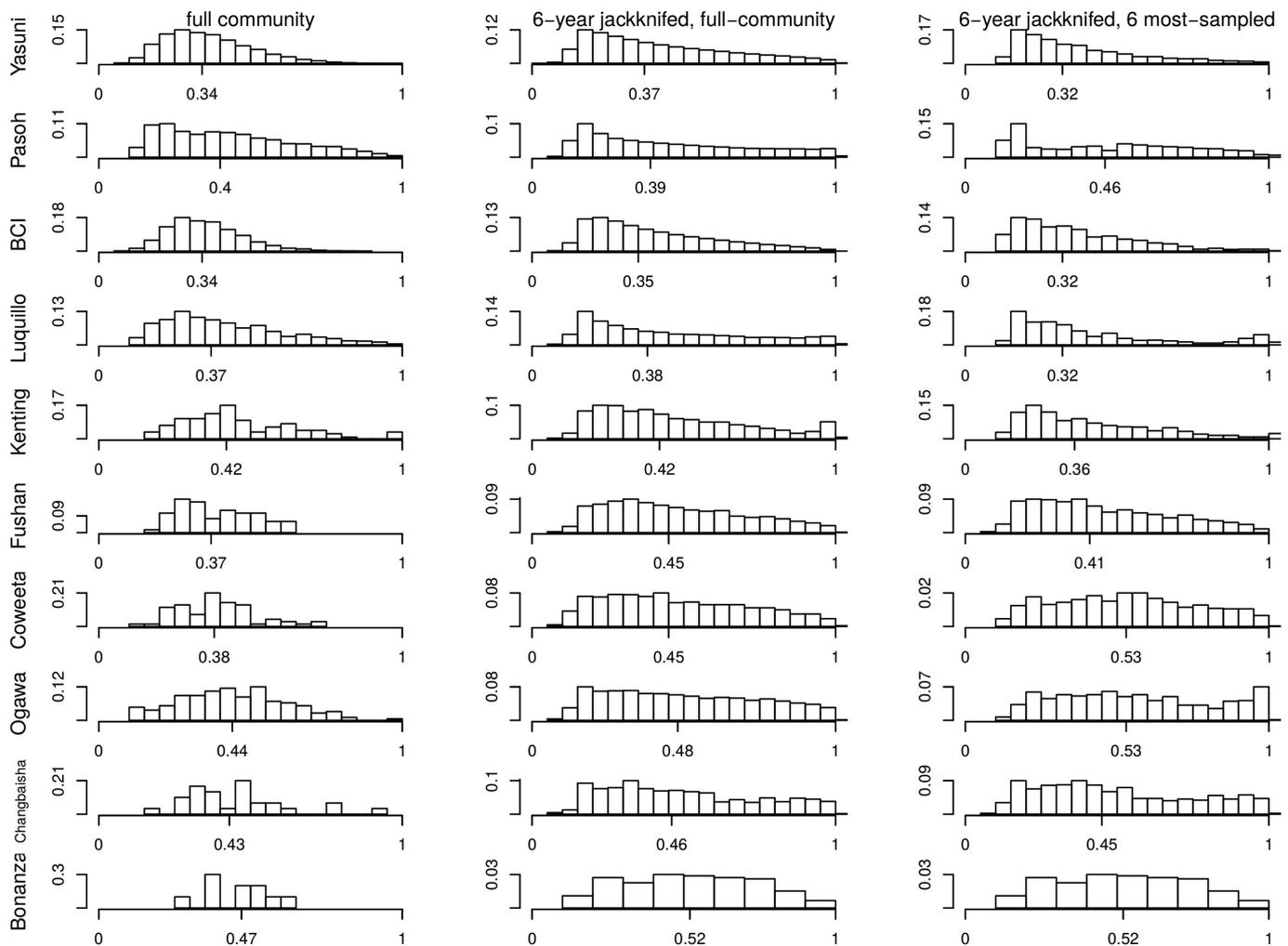
One implication of assuming an annual timescale for $R(t)$ is that equation (3) will not capture any storage effects that emerge if species recruit seedlings at sub-annual (monthly) timescales. It is likely that sub-annual recruitment would augment the observed patterns, as tropical forests provide relatively more opportunity for within-year differentiation than do temperate or boreal ones. Investigating this will require data on monthly seedling dynamics, which are currently unavailable for most of our sites. Additional parameterizations of the forest dynamics model include letting $d_i \rightarrow 1$ ($d_i = 0.99$ in numerical calculations) and $f_i = 0.6$ for all species²³. Our goal is to adopt biologically plausible values while removing differences between species, because asymmetries between species in survival at either stage can augment coexistence; we have taken a conservative approach by focusing only on the storage effect.

The calculated values of $A_{ij}A_{ji}$ are influenced by seedling time series length; median values of $A_{ij}A_{ji}$ were smaller for shorter datasets (Pasoh and Kenting forests). To account for possible bias caused by variation in time series length, we applied a jack-knife approach to recalculate $A_{ij}A_{ji}$ for each forest using randomly chosen subsets equal in length to the shortest records (six years, from Kenting) (Fig. 1, and 'X's and dashed line in Extended Data Fig. 3). To account for possible bias caused by different numbers of species between sites, or by rarer (and therefore less frequently sampled) species, we also applied the jack-knife approach with six year subsets that retained only the six species with the largest sample sizes from each site (to match the species number of the least diverse site, Bonanza Creek) (Fig. 1, open squares and dotted line, Extended Data Fig. 3). The six-year jack-knifed, six most-sampled species datasets give the same qualitative results as the six-year jack-knifed, full forest community datasets, suggesting that rare species did not bias the results. Therefore, we drew our main conclusions from calculations of $A_{ij}A_{ji}$ using the six-year jack-knifed, full community datasets, since they represent the full variety of species-specific responses in each forest.

Code availability. Example code used to produce these analyses (written in R) can be found at Figshare: <https://figshare.com/s/c06397c5c37eb78e64ba>.

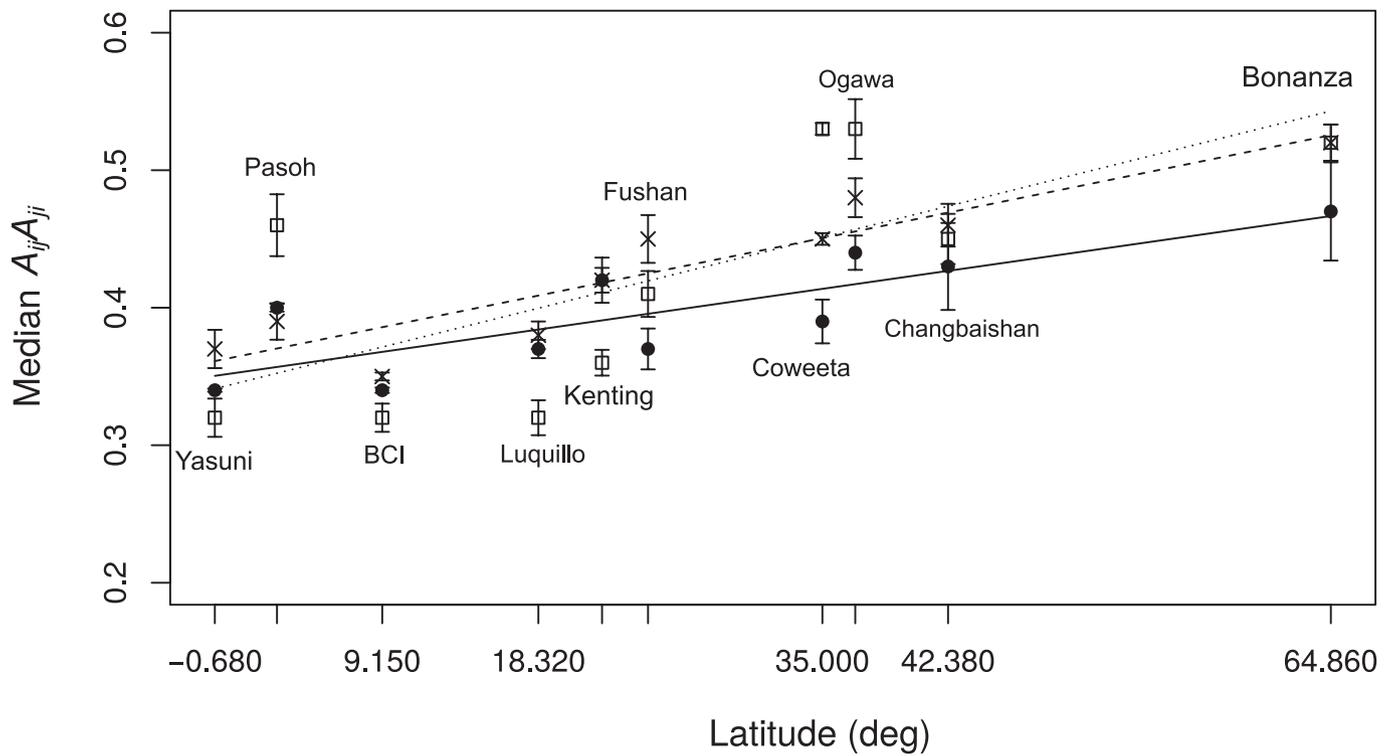
Data availability. The data that support the findings in this manuscript can be found at Figshare: <https://figshare.com/s/c06397c5c37eb78e64ba>.

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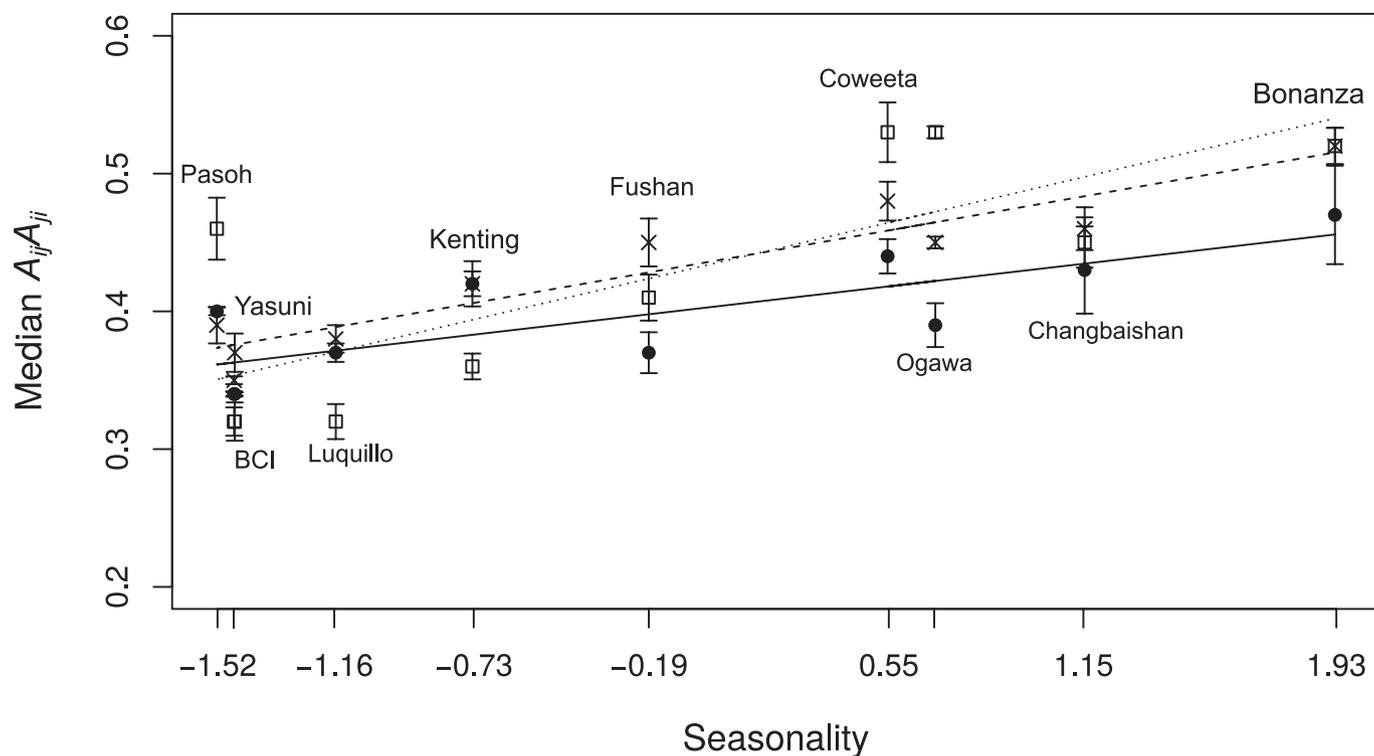
Extended Data Figure 1 | Frequency distributions of A_{ij}/A_{ji} for each forest community, calculated with three different approaches (columns 1–3). The first column is calculated for the full-community datasets (variable number of years and species between sets), the second

column for the six-year jack-knifed, full-community datasets (variable number of species), and the third column is for six-year jack-knifed, six most-sampled species datasets. See Extended Data Table 1 for sample sizes (number of species per forest).



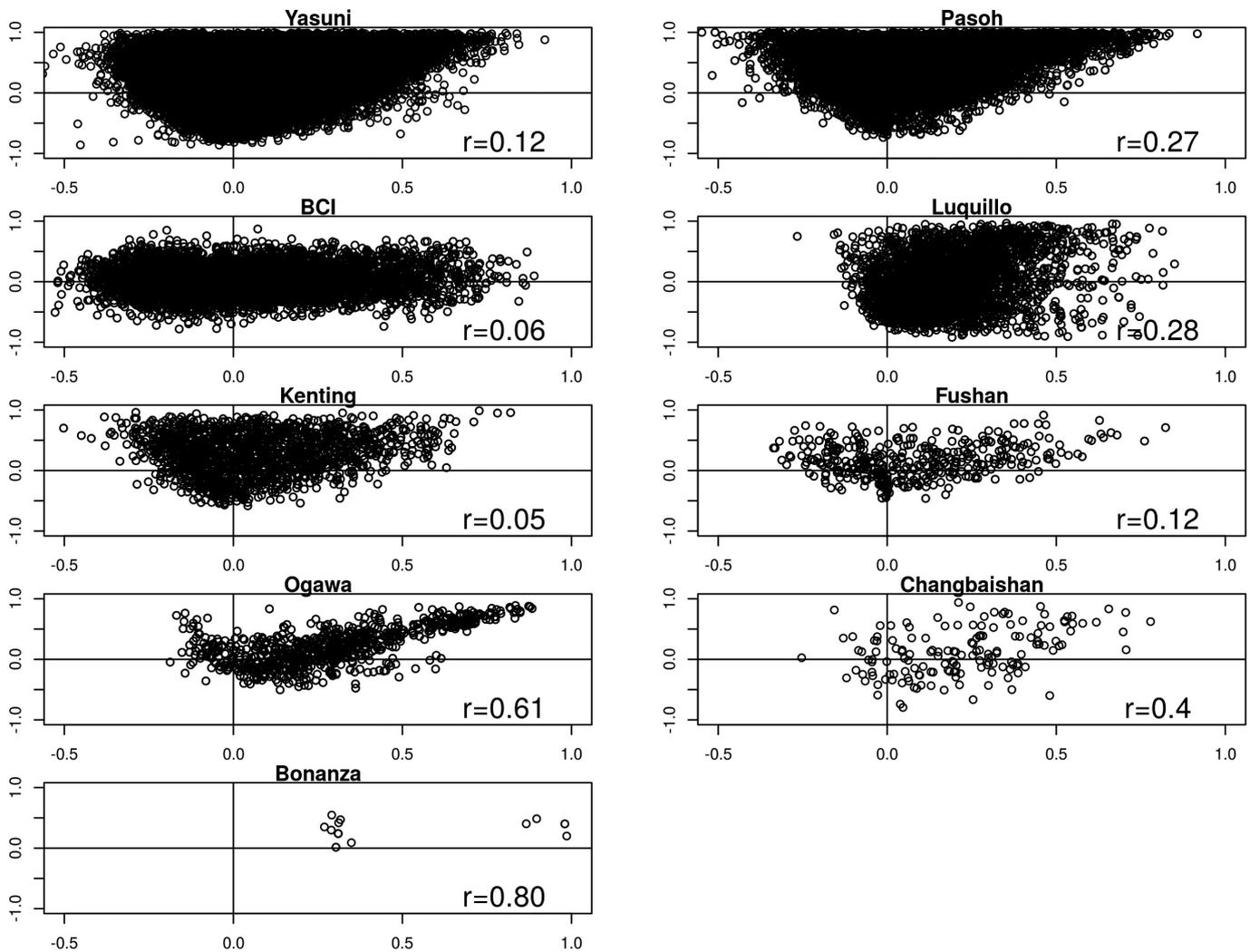
Extended Data Figure 2 | The median values of pairwise competition coefficients $A_{ij}A_{ji}$ are correlated with latitude for three different methods of calculation. Each combination of symbols and fitted lines corresponds to an approach for calculating $A_{ij}A_{ji}$, including standard error bars. Solid line and solid circles: all years in each dataset (slope = 0.0018, $R^2 = 0.63$, $P = 0.004$); dashed line and 'X's: repeated jack-knifing of six-year

subsets of the full dataset (slope = 0.0025, $R^2 = 0.83$, $P < 0.001$); dotted line and open squares: jack-knifing six-year subsets containing only the top six seedling-producing species in each forest (slope = 0.0031, $R^2 = 0.42$, $P = 0.03$). See Extended Data Table 1 for sample sizes (number of species per forest).



Extended Data Figure 3 | The median values of pairwise competition coefficients $A_{ij}A_{ji}$ are correlated with growing season for three different methods of calculation. The metric of growing season is the log of the sum of coefficients of variation (CV) for monthly solar insolation, minimum temperatures, and maximum temperatures, $\log(CV_I + CV_X + CV_N)$ (Methods, Extended Data Table 2). Lower values correspond to a longer growing season. Symbols and fitted lines represent different

methods of calculating $A_{ij}A_{ji}$, including standard error bars. Solid line and solid circles: all years in each dataset (slope = 0.027, $R^2 = 0.57$, $P = 0.007$); dashed line and 'X's: repeated jack-knifing of six-year subsets of the full set (slope = 0.041, $R^2 = 0.87$, $P < 0.001$); dotted line and open squares: jack-knifing six-year subsets containing only the top six seedling producing species in each forest (slope = 0.055, $R^2 = 0.55$, $P = 0.009$). See Extended Data Table 1 for sample sizes (number of species per forest).



Extended Data Figure 4 | The correlation between within-year pairwise synchrony and among-year synchrony was positive for all ten forests. Within-year and among-year synchronies are calculated as the within-year and among-year portions of the correlation (see Fig. 2, Methods). The correlation between these two scales of synchrony was also calculated

using the Pearson's correlation, given as r in the lower right corner of each panel. The median correlation across all forests was 0.28, and it ranged from 0.05 (BCI) to 0.80 (Bonanza Creek). See Extended Data Table 1 for sample sizes (number of species per forest).

Extended Data Table 1 | A summary of the selected forests and available data

Site name	Δ Elevation a.s.l	CV_I	CV_p	CV_x	CV_n	Species	Years	Species: seeds	Species: seedlings
Yasuni: 0°40'S, 76°24'W	213 - 237 m	0.173	0.301	0.030	0.028	1104	12	630	172
Pasoh: 2°58'N, 102°18'E	68 - 92 m	0.171	0.252	0.029	0.018	816	8	143	106
Barro Colorado Island: 9°09'N, 79°51'W	120 - 160m	0.198	0.584	0.019	0.013	300	17	103	86
Luquillo: 18°19'N, 65°49'W	333 - 446m	0.194	0.226	0.060	0.061	138	6	78	41
Kenting: 22°03'N, 120°51'E	310 - 330m	0.239	0.692	0.108	0.133	95	6	57	36
Fushan: 24°45'N, 121°33'E	600 - 730m	0.310	0.451	0.225	0.291	46	12	28	10
Coweeta: 35°00'N, 83°30'W	717 - 1037m	0.362	0.155	0.351	1.287	48	23	NA	16
Ogawa: 36°55'N, 140°34'E	633 - 658m	0.324	0.747	0.384	1.019	49	23	23	20
Changbaishan: 42°22'N, 128°04'E	791 - 809m	0.336	0.940	1.657	1.177	26	10	18	8
Bonanza Creek: 64°51'N, 147°51'W	206 - 405m	0.807	0.730	4.275	1.778	6	18-23	6	6

Site name, site name with latitude and longitude. Seasonality given by the CVs of monthly solar insolation (CV_I), precipitation (CV_p), maximum temperature (CV_x), and minimum temperature (CV_n). Species, total number of species in censused adults. Years, total length of seedling censuses. Species: seeds, the total number of species retained in filtered seed dataset. Species: seedlings, the total number of species retained in filtered seedling datasets.

Extended Data Table 2 | Statistical models using CVs of four different climate variables to predict community-wide averages of within-year interspecific synchrony, among-year interspecific synchrony, and the metric $A_{ij}A_{ji}$

	Intercept	CV_I	CV_p	CV_x	CV_n	R^2	AIC
Within-year correlations	-0.04702	0.7161				0.8367	-15.5
	0.002858		0.3016			0.2342	-3.2
	0.05437			0.2216		0.853	-16.4
	0.09179				0.09715	0.7682	-12.7
	0.0273	0.5977	-0.1977	0.2388	-0.0657	0.9447	-18.2
Among-year correlations	0.0728	0.2777				0.2308	-8
	0.1189		0.06919			0.0226	-6.1
	0.1165			0.07762		0.1919	-7.6
	0.128				0.03598	0.1932	-7.6
	0.08091	0.495	-0.1323	0.08533	-0.05549	0.2811	-2.5
$A_{ij}A_{ji}$	0.3499	0.2394				0.7096	-32.3
	0.3711		0.1037			0.2689	-24
	0.05437			0.07588		0.8663	-39.3
	0.09179				0.03066	0.5824	-29
	0.3318	0.158	0.04281	0.05531	-0.01621	0.9027	-36.1

The model AICs and R^2 are given to compare the explanatory power of the CV for monthly solar insolation (CV_I), precipitation (CV_p), maximum temperature (CV_x), and minimum temperatures (CV_n) individually, as well as the combination of all four (which we use as a metric of site seasonality). Each variable has substantial explanatory power, but the best models included all four variables.

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

Forest sites: Only forest sites with time series of seed and seedling production of at least 6 years were considered.
Seed and seedling records (from the methods): Both seed and seedling counts were filtered to consider only species that were well sampled over the duration of data collection. Yearly seed counts were only used for species with more than 50 records of seeds occurring in 3 separate years, and with adults occurring in the experimental plot. Seedling counts were only used for species with at least 25 records of recruitment occurring in 3 separate years, and with adults occurring within the plot. In all forests, more species were retained in the seed data sets than in the seedling data sets.

2. Data exclusions

Describe any data exclusions.

Forest sites: Only forest sites with time series of seed and seedling production of at least 6 years were considered.
Seed and seedling records (from the methods): Both seed and seedling counts were filtered to consider only species that were well sampled over the duration of data collection. Yearly seed counts were only used for species with more than 50 records of seeds occurring in 3 separate years, and with adults occurring in the experimental plot. Seedling counts were only used for species with at least 25 records of recruitment occurring in 3 separate years, and with adults occurring within the plot. In all forests, more species were retained in the seed data sets than in the seedling data sets.

3. Replication

Describe whether the experimental findings were reliably reproduced.

NA

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

NA

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

NA

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
- A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- A statement indicating how many times each experiment was replicated
- The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
- A description of any assumptions or corrections, such as an adjustment for multiple comparisons
- The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted
- A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
- Clearly defined error bars

See the web collection on [statistics for biologists](#) for further resources and guidance.

► Software

Policy information about [availability of computer code](#)

7. Software

Describe the software used to analyze the data in this study.

All analyses were done with R, R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* [guidance for providing algorithms and software for publication](#) provides further information on this topic.

► Materials and reagents

Policy information about [availability of materials](#)

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.

No unique materials were used.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).

No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.

No eukaryotic lines were used.

b. Describe the method of cell line authentication used.

No eukaryotic lines were used.

c. Report whether the cell lines were tested for mycoplasma contamination.

No eukaryotic lines were used.

d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by [ICLAC](#), provide a scientific rationale for their use.

No cell lines were used.

► Animals and human research participants

Policy information about [studies involving animals](#); when reporting animal research, follow the [ARRIVE guidelines](#)

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.

No animals were used.

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.

No humans were used.