

Coexistence in tropical forests through asynchronous variation in annual seed production

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Abstract. The storage effect is a mechanism that can facilitate the coexistence of competing species through temporal fluctuations in reproductive output. Numerous natural systems have the prerequisites for the storage effect, yet it has rarely been quantitatively assessed. Here, we investigate the possible importance of the storage effect in explaining the coexistence of tree species in the diverse tropical forest on Barro Colorado Island, Panama. This tropical forest has been monitored for more than 20 years, and annual seed production is asynchronous among species, a primary requirement for the storage effect. We constructed a model of forest regeneration that includes species-specific recruitment through seed, sapling, and adult stages, and we parameterized the model using data for 28 species for which information is known about seedling germination and survival. Simulations of the model demonstrated that the storage effect alone can be a strong mechanism allowing long-term persistence of species. We also developed a metric to quantify the strength of the storage effect in a way comparable to classical resource partitioning. Applying this metric to seed production data from 108 species, the storage effect reduces the strength of pairwise interspecific competition to 11–43% of the strength of intraspecific competition, thereby demonstrating strong potential to facilitate coexistence. Finally, for a subset of 51 species whose phylogenetic relationships are known, we compared the strength of the storage effect between pairs of species to their phylogenetic similarity. The strength of the storage effect between closely related species was on average no different from distantly related species, implying that the storage effect can be important in promoting the coexistence of even closely related species.

Key words: *asynchrony; Barro Colorado Island, Panama; community dynamics; competition; phylogenetic analysis; resource partitioning; seed production; storage effect; tree recruitment; tropical forest diversity.*

INTRODUCTION

The stable coexistence of competing species requires species to differ so that interspecific competition is, on average, weaker than intraspecific competition. This limits the ability of a superior competitor to reach sufficiently high densities to drive other species extinct. The most familiar, widespread, and well-studied coexistence mechanism is classical resource partitioning, in which species use different resources. Classical resource partitioning implies that conspecifics are more likely to be limited by the same resources than are heterospecifics, which makes intraspecific competition more severe than interspecific competition (MacArthur and Levins 1967, Chesson 2000). Even if species use the same resources, however, they may still coexist due to temporal variability. Recruitment fluctuations in the presence of overlapping generations can enable coexistence by producing resource partitioning through time, a mechanism referred to as the storage effect (Chesson and Warner 1981).

The storage effect was first identified in a lottery model of recruitment that was developed for species of territorial reef fishes (Chesson and Warner 1981). The original lottery model assumes that there are two competing species, each of which has two life stages. There are two essential features in the lottery model as it was first presented that together promote coexistence: (i) adults are long-lived in the sense that there is significant overlap between successive generations, and (ii) reproduction varies asynchronously among species through time due to species-specific environmental responses (Chesson 2003, Angert et al. 2009). More generally, (i) can refer to any long-lived stage in a population and (ii) to any mechanism that leads to asynchronous variation in recruitment. Asynchronous recruitment variation causes each species to have time periods when its juveniles are present in relatively large numbers and therefore experience high intraspecific competition relative to interspecific competition. The resulting covariance between competition and environmentally driven recruitment leads to facilitated coexistence (Chesson 2000). The long-lived stage ensures that occasional highly successful recruitment events sustain populations, even through periods of low or no

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recruitment; the importance of this long-lived stage led to the name “storage effect.”

The basic prerequisites for the storage effect can be found in numerous systems. Many animal species show high reproductive variability, most notably invertebrates (Thorson 1950) and marine fish (Secor 2007). Annual plants may fulfill the prerequisites of the storage effect when seeds form a relatively long-lived seed bank (Pake and Venable 1995). The same is true for many perennial plants with variable seed production and a long-lived adult stage, and forest communities especially have been observed as having very high reproductive variability (Herrera et al. 1998). Despite the likely importance of the storage effect for numerous systems, there is only a handful of studies that quantify the storage effect for specific communities (Pake and Venable 1996, Cáceres 1997, Kelly and Bowler 2002, Adler et al. 2006, Secor 2007, Angert et al. 2009).

Tropical forests appear to have all the prerequisites for the storage effect (Runkle 1989). Tropical trees are long-lived. Estimates of the mortality rates of adults average less than 2.55% mortality per year at Barro Colorado Island (BCI), a tropical moist forest in Panama, and less than 1.46% at Pasoh Forest, a tropical moist forest in Malaysia (Swaine et al. 1987, Dalling et al. 1997). A comparative study across four tropical forests found that interannual variability in seedling recruitment is high, ranging from a community average coefficient of variation (CV) of 40% at BCI to 117% at Pasoh (Metz et al. 2008). Investigations of seedling dynamics also indicate that interspecific correlations between annual seedling recruitment on BCI are typically much less than 1.0, indicating asynchronous variation in recruitment (Wright et al. 2005). Although Kelly and Bowler (2002) present evidence supporting the role of the storage effect in allowing coexistence of phylogenetically related pairs of tropical tree species, this evidence is based solely on the size structure of tree populations, rather than direct demonstration of the prerequisites of the storage effect. To our knowledge, there has been no attempt to quantify the magnitude and extent to which the storage effect could maintain diversity in tropical forests.

Here, we analyze the role of the storage effect in facilitating coexistence in the BCI forest. We first introduce a stochastic model of tree recruitment dynamics. Our model includes a species-specific reproduction parameter that we fit directly using a combination of 23 years of seed production and 14 years of seedling recruitment data for a subcommunity of 28 species. We use the fitted model to simulate forest dynamics and ask how many species the storage effect by itself can allow to coexist. We then derive a metric that quantifies the storage effect in terms of the reduction in interspecific competition relative to intraspecific competition, and apply this metric to the BCI data. We show that our metric is relatively insensitive to differences among species in germination or survival

rates, thereby allowing us to expand our analysis to include 108 species for which we have data on seed production but not seed germination or survival. This provides an overall quantification of the potential importance of the storage effect to explain the coexistence of these species and the diversity of the BCI forest.

Extensive studies have shown that classical resource partitioning probably does occur among tropical tree species (Harms et al. 2000, Paine et al. 2008, Comita et al. 2010), and we expect the storage effect to operate in concert with classical resource partitioning. Resource competition will likely be strongest between species sharing similar traits that dictate their resource requirements, yet identifying resource requirements for tropical tree species is difficult, and many ecological traits of the species in our data set are unknown. Therefore, we addressed this issue using a phylogenetic approach. It is typically assumed that closely related species are ecologically similar (Webb et al. 2002, Cavender-Bares et al. 2004) and, hence, we might expect classical resource partitioning to be less effective at promoting coexistence between closely related species. We asked whether the storage effect between closely related species could be sufficiently strong to explain their coexistence.

Forest dynamics model

We built a model of forest dynamics that includes the possibility of both classical resource partitioning among seedlings and the storage effect through variation in recruitment. Although we focus on the latter, by incorporating both coexistence mechanisms, we make it possible to compare them. We first provide biological motivation for the model and then build it mathematically.

Treefall gaps are essential for the establishment of most tropical trees (Augspurger 1984, Runkle 1989, Hubbell et al. 1999) because they make available resources (primarily light) that are necessary for seedling establishment and sapling growth (Augspurger 1983, Schupp et al. 1989). When a tree falls, the gap is filled by an individual either from an already existing population of shade-tolerant saplings that populate the understory, or by light-demanding species that germinate and grow quickly enough to overtop more shade-tolerant saplings (Brokaw 1985, Dalling et al. 1997). Here, we use the term “shade tolerant” to refer to those species with seedlings and saplings that can maintain a positive growth rate in shade (Wright et al. 2003) and experience low mortality under canopy conditions (De Steven and Wright 2002, Comita et al. 2010). The majority of species at BCI fall into the shade-tolerant category, and we selected only shade-tolerant species for the analyses. Due to the low mortality rate of saplings, the likelihood of a gap being filled by a member of any species is approximately proportional to its sapling population. This suggests that competition to fill gaps is of the lottery type (Runkle 1989). We acknowledge, however, that even though it is not incorporated into the model,

the actual likelihood integrates relative abundance of saplings, initial height of the saplings in the gap, and species-specific growth responses to gaps.

Recruitment of seedlings into the sapling population is set by a combination of seed production and survival. Annual variation in seed production is large, and years of high seed production vary among species. The mortality of seedlings in the first year is generally very high, estimated at >90% for some species (Augsburger 1983, Clark and Clark 1984). Mortality is caused by a combination of both density-dependent and density-independent factors, including desiccation (Engelbrecht et al. 2002), herbivory (Connell 1978), and pathogens (Mangan et al. 2010). Density-dependent mortality for most species in the first year of germination suggests strong competition (including apparent competition mediated by herbivores and pathogens) among seedlings to join the sapling population, and species' differences that contribute to survival rates are large during this stage (Harms et al. 2000). Once seedlings are established, mortality drops rapidly as they transition into the sapling population (De Steven 1994, De Steven and Wright 2002), where they continue to experience low levels of density-dependent mortality mediated largely by herbivores and pathogens (Svenning et al. 2008, Comita et al. 2010, Mangan et al. 2010). In our model, we focus on annual variation in seedling recruitment, rather than seasonal variation, for two reasons. First, the annual time scale is more appropriate to capture ontogenetic changes in tree demographics, as seedlings transition within a year into the sapling stage with lower mortality. Second, germination of seeds may not be immediate, so seasonal fluctuations in seed production may be blurred during entry into the seedling stage. Using an annual time step in the model would be conservative, in the sense that within-year asynchrony probably would add to the storage effect.

Mathematically, we represent the life history of tropical trees as a stage-structured model for n competing species. We explicitly model two stages: established saplings and long-lived reproductive adults, with density-dependent and independent survival of seeds and young (<1-year-old) seedlings incorporated implicitly into recruitment. Recruitment into the sapling stage is governed by a Leslie-Gower competition model (Leslie 1958), with the density of species i ($i = 1, \dots, n$) in the sapling population in year $t + 1$, $s_i(t + 1)$, given by

$$s_i(t + 1) = \frac{f_i s_i(t)}{1 + \beta_{ii} s_i(t) + k_{ii} x_i(t)} + \frac{R_i(t) x_i(t)}{1 + \sum_{j=1}^n \alpha_{ij} x_j(t) R_j(t)}. \tag{1}$$

The second term on the right side of Eq. 1 captures recruitment into the sapling population. The abundance of adults of species i , $x_i(t)$, is multiplied by the recruitment rate $R_i(t)$, expressed as seedling production per adult. All of the $R_i(t)$ taken together define an n -

dimensional random variable, matrix $\mathbf{R}(t)$, that captures the mean, variance, and correlation among species in recruitment into the seedling stage. We assume that all germination occurs within the year of seed production, an assumption that is valid for shade-tolerant tree species on BCI (Garwood 1983, Sautu et al. 2006). The rate of seedling establishment is negatively density dependent; a proportion of the seeds germinate and survive to the sapling stage, calculated as follows:

$$\left(1 + \sum_{j=1}^n \alpha_{ij} x_j(t) R_j(t) \right)^{-1}.$$

The impact of both conspecific and heterospecific recruits on seedling establishment is discounted by the coefficients α_{ij} that measure the per capita effect of species j on species i . These coefficients are usually interpreted as a measure of resource competition; however, several studies suggest that resource competition among seedlings is weak (Paine et al. 2008, Svenning et al. 2008). Nonetheless, apparent competition resulting from herbivory or pathogens can be strong (Mangan et al. 2010), and α_{ij} can be interpreted as a measure of apparent competition.

The first term on the right side of Eq. 1 captures sapling survival of species i from the previous year, where f_i is the density-independent survival of saplings. The terms β_{ii} and k_{ii} represent intraspecific competition experienced by saplings from other saplings and from adults, respectively; we model only intraspecific competition on saplings, because there is little evidence of interspecific competition at this stage (Comita et al. 2010).

To model the adult stage, we assume that adults have some high probability d_i of surviving each year, and when death occurs it creates a gap in the canopy for which individuals in the sapling population compete. Thus, the dynamics of adults are given by the lottery model:

$$x_i(t + 1) = d_i x_i(t) + \left(1 - \sum_{j=1}^n d_j x_j(t) \right) \frac{s_i(t)}{\sum_{j=1}^n s_j(t)}. \tag{2}$$

Eqs. 1 and 2 together give our forest dynamics model.

Barro Colorado Island tree recruitment data

Barro Colorado Island, Panama (9°9' N, 79°51' W) is a tropical moist forest experiencing a four-month dry season (December–April) with annual rainfall averaging 2600 mm. Flowering and fruiting of at least some species occur across all 12 months, but for the majority of tree and liana species, reproduction coincides with the dry season, with a second smaller peak in September–October (Zimmerman et al. 2007). BCI is perhaps the best-studied tropical forest, and numerous detailed descriptions of its climate, environment, flora, and fauna

are available (Croat 1978, Leigh and Wright 1990, Windsor 1990, Leigh 1999).

The key piece of information needed for our analysis is the per capita recruitment rate, $R_i(t)$, which incorporates seed production, survival, germination rates, and the survival of young seedlings. Seed production at BCI has been quantified weekly since January 1987, at 200 sampling stations located within a 50-ha Forest Dynamics Plot; detailed descriptions of the census methodology are given by Wright et al. (1999, 2005). Weekly seed counts are assigned to annual totals in a four-step process. First, seeds are tallied by month for the entire record. Second, a month with zero seed production is identified for each species. Third, a value for annual production is calculated by summing over 12 months beginning with the month identified in step two. Fourth, each annual sum is assigned to a calendar year according to the mean date of seed production. The final step is necessary because some species produce seeds across December–January, thus creating an annual reproductive event that spans two calendar years.

These censuses provide 22 years of annual seed production for nearly 260 species, from which we selected 108 species of trees and lianas. The 108 species have at least four seed-bearing individuals in close proximity to seed traps, produce seeds large enough to be captured by the 1-mm mesh seed traps, have seeds identifiable to species (which excludes all *Ficus* and all but one *Inga* species), and have more than 75 seeds plus fruit captured during the 22-year record (for further details, see Wright et al. 2005). In addition, *Hyeronima alchorneoides* was excluded it produces seeds twice each year. The remaining species each produce seeds just once in a year. Furthermore, individuals within each species have highly synchronized seed production over the course of a year (Zimmerman et al. 2007); this within-year synchrony implies the possibility of strong intraspecific competition during recruitment. The 108 species are approximately uniformly distributed by abundance class from a high of 13.3% (*Hybanthus prunifolius*) to 0.01% (*Anacardium excelsium*) of total stems. Seed production, as measured by presence or absence of a species from individual traps over all 22 years, is also approximately uniformly distributed across abundance classes from a high of 9.4% (*Alseis blackiana*) to 0.01% (*Mascagnia hippocrateoides*) of total occurrences. All 108 species account cumulatively for 68% of stems in the plot and 78% of recorded seeds.

We also consider in greater detail a subset of 28 species for which the most information on local seedling recruitment is available. Specifically, at the 200 sampling stations there are three permanent 1-m² plots adjacent to each seed trap. Each seedling is tagged and identified in annual censuses conducted each dry season. The subset of 28 species had seedling recruits at 30 or more stations for the 14-year period starting in 1993, 10 or more recruits during a single annual event recorded at a single station, and seeds or fruit recorded at 50 or more

stations over the 14-year interval. The 28 species are mostly in the top 10% of both stem abundance and seed production categories from the larger set of 108 species. This subset includes 38% of total stems in the plot and 40% of seed records.

For the groups of 28 and 108 species, we set $R_i(t)$ to represent different processes. For the subset of 28 species, we use $R_i(t) = g_i(t)$, where $g_i(t)$ is the species-specific rate of seedling recruitment incorporating multiple post-dispersal processes that determine seedling densities at the time of the annual census. For the full set of 108 species, we ignored the (unknown) seedling recruitment rates by setting $R_i(t) = r_i(t)$, where $r_i(t)$ denotes seed production as determined by the seed traps.

Simulations of the storage effect

We first illustrate the model by simulating the case of two species, *Spondias mombin* and *S. radlkoferi*, to show how asynchronous fluctuations in recruitment $R_i(t)$ and adult longevity facilitate coexistence. The annual fluctuations in seed production, $r_i(t)$, for the two *Spondias* species have variances $\sigma_{S,mom}^2 = 1.68$ and $\sigma_{S,rad}^2 = 0.66$, and are asynchronous with correlation coefficient $\rho = -0.16$ (Fig. 1A). We fit these seed production data to a first-order autoregressive model (Box et al. 1994), which we then used to simulate recruitment (Fig. 1B). The autoregressive model allowed us to simulate different degrees of synchrony; the case of $\rho = 0.9$, where both species are almost completely synchronous, is illustrated in Fig. 1C.

The storage effect on coexistence can be illustrated by testing for mutual invasibility, that is, whether either species can invade a population of the other species when the latter is established at its stochastic stationary distribution (Turelli 1978). For any pair of species, the outcome of competition will depend on both the strength of the storage effect (given by variability in $R_i(t)$) and any asymmetry in the overall success of the competing species (given by the mean values of $R_i(t)$). Although we have data to account for asymmetries in seed production and seedling recruitment, we have no information about other sources of asymmetry. In the absence of information, and to focus on the storage effect, we assume that the mean values of $R_i(t)$ are the same for both species.

The other parameters in the model are, for both *S. mombin* and *S. radlkoferi*, seedling survival $f_i = 0.6$ and adult survival $d_i = 0.975$. Adult survival is based on the plot-wide averages found in Swaine et al. (1987) and Condit et al. (1999). Although model behavior is largely insensitive to the value of f_i as long as it is less than d_i (Appendix A), we chose the value based on the survival rate of individuals between 2 and 20 years of age taken from De Steven and Wright (2002). Intraspecific competition from saplings β_{ii} and adults κ_{ii} are set to zero to provide a lower bound on potential coexistence, because positive β_{ii} and κ_{ii} coefficients increase the likelihood of coexistence (Appendix A). Finally, we remove the

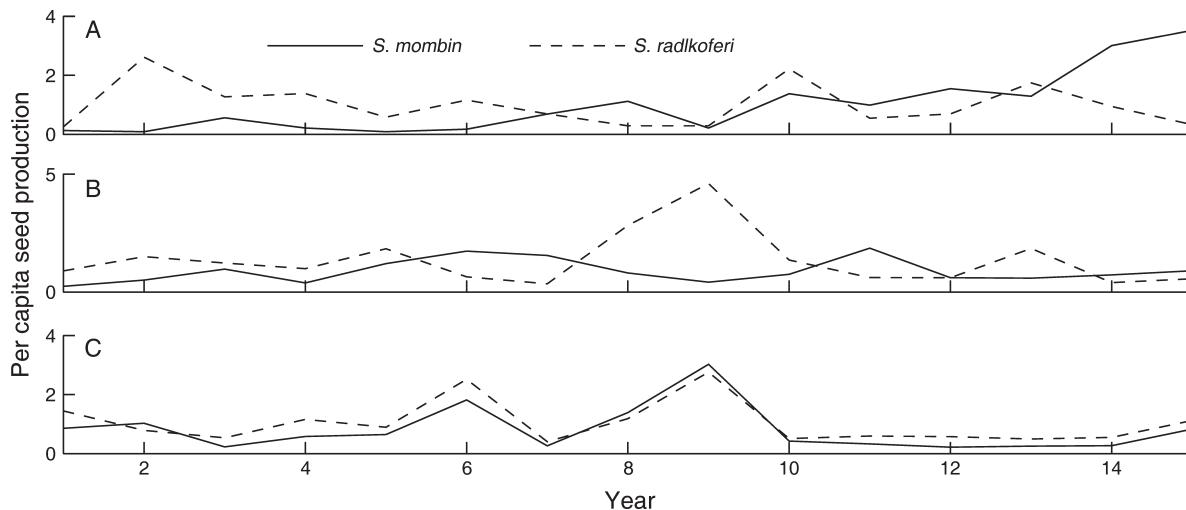


FIG. 1. (A) Fluctuations in seed production, $r_i(t)$, standardized by the means for the tropical trees *Spondias mombin* and *S. radlkoferi*. (B) Example trajectories of autoregressive models fit using parameter values estimated from the data in panel (A) with interspecific correlations (ρ), variances (σ^2) of the species, and means: $\rho = -0.16$, $\sigma_{S.mom}^2 = 1.68$, $\rho_{S.rad} = 0.66$, and $\bar{R}_i = \bar{R}_j = 1$. (C) Example trajectories simulated with $\rho = 0.9$ and other parameters as in panel (B).

possibility of coexistence through classical resource partitioning by setting the intra- and interspecific seedling competition coefficients to 1 ($\alpha_{ii} = \alpha_{ij} = \alpha_{ji} = 1$).

In the simulation, coexistence is possible for the observed correlation, ρ , and variance, σ^2 , in interannual seed production $R_i(t)$ (Fig. 2). When we separately reduced the asynchrony in seed production by setting $\rho = 0.9$ and reduced adult longevity by decreasing d_i from 0.975 to 0.1, *S. radlkoferi* outcompeted *S. mombin* (Fig. 3A, B), showing that both asynchrony and adult longevity are required for the storage effect. Finally, even when asynchrony is weak ($\rho = 0.9$), increasing the variance in recruitment of *S. mombin* by fivefold allows coexistence (Fig. 3C). Thus, two species can be highly correlated in terms of good recruitment years and still coexist if each species can occasionally produce significantly larger numbers of recruits.

We applied the procedure that we illustrated with the two *Spondias* species to assess the potential contribution of the storage effect to coexistence for the subset of 28 species with $R_i(t) = g_i(t)$. Autoregressive models of annual seedling production were fit for each species. Autocorrelation was found in only 8 of the 28 species, with only 3 of these species showing lags greater than 1; performing simulations without these autocorrelations did not change the results. Correlations in annual seedling production rates were calculated between all species pairs; the average pairwise correlation was 0.059 and ranged from -0.629 to 0.971 (Appendix B). We tested coexistence by simulating the 28-species community for 10 000 years, with persistence scored when a given species had a nonnegative population growth rate, on average, for the final 5000 years. Repeating this simulation 100 times, 43% of species persisted in every simulation, and 54% persisted in the majority of

simulations (Appendix C). For comparison, we repeated this procedure assuming that the pairwise correlations in seed production were all $\rho = 0.9$. In this case 3 of 28 species coexisted in 65% of the simulations, with a single species typically dominating in the remaining cases, yielding 2.3 as the average number of species persisting for the final 5000 years. The contrast between simulations with naturally occurring asynchrony (average $\rho = 0.059$) and reduced asynchrony ($\rho = 0.9$) demonstrates the potential importance of the storage effect.

Measuring inter- vs. intraspecific competition

A simple expression can be derived for our forest dynamics model that gives the strength of inter- to intraspecific competition and the potential role of the storage effect in coexistence. To derive this expression, we first assume that $\beta_{ii} = 0$ and $\kappa_{ii} = 0$, implying no intraspecific competition between saplings. Positive β_{ii} and κ_{ii} increase the likelihood of coexistence by increasing intraspecific competition, and therefore their removal provides a lower bound on potential coexistence (Appendix A). In addition, we take the limit as $d_i \rightarrow 1$, when adults become very long lived. In this case, the expected rate of population increase of species i invading species j is given approximately by the following:

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

where E denotes the expectation of the quantity in brackets (Appendix D). If $D_{ji} > 1$, then species i can invade species j , so coexistence requires that $D_{ij} > 1$ and

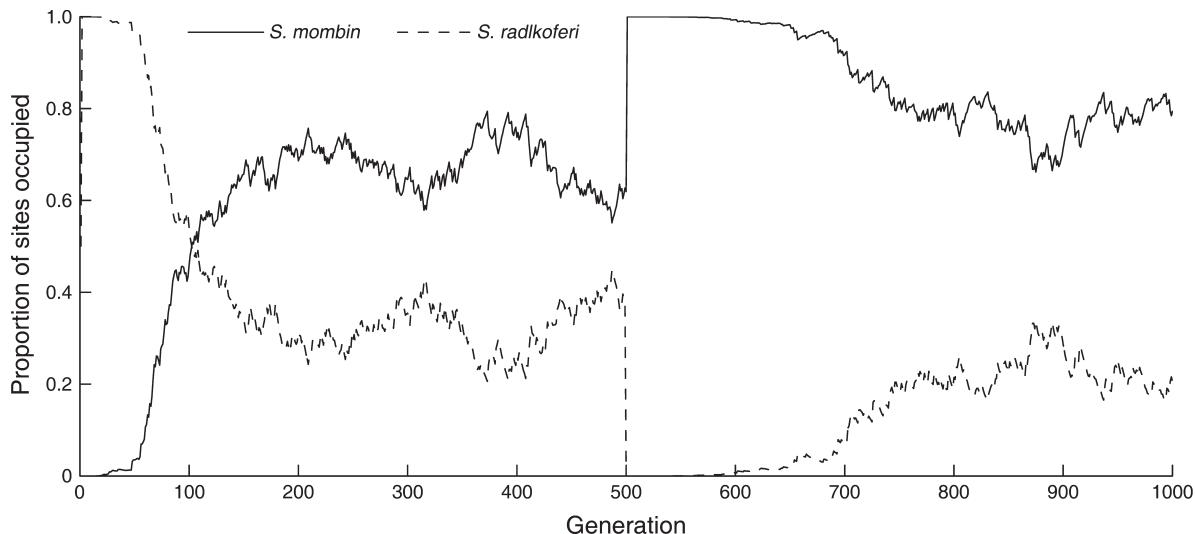


FIG. 2. Invasibility analysis for *S. mombin* and *S. radlkoferi*. Generations 0 to 500 demonstrate *S. mombin* invading *S. radlkoferi*, and in generation 501 the reverse invasion is demonstrated. The reproduction rates, $R_i(t)$, were fit to the seed production data to capture magnitudes (σ^2) and correlations (ρ) of recruitment fluctuations standardized to means $\bar{R}_i = \bar{R}_j = 1$: $\rho = -0.16$, $\sigma_{S,mom}^2 = 1.68$, $\sigma_{S,rad}^2 = 0.66$ (as in Fig. 1). Other parameters of the forest dynamics model include interspecific and intraspecific seedling competition, $\alpha_{ij} = \alpha_{ji} = \alpha_{ii} = \alpha_{jj} = 1$; survival rates of adults, $d_i = d_j = 0.975$; intraspecific sapling competition, $\beta_{ii} = \beta_{jj} = 0$; intraspecific competition between saplings and adults, $\kappa_{ii} = \kappa_{jj} = 0$; and survival rate of saplings, $f_i = f_j = 0.6$.

$D_{ji} > 1$ simultaneously. Therefore, $D_{ij}D_{ji} > 1$ is a necessary (but not sufficient) requirement for coexistence. If we define $A_{ij} = 1/D_{ji}$ so that $A_{ij}A_{ji} < 1$ is a necessary condition for coexistence, this expression is consistent with the classical result for coexistence; coexistence requires the product of the alpha competition coefficients to be less than one, with A_{ij} playing the

role of alpha competition coefficients that incorporates the storage effect.

To illustrate how Eq. 3 can be used to determine coexistence, first consider the case in which seedling survival is the same for both species ($f_i = f_j$), seedling competition coefficients, α_{ij} , equal 1 (so intra- and interspecific seedling competition are equal), and there is

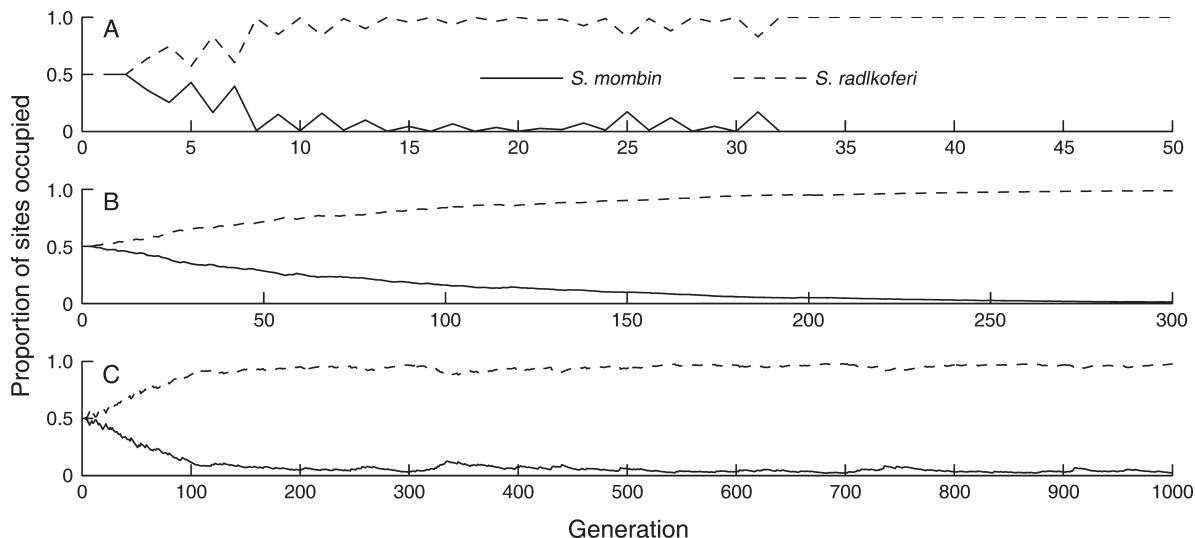


FIG. 3. Simulations of the model for *S. mombin* and *S. radlkoferi*. In panel (A), asynchrony in recruitment has been reduced by setting $\rho = 0.9$ while retaining species values of the variance $\sigma_{S,mom}^2 = 1.68$, $\sigma_{S,rad}^2 = 0.66$, and normalized means $\bar{R}_i = \bar{R}_j = 1$. Extinction of *S. mombin* indicates that asynchronous fluctuations are necessary for the storage effect. In panel (B), the survival of adults is reduced to 0.1 while retaining asynchrony, $\rho = -0.16$ (with $\sigma_{S,mom}^2 = 1.68$ and $\sigma_{S,rad}^2 = 0.66$); extinction of *S. mombin* demonstrates that the storage effect depends on a long-lived stage. In panel (C), even with reduced asynchrony ($\rho = 0.9$), a fivefold increase in the variance in recruitment of *S. mombin* ($\sigma_{S,mom}^2 = 8.5$) allows coexistence. Other model parameters are: $\alpha_{ij} = \alpha_{ji} = \alpha_{ii} = \alpha_{jj} = 1$, $d_i = d_j = 0.975$, $\beta_{ii} = \beta_{jj} = 0$, $\kappa_{ii} = \kappa_{jj} = 0$, and $f_i = f_j = 0.6$.

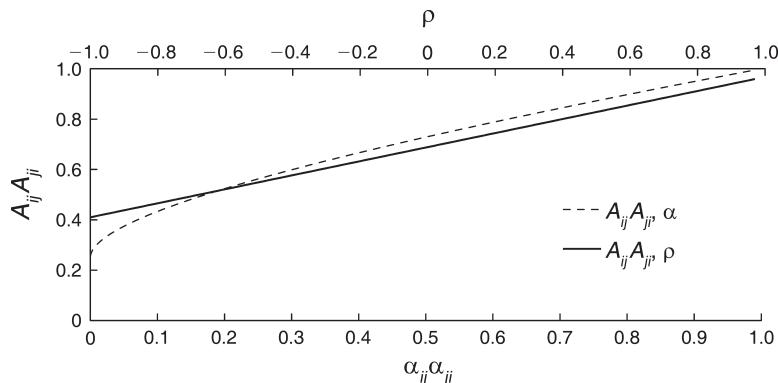


FIG. 4. The quantity $A_{ij}A_{ji}$ gives a synoptic measure of facilitated coexistence, appropriate for either classical resource partitioning or the storage effect. The relationships between $A_{ij}A_{ji}$ and resource partitioning ($\alpha_{ij}\alpha_{ji}$) and the storage effect (ρ) were computed for the model parameterized for *S. mombin* and *S. radlkoferi*. Parameter values are: $\bar{R}_i = \bar{R}_j = 1$, $\rho = \sigma^2 = 0$ for resource partitioning; $\alpha_{ij} = \alpha_{ji} = \alpha_{ii} = \alpha_{jj} = 1$, $\sigma_{S,mom}^2 = 1.68$, $\sigma_{S,rad}^2 = 0.66$ for the storage effect; and $d_i = d_j = 0.975$, $\beta_{ii} = \beta_{jj} = 0$, $\kappa_{ii} = \kappa_{jj} = 0$, and $f_i = f_j = 0.6$ for both.

no variability in recruitment. In this case,

$$A_{ji} = E \left[\frac{\sum_{\tau=1}^t f_i^\tau \frac{R_i(t-\tau-1)}{1+R_j(t-\tau-1)}}{\sum_{\tau=1}^t f_j^\tau \frac{R_j(t-\tau-1)}{1+R_j(t-\tau-1)}} \right]^{-1} = \frac{\bar{R}_j}{\bar{R}_i} \quad (4)$$

where \bar{R}_i is the (constant) value of $R_i(t)$. From Eq. 4, there is no possibility for coexistence, because $A_{ij}A_{ji} = 1$. However, if there is classical resource partitioning in seedling establishment, with $\alpha_{ij} < \alpha_{ii}$ and $\alpha_{ij} < \alpha_{jj}$, then $A_{ij}A_{ji} = [(1 + \alpha_{ij}\bar{R}_j)(1 + \alpha_{ji}\bar{R}_i)] / [(1 + \alpha_{ii}\bar{R}_i)(1 + \alpha_{jj}\bar{R}_j)] < 1$, so coexistence is possible.

For the storage effect, we can relate A_{ij} to the correlation and variances in recruitment rates $R_i(t)$. To give a simple mathematical expression, we set $f_i = f_j = 0$ and remove resource partitioning ($\alpha_{ij} = 1$) so that

$$A_{ij} = E \left[\frac{R_i(t)}{R_j(t)} \right]^{-1} \quad (5)$$

A_{ij} can then be approximated using a Taylor expansion around the mean values of $R_i(t)$ and $R_j(t)$ to give

$$A_{ij} \approx \left[\frac{\bar{R}_i}{\bar{R}_j} \left(1 - \frac{\rho_{ij}\sigma_i\sigma_j}{\bar{R}_i\bar{R}_j} + \frac{\sigma_j^2}{\bar{R}_j^2} \right) \right]^{-1} \quad (6)$$

From this relationship we see explicitly that $A_{ij}A_{ji}$ decreases with decreasing correlation between $R_i(t)$ and $R_j(t)$, and with increasing variances in $R_i(t)$ and $R_j(t)$, thereby making coexistence more likely.

Although we have only illustrated this with special cases, in general the metric $A_{ij}A_{ji}$ is monotonically related to both the ratio of inter- to intraspecific seedling competition coefficients, $\alpha_{ij}\alpha_{ji}/(\alpha_{ii}\alpha_{jj})$, and the degree of synchrony in recruitment variation between species, ρ (Fig. 4). One way of interpreting $A_{ij}A_{ji}$ is to recognize that this product corresponds to a range of values of mean recruitment rates that allow coexistence (Appen-

dix A); the smaller the value of $A_{ij}A_{ji}$, the greater the range of values of \bar{R}_j/\bar{R}_i that allow coexistence (Appendix A; Fig. A1.1). Thus, quantifying the competitive effect of one species on another using $A_{ij}A_{ji}$ provides a measure of the ease of coexistence.

These results are a special case of the more general set of models and tools to link fluctuating population dynamics to coexistence (Chesson 1994, 2003). For example, Eq. 5 is essentially identical to Eq. 13 in Chesson (2003) for the same special case. Nonetheless, rather than starting our analyses with the general case, instead we have started with our specific model tailored for tropical forests, sacrificing generality in order to simplify the presentation.

Quantifying the storage effect at BCI

We calculated $A_{ij}A_{ji}$ for each pair of species in the 28-species subset for which we have seedling establishment data, setting $R_i(t) = g_i(t)$. For these calculations, we set all $\alpha_{ij} = \alpha_{ii} = 1$; adding seedling resource partitioning (setting $\alpha_{ij} < 1$) will further decrease the values of $A_{ij}A_{ji}$, although the proportional reduction of $A_{ij}A_{ji}$ by the storage effect remains roughly the same (results not presented). For the collection of 28 species, all values of $A_{ij}A_{ji}$ are distributed between 0 and 0.8, with an average of 0.35 (Fig. 5A). This represents a strong overall decrease in interspecific competition relative to intraspecific competition.

To expand the analyses to all 108 species for which we have seed production data, $r_i(t)$, but not seedling establishment rates needed to estimate $g_i(t)$, we calculated $A_{ij}A_{ji}$ assuming $R_i(t) = r_i(t)$. We did this first for the subset of 28 species so that we could see the potential effects of ignoring species-specific germination and seedling establishment rates. For the subset of 28 species, the values of the $A_{ij}A_{ji}$ were lower using $R_i(t) = r_i(t)$ than $R_i(t) = g_i(t)$ (mean of 0.26 vs. 0.39, respectively; Fig. 5B). Thus, the inclusion of more information on seedling recruitment rates generally has

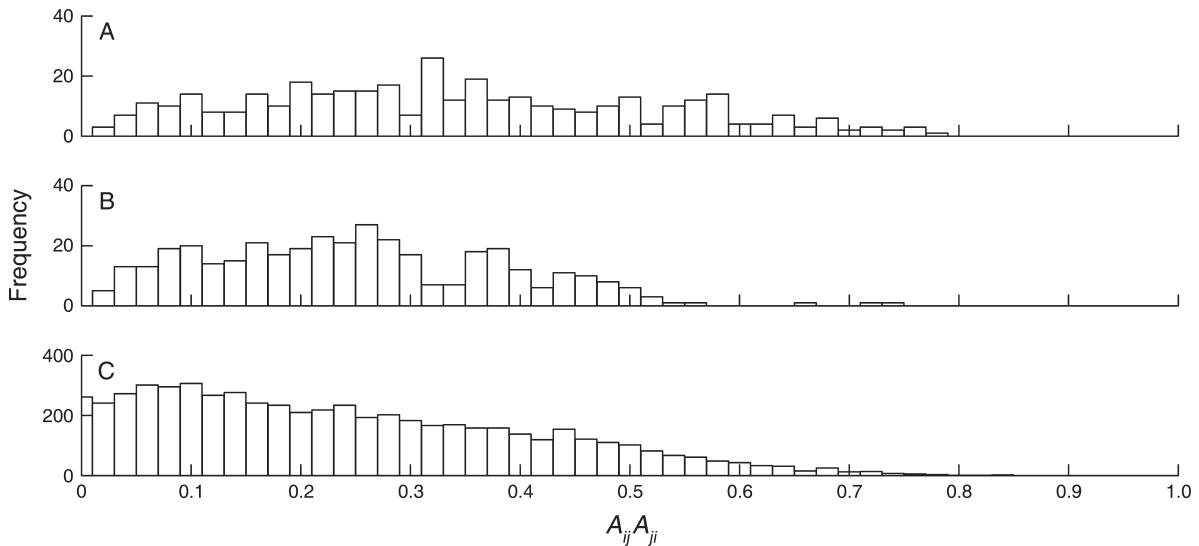


FIG. 5. Frequency distributions of competition coefficients calculated for (A) the subset of 28 species with $R_i(t)$ defined as per capita annual seedling production, $R_i(t) = g_i(t)$; (B) for the same subset of species with $R_i(t)$ defined as per capita seed production alone, $R_i(t) = r_i(t)$; and (C) for 108 species when $R_i(t) = r_i(t)$.

the effect of increasing $A_{ij}A_{ji}$. This occurs because some species experience strong negative intraspecific density dependence in the transition from seed to seedling (Wright et al. 2005). With negative density dependence, the magnitude of recruitment during large fruiting events is reduced, thereby reducing the benefit of good environmental conditions to otherwise rare species. The effect of negative density dependence can be seen from Eq. 5; decreasing the maximum values of $R_i(t)$ in a nonlinear way (e.g., according to the power functions used to model the seed-to-seedling transition in Wright et al. [2005]) causes the variance in $R_i(t)$, σ_i^2 , to decrease. This will in turn cause A_{ij} to increase.

For the entire 108-species data set using $R_i(t) = r_i(t)$ (Fig. 5C), the mean value of $A_{ij}A_{ji} = 0.25$ is similar to that of the 28 species subset with $R_i(t) = r_i(t)$ (0.26). Although the 28 species subset contains species that are relatively abundant and thus well represented in both seed and seedling data, the 108-species data set contained a greater number of rare species. Small sample sizes and the consequent sampling error could lead to overestimates of fruiting asynchrony, because sampling error would introduce variability that is uncorrelated among species. However, this would be expected to produce a higher mean value of $A_{ij}A_{ji}$ for the larger data set, which was not the case. We further explored the possibility of sampling error causing overestimates in asynchrony by examining the association between the pairwise synchrony in seed production between species and their mean abundances; the absence of the expected association (rare species have greater asynchrony) suggests little effect of sampling error on our results.

Arguing from the 28 species, estimates of $A_{ij}A_{ji}$, ignoring post-dispersal processes captured by species-

specific seedling recruitment rates should lead to slight overestimates of the importance of the storage effect in facilitating coexistence (Fig. 5B vs. 5A). Nonetheless, this analysis still provides a useful first approximation of the potential importance of the storage effect in the absence of detailed seed-to-seedling transition data.

The storage effect and phylogenetic similarity

We obtained the high-resolution phylogenetic tree for 51 of the 108 species from Kress et al. (2009) that was constructed from DNA barcodes. We computed species similarities as the shared branch lengths between species. Under the assumption that evolution occurs in a Brownian motion fashion, in which continuous-valued traits increase or decrease in magnitude with equal probability through evolutionary time, the shared branch lengths of species on the phylogenetic tree are proportional to the covariance in trait values between species (Martins and Hansen 1997, Garland and Ives 2000). Therefore, the resulting covariance matrix computed from the phylogeny gives a measure of phylogenetic similarity among species. Because the DNA barcode phylogeny is not ultrametric (i.e., the tips are not contemporaneous), we converted the covariance matrix into a correlation matrix so that phylogenetic similarity between species scales between zero (no phylogenetic relationship) and 1 (phylogenetic identity).

The strength of the storage effect, $A_{ij}A_{ji}$, was unrelated to the phylogenetic similarity of species (Fig. 6A); even closely related species could experience large reductions in interspecific competition. This indicates that closely related species do not show strong synchrony in seed production. We also investigated whether there are some species for which the storage effect will be relatively more important. To address this,

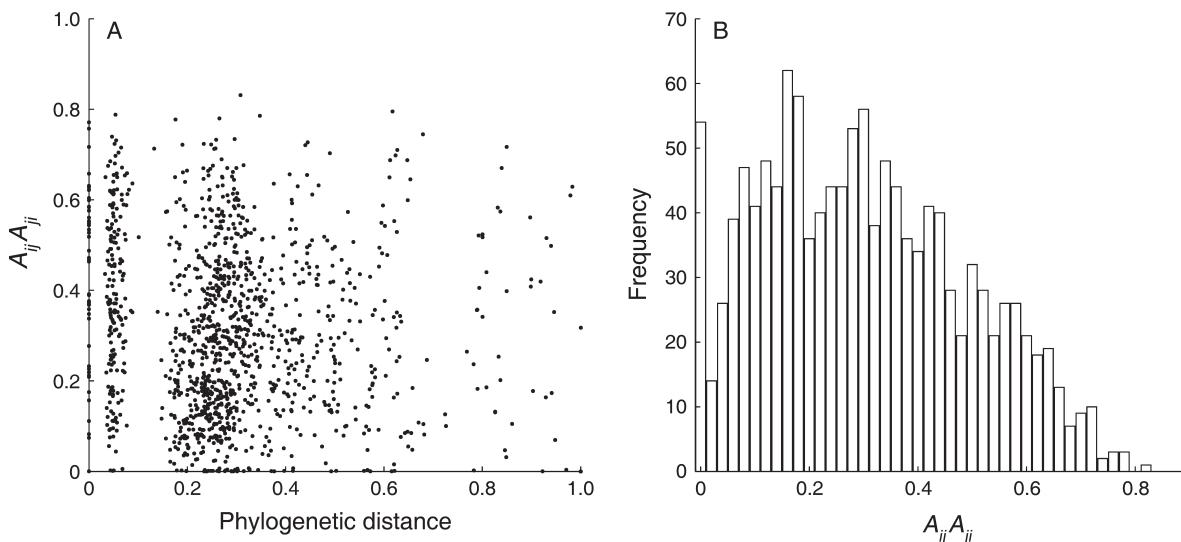


FIG. 6. (A) The relationship between the storage effect measured by $A_{ij}A_{ji}$ and the phylogenetic similarity between species. Phylogenetic similarity was measured by creating a phylogenetic covariance matrix given by the shared branch lengths between species, and then converting this to a correlation matrix so that similarity scales from 0 (no phylogenetic relationship) to 1 (phylogenetic identity). This is done for 51 species with phylogenetic data available. (B) The mean $A_{ij}A_{ji}$ for the same 51 species. No phylogenetic signal was found in the mean values.

we calculated the mean value of $A_{ij}A_{ji}$ for each species and plotted a histogram of these values (Fig. 6B). We tested for phylogenetic signal in mean values of $A_{ij}A_{ji}$ using two metrics, d from the Ornstein-Uhlenbeck model of evolution, and Pagel's λ (Lavin et al. 2008), both of which have values 0 when there is no phylogenetic signal. The estimated values were $d = 0$ and $\lambda = 0.11$, with the 95% confidence interval of λ including 0, indicating no statistically significant phylogenetic signal.

DISCUSSION

We have demonstrated the potentially large role that the storage effect can have in facilitating coexistence for a tropical tree community. The average estimate of competition coefficients $A_{ij}A_{ji}$ was 0.35 for the subset of species with estimates of seed-to-seedling transition rates, and 0.25 for all 108 species when post-dispersal processes were not factored into the calculations of recruitment $R_i(t)$. These results indicate that the observed temporal variability and asynchrony in seed and seedling production translate into large reductions in interspecific competition and corresponding increased likelihoods of coexistence.

In simulations, we found that the storage effect alone is sufficient to allow coexistence of a large proportion of species. However, this does not rule out the importance of other mechanisms such as classical resource partitioning that might also facilitate coexistence. Furthermore, for those species for which the storage effect is not strong enough by itself to allow coexistence, it could nonetheless, in conjunction with classical resource

partitioning, allow coexistence; both classical resource partitioning and the storage effect can act in concert.

The high levels of asynchrony in recruitment underlying the storage effect probably represent species-specific responses to different factors. Several studies have shown that seed production and germination of the BCI tree community are partially synchronized by rainfall and irradiance both within years (Zimmerman et al. 2007) and among years, with among-year patterns corresponding to global climate patterns, i.e., the Southern Oscillations (Wright et al. 1999, Wright and Calderon 2006). Climate anomalies that reduce cloud cover and increase levels of photosynthetically active radiation reaching the forest canopy are associated with increases in seed production in many, but not all, species. This particular climate anomaly coincides with many El Niño events in central Panama. When there are long, multiyear periods without El Niño, the levels of seed production are unrelated among species. When an El Niño event does occur, as in the years 1992 and 1997, many species produce large seed crops within a year. Thus, the level of asynchrony in seed production and establishment depends on both the occurrence of specific environmental events and differences in the sensitivities of species to these events.

Our phylogenetic analysis showed that closely related species were not more likely to experience a weaker storage effect; this occurs because synchronous fluctuations in seed production are not stronger for closely related species. We do not attempt to explain why even closely related species show highly asynchronous levels of seed production. Nonetheless, this result has possibly important consequences for coexistence. Phylogenetical-

ly related species are often assumed to experience greater resource competition (Darwin 1859, Webb et al. 2002, Cavender-Bares et al. 2004), although we recognize that adaptive pressures can lead to divergence of closely related species or convergence of distantly related species (Lawlor and Smith 1976, Kelly and Bowler 2002, Losos et al. 2003). If closely related species did show reduced classical resource partitioning, then coexistence of closely related species would be more difficult. Because the magnitude of the storage effect for the species that we investigated is independent of phylogeny, the storage effect could explain the coexistence of species that would not be expected to coexist through classical resource partitioning.

Our model contains basic features thought to be important in tropical tree dynamics. In the model there is no seed dormancy. Although many pioneer species produce seeds that have dormancies greater than a year (Dalling et al. 2002, Dalling and Brown 2009), seed dormancy is rare among shade-tolerant species (Garwood 1983, Vazquez-Yanes and Orozco-Segovia 1993, Sautu et al. 2007) that we analyzed. The model assumes that heterospecific seedlings have a negative, density-dependent effect on one another prior to establishment and thus allows for competition-driven coexistence mechanisms (e.g., classical resource partitioning) within this early stage of growth. Negative density dependence has been observed for individual species by directly monitoring annual seedling survival (De Steven and Wright 2002) and has been measured more broadly for a subset of 51 species using documented rates in the seed-to-seedling transition by Harms et al. (2000). Once seedlings have passed through a competitive bottleneck, however, survival is high (De Steven and Wright 2002), even though intraspecific density dependence still occurs (Comita et al. 2010, Mangan et al. 2010). Finally, the model assumes that replacement of adult trees involves lottery competition among saplings to fill gaps in the canopy. We assume that this is a pure lottery, in which every sapling regardless of age or species has the same chance of winning. Although our model is necessarily an approximation of tropical forest dynamics, it nonetheless captures essential features driving the replacement of tree species.

We have used the model primarily to make comparisons between the storage effect and resource partitioning as a mechanism facilitating coexistence. Our metric $A_{ij}A_{ji}$ translates patterns of asynchronous seed production into the population-level strength of interspecific relative to intraspecific competition. It similarly extrapolates classical resource partitioning in seedling competition to the population level. Although longitudinal cohort studies of seedling/sapling survival suggest strong apparent competition in early seedling establishment, we do not have estimates of the strength of interspecific relative to intraspecific competition. Therefore, we cannot make an explicit comparison between the strength of the two coexistence mechanisms for this

forest system. Nonetheless, the degree of asynchrony in annual seed production is sufficiently large that the corresponding decreases in $A_{ij}A_{ji}$ argue for an important contribution of the storage effect to coexistence regardless of the strength of classical resource partitioning.

Our study joins other work supporting a widespread role for the storage effect. Specific features of communities that lead to the storage effect are common, suggesting that it may be important in many more systems. For example, Angert et al. (2009) found that fluctuations in the density of germinating seeds in a desert annual community are tied directly to a functional trade-off between rapid photosynthesis rates and drought tolerance, suggesting a general mechanism that can lead to the storage effect. Adler et al. (2006) demonstrated that climate variability, when it is coupled to growth rates, can lead to the storage effect in perennial plants. However, Adler et al. (2009) found that the presence of species-specific responses to temporal variation was not enough to promote coexistence in a sagebrush steppe community, because competition itself did not covary with environmental response. This emphasizes the importance of meeting all conditions for the storage effect simultaneously.

Our general approach has been to measure the storage effect in a way that translates into population-level alpha competition coefficients, $A_{ij}A_{ji}$. While this approach is not as general as that provided by Chesson's formalism (Chesson 1994, 2003), it nonetheless has the intuitive appeal of making the storage effect easily comparable to classical resource partitioning. Furthermore, rather than summarize the net effect of competition by averaging across the entire community (Angert et al. 2009), we have instead retained the identity of species involved in pairwise interactions. This allowed us to ask whether phylogenetically related species are less likely to experience a strong storage effect. Our approach easily can be applied to other tropical and temperate forests. Comparison among different forests could reveal whether the storage effect is ubiquitous and strong, and whether its magnitude varies consistently among different forest types.

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SUPPLEMENTAL MATERIAL

Appendix A

Comparison of coexistence in the forest dynamics model under different parameter values (*Ecological Archives* E093-198-A1).

Appendix B

Pairwise correlations in annual seedling recruitment for 28 species at Barro Colorado Island, Panama (*Ecological Archives* E093-198-A2).

Appendix C

Number of species persisting in simulations of the forest dynamics model for a 28-species subcommunity (*Ecological Archives* E093-198-A3).

Appendix D

Derivation of the invasion rates, D_{ij} , given in Eq. 3 (*Ecological Archives* E093-198-A4).