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SYNTHESIS

Community Synchrony in Seed Production is Associated With Trait Similarity and Climate Across North America

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ABSTRACT

Mast seeding, the synchronous and highly variable production of seed crops by perennial plants, is a population-level phenomenon and has cascading effects in ecosystems. Mast seeding studies are typically conducted at the population/species level. Much less is known about synchrony in mast seeding between species because the necessary long-term data are rarely available. To investigate synchrony between species within communities, we used long-term data from seven forest communities in the U.S. Long-Term Ecological Research (LTER) network, ranging from tropical rainforest to boreal forest. We focus on cross-species synchrony and (i) quantify synchrony in reproduction overall and within LTER sites, (ii) test for relationships between synchrony with trait and phylogenetic similarity and (iii) investigate how climate conditions at sites are related to levels of synchrony. Overall, reproductive synchrony between woody plant species was greater than expected by chance, but spanned a wide range of values between species. Based on 11 functional and reproductive traits for 103 species (plus phylogenetic relatedness), cross-species synchrony in reproduction was driven primarily by trait similarity with phylogeny being largely unimportant, and synchrony was higher in sites with greater climatic water deficit. Community-level synchrony in masting has consequences for understanding forest regeneration dynamics and consumer-resource interactions.

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1 | Introduction

Mast seeding, defined as the synchronous and highly variable production of seeds across years by a population of perennial plants (Bogdziewicz et al. 2024; Janzen 1976; Kelly 1994; Silvertown 1980), is common across a wide range of species (Kelly and Sork 2002; Koenig and Knops 2000; Pearse, LaMontagne, and Koenig 2017; Pearse et al. 2020). The booms and busts of seed production associated with mast seeding, with large pulses of reproduction by plants, have a major effect on the regeneration of trees and a cascading effect across trophic levels through driving the population dynamics of seed-eating mammals and birds, and zoonotic disease (Jones et al. 1998; Kelly, Koenig, and Liebhold 2008; Ostfeld and Keesing 2000; Peters, Macdonald, and Dale 2006; Rossi et al. 2012).

The two predominant evolutionary hypotheses to explain mast seeding are the predator satiation hypothesis and the pollination efficiency hypothesis. Both operate through an 'economy of scale' in which synchronous, large reproductive events lead to higher survival of viable seeds (Norton and Kelly 1988; Pearse, Koenig, and Kelly 2016). The predator satiation hypothesis argues that poor seed crops limit granivorous populations such that during a high-abundance 'mast crop' a large fraction of seeds survive to potentially regenerate (Janzen 1971). A meta-analysis of the predator satiation hypothesis found that mast seeding led to satiation of invertebrate but not vertebrate seed predators, and that satiation was more effective in temperate and boreal latitudes, and indicated that seed losses may be more reduced when plant communities had lower diversity (Zwolak, Celebias, and Bogdziewicz 2022). The pollination efficiency hypothesis refers to positive density dependence in pollination, such that mast-seeding events are associated with greater conspecific synchrony in reproduction and higher pollination, and thus a higher rate of fertilisation (Allen and Platt 1990; Bogdziewicz et al. 2020; Rapp, McIntire, and Crone 2013). Pollination efficiency has been most widely cited for wind pollinated species in the mast seeding literature (Kelly, Hart, and Allen 2001), but density dependent pollination efficiency is also common in animal-pollinated plants (Ghazoul 2005).

Most mast seeding studies typically focus on a single species (Wang et al. 2017). Single-species studies have provided insight into the role of weather conditions as proximate drivers of reproduction (Kelly et al. 2013; Krebs et al. 2012), levels of intraspecific synchrony (Koenig and Knops 2000; LaMontagne et al. 2020; LaMontagne and Boutin 2007; Liebhold et al. 2004; Moreira et al. 2014), and the effectiveness of predator satiation (Fletcher et al. 2010; Kelly et al. 2008; Soler et al. 2017). Studies that include multiple taxa often either analyse species-specific relationships with environmental variables (Bogdziewicz et al. 2023; Chen et al. 2018; Koenig et al. 2016; LaMontagne et al. 2021), or have been used to ask questions about the broad patterns and drivers of mast seeding over space and time at continental to global scales (Hacket-Pain et al. 2022; Koenig and Knops 2000; Pearse, LaMontagne, and Koenig 2017). These global mast-seeding analyses have primarily focused on variability, with the exception of (Qiu et al. 2023) who explored intraspecific patterns of mast-seeding synchrony. Analyses of synchrony in mast seeding among species within a community are rare, in part because long-term seed production data on co-located species are rare (Koenig and Knops 2013, 2014; Wang et al. 2017); however, synthesis of multiple long-term data sets provides an opportunity to close this gap in our knowledge and clarify the extent to which community synchrony in plant reproduction may be ecologically important.

A starting place for this is to ask, if there is no selective benefit to community synchrony, how much synchrony between unrelated species might we expect in the same site, and if this is not zero, what non-selective factors could drive that pattern? A mathematical null hypothesis is simple to test: is the correlation between pairs of time series of seeding zero? However, two species may show modest positive synchrony for non-adaptive reasons because they inhabit the same variable environment. A Moran effect (Moran 1953) null hypothesis would expect that 'good' years are largely productive for most plant species, with a species-specific development delay. It is challenging to define how much the correlation of time series should depart from this in order to be significant, since selection may act to increase or decrease synchrony depending on the driving factors.

Multiple hypotheses based on evolutionary or ecological mechanisms predict conditions under which mast-seeding synchrony among species should be synchronous, uncorrelated, or even anti-synchronous. At the evolutionary level, the selection pressure of granivory is unlikely to operate independently among plant species, and thus high levels of synchrony among species would facilitate predator satiation among generalist seed predators (Curran and Leighton 2000; Schauber et al. 2002; Shibata, Tanaka, and Nakashizuka 1998). The effects of synchrony in seed production across species could thus have cascading ecological consequences on consumers and plant populations. Alternatively, if there is competition for pollinators in a primarily animal-pollinated community, relatively low synchrony may be predicted.

Similarity of plant traits that relate to life-history strategies, reproduction, or belowground resource acquisition (Appendix S1: Table S1) could predict the direction and strength of synchrony observed in mast-seeding patterns across species within a community. Species-level traits such as pollination vector and the length of time for seed development are related to measures of temporal variability in mast seeding (LaMontagne et al. 2021; Qiu et al. 2023). Higher similarity in traits among species could also promote synchrony between species through the potential for similar patterns of resource allocation (e.g., leaf longevity, growth form, shade tolerance and mycorrhizal association) or reproduction (e.g., fleshy fruit, seed mass and sexual system), or anti-synchrony could result from competition for environmental resources. Species with higher trait similarity are also likely to respond more similarly to environmental conditions, resulting in synchrony between populations in a community (Rocha et al. 2021). Climatic conditions can influence synchrony through reproductive vetoes (Pesendorfer et al. 2016), that may be more frequent for species that occupy habitats prone to drought (Wion et al. 2021). Therefore, sites with more extreme climate conditions, such as more arid regions with high water deficits or boreal and subalpine regions with high seasonality and short growing seasons, may promote interspecific synchrony in reproduction as a consequence of greater or more frequent climatic constraints through environmental vetoes that synchronise reproduction across the community. Pollinator and frugivore diversity is greater at lower latitudes (Fleming, Breitwisch, and Whitesides 1987; Ollerton 2017). Thus, in less environmentally extreme habitats, there may be a higher likelihood of having both animal pollinators and seed dispersers available, with lower levels of synchrony in reproduction among plant species to maintain a high abundance among those animal populations.

To investigate synchrony in woody plant reproduction between species and test how it is related to similarity in species traits and climate, we synthesised and analysed data from seven U.S. Long-Term Ecological Research (US-LTER, hereafter, LTER) forest sites spanning tropical rainforest to boreal biomes (Figure 1). These data included long-term records of interannual variation in woody plant reproduction between 10 and 58 years in length. We asked: (Q1) what is the direction and magnitude of synchrony between co-occurring species in woody-plant reproduction?, (Q2) how does synchrony vary among LTER sites and how is it related to climate variation across LTER sites?, (Q3) is synchrony associated with shared species attributes and phylogenetic relatedness? and (Q4) what is the relative contribution of climate, traits and phylogeny to variation in synchrony across the range of LTER sites and species?

If there is an advantage to synchronous patterns of reproduction between species due to shared seed predators, shared pollinators, shared plant traits or phylogeny, we predicted high correlations in pairwise time series of seed production between species. Conversely, if there is no advantage to synchronous seed production or if traits differ across species, we predicted that cross-species correlations in seed production would generally be non-significant, asynchronous, or anti-synchronous. We also predicted that patterns in synchrony would vary among LTER sites due to differences in community composition and environmental conditions. We predicted that LTER sites in more extreme environments, specifically sites with a greater climatic water deficit or lower actual evapotranspiration, would have greater synchrony in reproduction. We predicted that species pairs with greater trait similarity and higher phylogenetic relatedness would have higher synchrony in reproduction between species.

2 | Materials and Methods

2.1 | Database Assembly and Inclusion Criteria

Our synthesis examined synchrony in reproduction between woody-plant species that co-occur within U.S. LTER sites. The LTER network was established in 1980 with the goal of

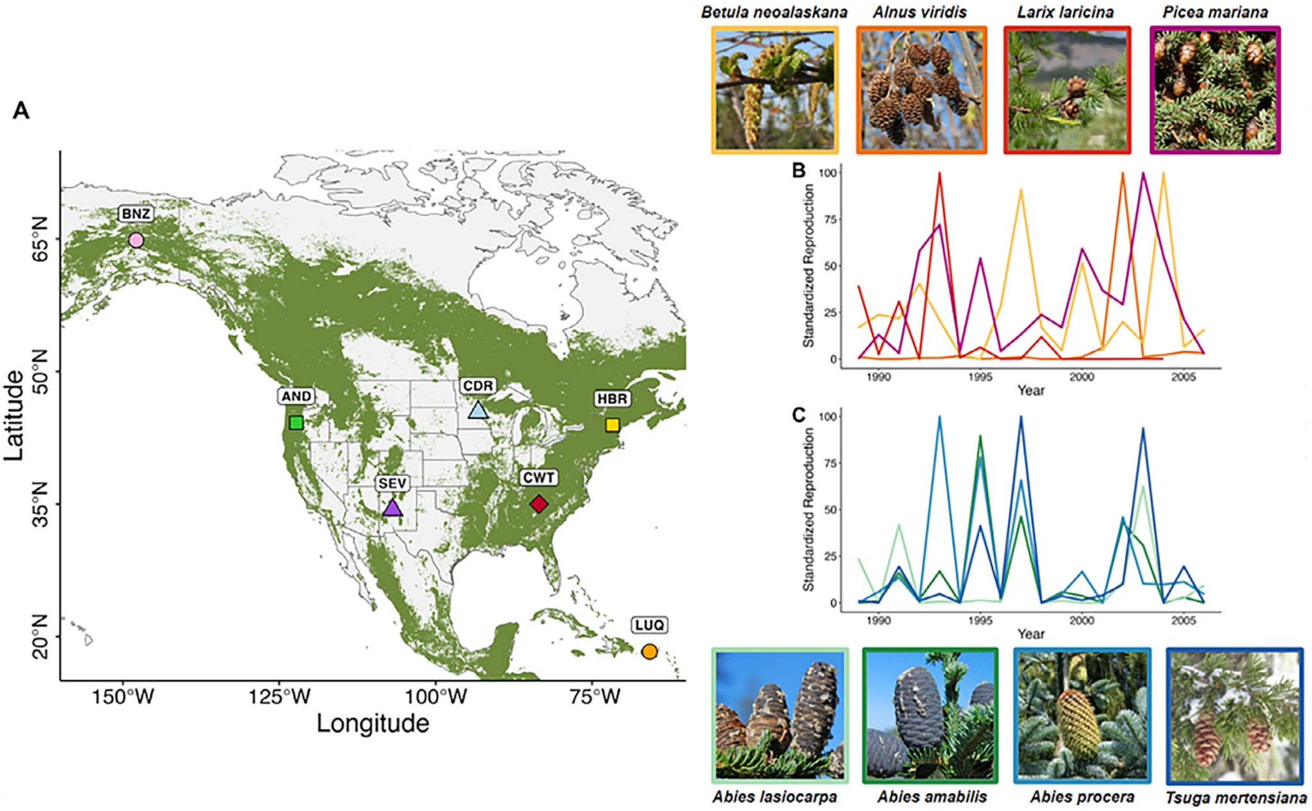

FIGURE 1 | Seed production data for two Long-Term Ecological Research (LTER) plots that differ in the degree of community-level synchrony. (A) Location of the LTER sites included in the synthesis overlaid on a map of forested area in North America shown in green (USGS EROS 2018). (B) Data from Bonanza Creek (BNZ—site FP5A); show little (and slightly negative) cross-species synchrony (minimum $r_S = -0.38$, maximum $r_S = 0.18$), while (C) the data from Andrews (AND—Mosquito Lakes) exhibit high reproductive synchrony (minimum $r_S = 0.57$, maximum $r_S = 0.79$). Reproductive counts for each species have been standardised to the range (0–100) for that species observed over 1989–2006. Images of reproductive structures are listed with the names of each species; border colours of images correspond to colours used in the time series plot. Photograph credits: J. Johnstone for BNZ; J. Bisbee, J. Grimshaw and J. Sutton, American Dendrological Society, Trees and Shrubs Online (www.treesandshrubsonline.org) for AND.

TABLE 1 | Summary of data used in the synthesis of cross-species synchrony in woody plant reproduction with seven Long-Term Ecological Research (LTER) sites.

LTER site[a]	Biome	# Species	# Variable pairwise traits	Mean (min–max) years overlap for synchrony	# Plots	Mean CWD (mm) (min–max)
CWT	Deciduous forest	17	12	23.9 (19–29)	7	40.8 (28.1–50.3)
LUQ	Tropical rainforest	62	11	20.2 (10–30)	1	54.5 (na)
HBR	Deciduous forest	3	6	26.1 (23–28)	10	55.6 (na)
CDR	Savanna and tallgrass prairie	4	3	17.0 (17–17)	1	119.3 (na)
BNZ	Boreal forest	6	6	22.3 (15–34)	8	149.2 (145.7–151.3)
AND	Coniferous forest	10	5	41.0 (13–58)	15	206.3 (75.7–286.7)
SEV	Desert and grassland	3	12	20.2 (20–21)	2	1223 (1193–1253)
Total		103	12	—	44	—

Note: Eleven species traits were assigned for each species, plus phylogenetic similarity between species pairs; the # variable pairwise traits column indicates the number of traits (out of a maximum of 12; including phylogenetic similarity) that varied across species pairs at each LTER site. Sites are ordered in the table by mean climatic water deficit (CWD), which shows the average 30-year normal CWD across all plots within each LTER site (parentheses denote the range of CWD values across the plots). For LTER sites where there was only one plot or where all the plots were located within the same climate site, then no range (i.e., 'na') is provided. LTER sites are ordered by increasing Climate Water Deficit (CWD). Biome data are from Jones and Driscoll (2022).

[a] Full names of LTER sites: AND = H.J. Andrews Experimental Forest; BNZ = Bonanza Creek; CDR = Cedar Creek; CWT = Coweeta; HBR = Hubbard Brook Experimental Forest; LUQ = Luquillo; SEV = Seviletta.

studying ecological processes across a broad range of ecosystem types (Kratz et al. 2003), and we focused our data synthesis on seven LTER sites that collected long-term data on woody plant reproduction (Table 1, Figure 1). These LTER sites included H.J. Andrews Experimental Forest (AND), Bonanza Creek (BNZ), Cedar Creek (CDR), Coweeta (CWT), Hubbard Brook Experimental Forest (HBR), Luquillo (LUQ) and Seviletta (SEV). We used LTER plant reproduction datasets published in the Environmental Data Initiative repository (https://edirepository.org/) (Fahey and Cleavitt 2021; Franklin and Schulze 2023; Van Cleve et al. 2022; Zimmerman 2022; Zlotin 2016) and other data associated with LTER sites (Clark, LaDeau, and Ibanez 2004; Koenig and Knops 2014). Two methods of seed production data collection were implemented at LTER sites: either direct individual-based counts of reproductive structures (cones, fruits and seeds) on marked individuals (AND, CDR and SEV), or seed trap studies that sample seeds from the woody plant community (BNZ, CWT, HBR and LUQ). The criteria we applied for including data in this synthesis were: (i) woody plant reproduction data (i.e., trees, shrubs and liana) at an LTER site included multiple co-occurring species; (ii) taxa were identified to species; (iii) the time series of reproductive counts included a minimum of 10 continuous years of data collection; (iv) sampling units (trees or seed traps) were replicated within LTER sites; and (v) geographic coordinates were available for all plots sampled within an LTER site to allow for climate data to be obtained. Data that originated from counts on individual trees were included only for years when counts were conducted on a minimum of 10 trees for a species. Datasets were aggregated to the stand level (here called 'plots') within LTER sites for each species and calendar year (mean reproduction per tree or mean seeds per trap). In consultation with LTER data leads, we excluded seed trap datasets for species that were rare at the site and/or were rarely captured in the seed traps, such that separation of seed production from sampling noise would not be possible. We screened tree count datasets for consistency of sample sizes over time, and plots where samples declined below 10 individuals were not included in analyses. Note that due to limitations in available data and losses of data in the filtering process, some LTER sites had woody-plant communities that were not fully represented. For instance, acorn and hickory nut data at CWT were identified only to the genus level (*Quercus* and *Carya* spp.), and therefore those data were filtered out prior to data analysis.

2.2 | Data Harmonisation and Filtering

In the final database used for this synthesis, a single time series was a set of seed production data (count or seed trap data) ordered across years, for one species at one plot. We used nonparametric correlations (Spearman rank) between the time series for species pairs to avoid having extreme seed production years unduly affect estimates of cross-species synchrony. We did not detrend time series in order to avoid having the beginning or end of a time series disproportionately affect trends. We performed all data wrangling, statistical analysis and data visualisation operations using R version 4.2.2 (R Core Team 2023). All R packages are cited in Appendix S1, the data used in these analyses are available in LaMontagne et al. (2024), which were originally compiled in a data paper (Nigro et al. in press).

2.3 | Trait and Climate Data

Across all LTER sites, a total of 103 woody plant species (Appendix S1: Table S2) met the inclusion criteria and we compiled data on these species for 11 traits. These traits included: (i) leaf longevity (deciduous and evergreen), (ii) dispersal syndrome (abiotic, endozoochory, and synzoochory), (iii) fleshy fruit (yes and no), (iv) growth form (tree, shrub, and liana), (v) mycorrhizal association (arbuscular [AM], ectomycorrhizal [EM], ericoid, and none), (vi) pollinator (animal and wind), (vii) seed bank (yes and no), (viii) seed development time (from bud differentiation to seed maturity: 1, 2, and 3 years), (ix) sexual system (dioecious, hermaphrodite, monoecious, and polygamo-dioecious), (x) shade tolerance (intolerant, intermediate, and tolerant) and (xi) seed mass (mg; continuous variable) (Appendix S1: Table S1). Broadleaf and needleleaf traits were not included as we only had one needleleaf-deciduous species (*Larix laricina*; the remainder were needleleaf-evergreen) and therefore deciduous-evergreen provided more variation across species. We extracted trait data from the TRY database (Kattge et al. 2011, 2020) and from the literature (Appendix S2). We also used phylogenetic relatedness between species, based on Zanne et al. (2014); 93 of our species matched exactly their phylogeny. Of the remaining 10 species, eight matched a genus on the Zanne et al. (2014) phylogeny, and are placed as polytomies at the genus level. The remaining two species did not match at the genus level, and they were placed as polytomies at the family level.

We performed nonmetric multidimensional scaling (NMS) across species on trait status (i.e., either 1 or 0 for each trait level) using the Jaccard distance measure (Jaccard 1912). We also included the natural logarithm of seed mass as the only non-binary input trait. We then fitted vectors for each trait to overlay trait-specific arrows indicating how particular traits were related to dissimilarity among points. Species found at more than one LTER site were included at all locations and resulted in directly overlapping points in the ordination. To maintain consistency with the NMS, overall trait similarity between pairs of species was calculated based on the Jaccard distance between a vector of pairwise shared traits (0 = different, 1 = same), difference in log(seed mass), and phylogenetic distance between the two species; continuous variables were also scaled between 0 and 1.

We extracted climate summaries based on the geographic coordinates of each of 44 plots across the LTER sites from TerraClimate (Abatzoglou et al. 2018), a global gridded monthly climate dataset with a resolution of 4 km, from 1958 to 2022. We summed monthly data for each year and then averaged the data across all years to provide a mean annual climate summary at each plot. Climate variables used in the analyses included two indices that combine temperature and precipitation: actual evapotranspiration (AET) and climate water deficit (CWD). Both AET and CWD are biologically meaningful measures of plant water balance and, collectively, are strongly correlated with vegetation distribution (Stephenson 1990). Areas of high AET represent plots with high availability of both water and energy and are strongly associated with plant productivity (Rosenzweig 1968; Stephenson 1990). An indicator of drought stress, CWD represents the amount of water by which potential evaporation exceeds actual evapotranspiration (Stephenson 1998). We log-transformed CWD for the analysis to compensate for the long-tailed distribution of this variable in our dataset. When multiple plots at an LTER site were located within the same 4 km climate grid zone the plots were pooled into single 'climate sites' for analysis (10 plots were grouped into a single climate site at HBR, eight plots were grouped into two climate sites at BNZ, seven plots were grouped into two climate sites at CWT).

2.4 | Analyses

We quantified synchrony in reproduction between species within woody-plant communities by calculating pairwise Spearman correlations for each pair of seed production time series for species within plots at LTER sites that overlapped for a minimum of 10 years; we refer to this as 'cross-species synchrony'. Temporal patterns of mast seeding are driven proximately by weather conditions at local to regional (air mass) scales, which vary spatially at a regional scale (Koenig 2002; LaMontagne et al. 2020; Wion et al. 2021), and synchrony is considered for species pairs within, but not across, LTER sites. To test if local cross-species synchrony was broadly positive or negative (i.e., if the mean of all correlations was significantly different from 0) across all LTER sites, we used permutation tests. We created random permutations of the time series to serve as our null distribution; for each species-pair, we randomised the order of seed production values in one time series and calculated a second correlation coefficient (i.e., the null correlation). We performed this randomisation and re-calculation operation 1000 times to generate a distribution of the random permutations. To assess how synchronous species pairs were within LTER sites, for each site we conducted a perANOVA (permutation ANOVA) with residual randomisation in the permutation procedure (RRPP) to assess the difference between observed correlations and the null model predictions based on permutation of the time series (Collyer and Adams 2018, 2023). This constitutes a test of the mathematical null hypothesis, that cross-species synchrony is zero when one of the datasets is completely randomised.

We tested for the influence of climate drivers on cross-species synchrony in reproduction by modelling the effects of two climate covariates using 30-year means for annual log-CWD and annual AET. We fit linear mixed effect models with pairwise correlations as the response variable, with the two climate variables (CWD and AET) as fixed effects, and climate site and species pair as random intercepts.

We tested for relationships between overall trait similarities for species pairs based on the Jaccard distance and cross-species synchrony using linear models for all data together and separately for species pairs within each of the LTER sites. Then, to assess the relative importance of trait similarity and phylogenetic distance on cross-species synchrony, we used multiple regression on distance matrices (MRM) using the 'ecodist' R package (Goslee and Urban 2007). All 'distance' variables were converted to similarity indices (Koenig et al. 2017). Cross-species synchrony was the response variable, and we transposed each of the 12 explanatory variables to range from 0 to 1; these included trait similarity for each species pair (Boolean scale; 0 = dissimilar, 1 = similar), seed mass similarity and phylogenetic similarity. The coefficient of the effect size and *p*-value were based on 1000 permutations of the data. While the structure of MRM does not allow for random effects (LTER site and species-pair could be regarded as random effects), the MRM analysis was used instead of linear-mixed effects models because the latter would not have accounted for the matrix-style structure of the data. We conducted analyses for all sites combined, and the significance of variables within the full model with all variables is reported. We also did sensitivity analyses, leaving out one LTER site at a time to evaluate the effect of individual sites on the overall results. MRM analyses were also conducted for each LTER site separately (Appendix S1: Table S3, Figures S1–S7).

For each trait, we tested for significant differences in cross-species synchrony based on actual trait combinations (e.g., for pollination vector, when a species pair was both wind pollinated, compared to both animal pollinated, compared to one species being wind pollinated and the other animal pollinated) using perANOVAs using the RRPP package (Collyer and Adams 2018, 2023).

Finally, we addressed the contribution of three fixed effects (i) site-level climate variables (AET and log-CWD), (ii) overall trait similarity and (iii) phylogenetic similarity to synthesise our long-term patterns of cross-species synchrony across a wide geographic range of LTER sites that span a wide range of biomes. We created a single linear mixed model with climate site and species pair as random effects using the 'lme4' package (Bates et al. 2015). All explanatory variables were scaled and centered for this analysis.

3 | Results

The seven LTER sites used in this synthesis included a variety of habitats from semi-arid woodland to tropical, temperate and boreal forests, ranging over 46.5° of latitude and 82° of longitude (Figure 1). These sites spanned climate conditions with mean annual precipitation ranging from 300 to 2716 mm and mean annual temperature ranging from −2.9°C to 21.8°C (Table 1). Mean number of years that time series overlapped for co-occurring species ranged from 17 to 41 years and included 2104 pairwise values of within LTER-site cross-species synchrony (Appendix S1: Table S4). The 103 woody plant species included trees, shrubs and lianas, with a range of attributes (Appendix S1: Tables S1 and S2).

3.1 | Levels of Cross-Species Synchrony

Over all the data, the distribution of synchrony in annual reproduction between woody plant species was greater than expected by chance (Figure 2; $p = 0.001$) and co-occurring species pairs showed levels of synchrony that ranged from highly synchronous to anti-synchronous (mean = 0.29, median = 0.31, range: −0.72 to 0.89). Within LTER sites, cross-species synchrony was uniformly positive at three LTER sites (SEV, AND and HBR) (Figure 3A; Appendix S1: Table S4). At the other four sites (BNZ, CDR, LUQ and CWT), cross-species synchrony was variable and spanned a range of negative to positive values. With the exception of CDR, cross-species synchrony was significantly more positive than expected compared to randomised time series (Figure 3A; Appendix S1: Table S4).

Cross-species synchrony in woody plant reproduction increased significantly as log-CWD increased (slope = 0.16 ± 0.06 [1 SE], $p = 0.03$), such that more arid areas had greater synchrony in seed production (Figure 3B). For plots with mean annual CWD >160 mm, synchrony in woody plant reproduction was always positive. There was no significant relationship between cross-species synchrony and AET (slope = 0.000 ± 0.000, $p = 0.44$).

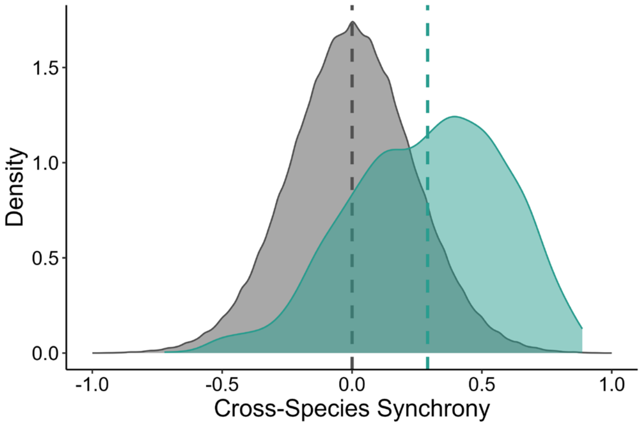

FIGURE 2 | The distribution of values for local-level cross-species synchrony (Spearman rank correlation coefficient) in woody plant reproduction for all plots at Long-Term Ecological Research (LTER) sites (green; $n = 2104$ cross-species correlations) is skewed towards more positive values compared to random permutations of the pairwise time series (grey). Dashed lines represent the means for each distribution.

3.2 | Trait Similarity and Phylogenetic Relatedness

Species in our synthesised dataset (Appendix S1: Table S2) covered a wide range of trait space (Figure 4A). Trait variability within an LTER site depended both on the number of species represented and the variation across those species; CWT (17 species) and LUQ (62 species) represented distinct areas of trait space, and these sites spanned the greatest range in trait variability, from species pairs that were dissimilar to species pairs that were very similar in their traits (Figure 4A,B; Appendix S1: Table S1). In contrast, SEV had only three species, and they were all relatively dissimilar with respect to traits, while AND had 10 species that were relatively similar in traits. Across the entire LTER dataset, from a linear model we found a significant positive relationship between overall trait similarity and cross-species synchrony ($F = 231$, $p = 0.001$; Figure 4B). For the analysis of each LTER site separately, the relationship between overall pairwise trait similarity and synchrony was significantly positive at two LTER sites (LUQ [$F = 80$, $p = 0.001$] and AND [$F = 34$, $p = 0.001$]) and significantly negative at HBR ($F = 6.5$, $p = 0.025$; Appendix S1: Figure S8).

Traits that were significant predictors of cross-species synchrony had pairwise synchrony values that were significantly different between species that shared the same trait vs. those that did not share the trait. In the full MRM model, when pairs of species within a site shared traits related to leaf longevity, fleshy fruit, pollinator type and mycorrhizal association, they were more likely to have greater synchrony in seed production (Figure 5; Appendix S1: Table S3). For shade tolerance and dispersal syndrome, sharing a trait had a small but significantly negative effect on synchrony. In the overall MRM model, trait similarity in growth form, seed bank, seed development time,

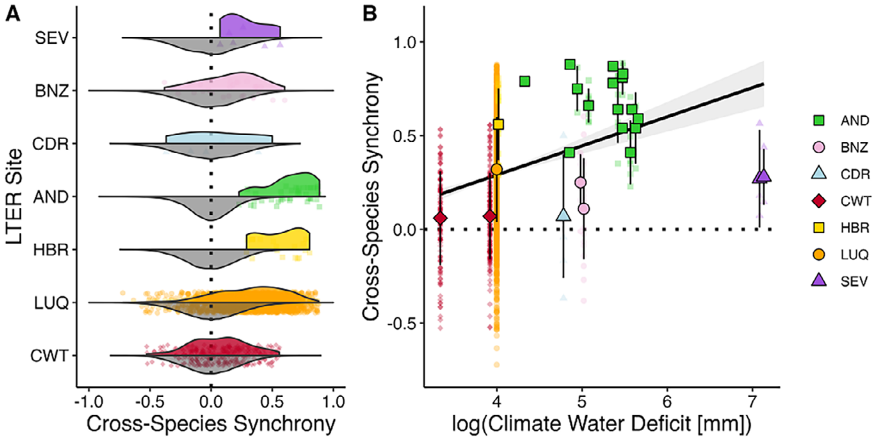

FIGURE 3 | (A) Frequency distribution of local-scale cross-species synchrony in woody plant reproduction (above horizontal lines and in colour, with random permutations of cross-species synchrony below the horizontal lines and in grey) within Long-Term Ecological Research (LTER) sites arranged in order of climate water deficit (CWD). (B) There is a significant positive relationship between log-CWD and local-scale cross-species synchrony. Error bars around points indicate standard deviation. Colours for LTER sites in panel B match those in panel A. AND = H.J. Andrews Experimental Forest; BNZ = Bonanza Creek; CDR = Cedar Creek; CWT = Coweeta; HBR = Hubbard Brook Experimental Forest; LUQ = Luquillo; SEV = Seviletta.

sexual system, seed mass, and phylogeny were not significant with respect to synchrony (Figure 5). Looking within an LTER site, the seed development effect (number of years from bud differentiation to seed maturity) showed a positive relationship between shared development time and synchrony in the MRM at two of the three sites that had species pairs with variability in seed development time (AND, CDR; Appendix S1: Table S3). The third site (SEV) showed the same relationship between shared development time and synchrony (Appendix S3) but because multiple traits at SEV varied in the same way, the MRM was unable to distinguish a significant effect in the context of other variables.

The sensitivity analysis conducted by iteratively removing individual sites showed that the results were largely consistent, with a few exceptions (Appendix S1: Table S5). For dispersal syndrome, the sensitivity analysis showed that removing any site except LUQ maintained the significant negative relationship between shared dispersal syndrome and synchrony between species; removing LUQ resulted in no significant effect of dispersal syndrome on synchrony (Appendix S1: Tables S3 and S5). The sensitivity analysis showed that in the absence of CWT or LUQ, shade tolerance was not significant, whereas removing any other single site from the overall dataset retained the negative effect of shared shade tolerance on synchrony (Appendix S1: Table S5). Phylogenetic similarity was not significant in the full MRM model or in most site-level full models (Appendix S1: Table S3); it was a significant predictor in two of the seven LTER site-level models (at HBR and CWT). Sensitivity analysis showed that removing any one site from the MRM analysis did not result in a significant phylogenetic signal (Appendix S1: Table S5).

Beyond overall pairwise trait similarity, actual trait combinations between species pairs were related to levels of cross-species synchrony in reproduction. Reproductive synchrony for animal-pollinated species pairs (mean ± SD = 0.31 ± 0.01) and wind-pollinated species pairs (0.38 ± 0.03) was significantly higher compared to species pairs where one species was animal pollinated and the other was wind pollinated (0.11 ± 0.02; $p < 0.001$; Figure 6). Conversely, for leaf longevity, evergreen species pairs had significantly higher synchrony in reproduction (0.34 ± 0.01) compared to species pairs that included a deciduous species ($p < 0.001$; Figure 6), including when both species were deciduous (0.14 ± 0.02) or one species was deciduous and the other species was evergreen (0.12 ± 0.02). Species pairs with endozoochorous dispersal were more synchronous than pairs of species that were both synzoochorous or both abiotic dispersed, and species pairs that both had fleshy fruit were more synchronous than pairs that included one or both species not having fleshy fruit (Appendix S3: Figure S1). For some traits (e.g., sexual systems and mycorrhizal associations) there was considerable variation in cross-species synchrony across the trait combinations (see Appendix S3: Figure S1 for all categorical species trait pairs).

3.3 | Relative Contribution of Climate, Traits and Phylogeny

To synthesise the long-term patterns of cross-species synchrony across a wide geographic range of LTER sites that spanned a wide range of biomes, we created a single model including trait similarity, phylogeny and site-level climate (mean annual CWD and AET). Cross-species synchrony in woody plant reproduction was most strongly positively associated with trait similarity between species pairs ($p < 0.001$) and was significantly greater in areas with higher log-CWD (i.e. hotter and drier environments; $p = 0.01$), while AET and phylogenetic distance were not significantly associated with cross-species synchrony (Table 2).

4 | Discussion

Temporal synchrony in reproduction within populations across years is, by definition, a key component of mast

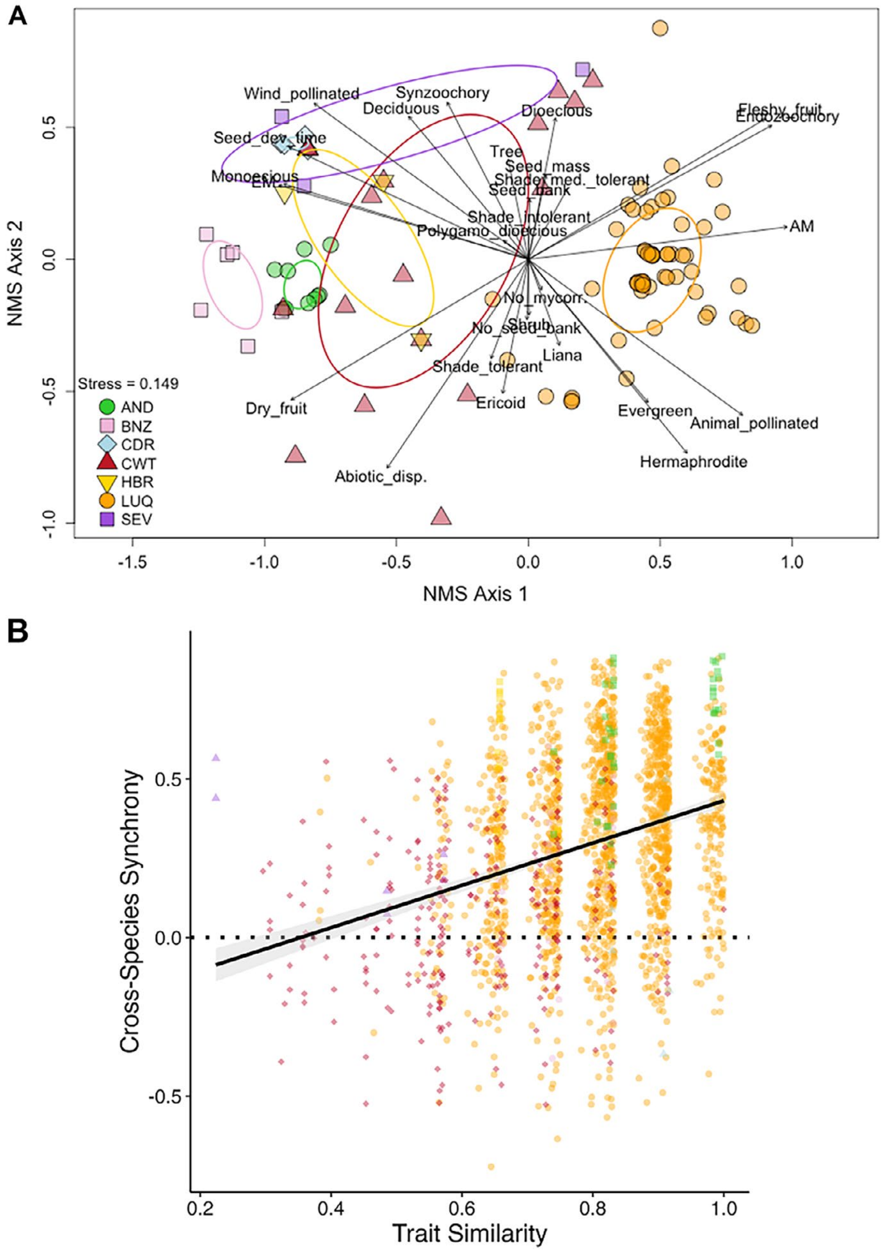

FIGURE 4 | (A) Trait space shown by nonmetric multidimensional scaling (NMS) at the seven Long-Term Ecological Research (LTER) sites. Ellipses indicate standard deviations around group centroids while each point indicates a particular species' position in 'trait space'. See Appendix S1: Table S1 for the full list of traits. (B) Pairs of species with more similar traits (*x*-axis, 0 = different, 1 = same, modified Jaccard index on 12 traits) have higher synchrony (*y*-axis, Spearman's correlation) than species with less similar traits. The solid black line shows the relationship across the full dataset (point colours correspond to individual sites as in panel A). Acronyms and LTER site names are defined in Table 1 and Appendix S1: Table S1.

seeding (Bogdziewicz et al. 2024; Janzen 1976; Kelly 1994; Silvertown 1980). While single-species studies of mast-seeding have been the norm, synchrony between species can affect forest community dynamics through reproduction, competition and trophic cascades (Wang et al. 2017; Yi, Yang, and Zhang 2011). By using long-term data on the reproductive output of woody plant species that co-occur in forest and woodland communities, here we found that the magnitude of temporal synchrony in reproduction between species had a wide range of values and was on average greater than expected by chance from data across all LTER sites. This skew towards positive synchrony was consistent at six of the seven sites we examined, indicating little support for the mathematical null hypothesis that cross-species synchrony is random. We found that greater trait similarity between species pairs was the most important factor in the level of cross-species synchrony and that species pairs in more extreme environments characterised by greater climate water deficits were more synchronous, supporting our predictions. Contrary to our hypothesis, phylogenetic relatedness among species pairs was a poor predictor of whether more closely related species had greater synchrony in reproduction.

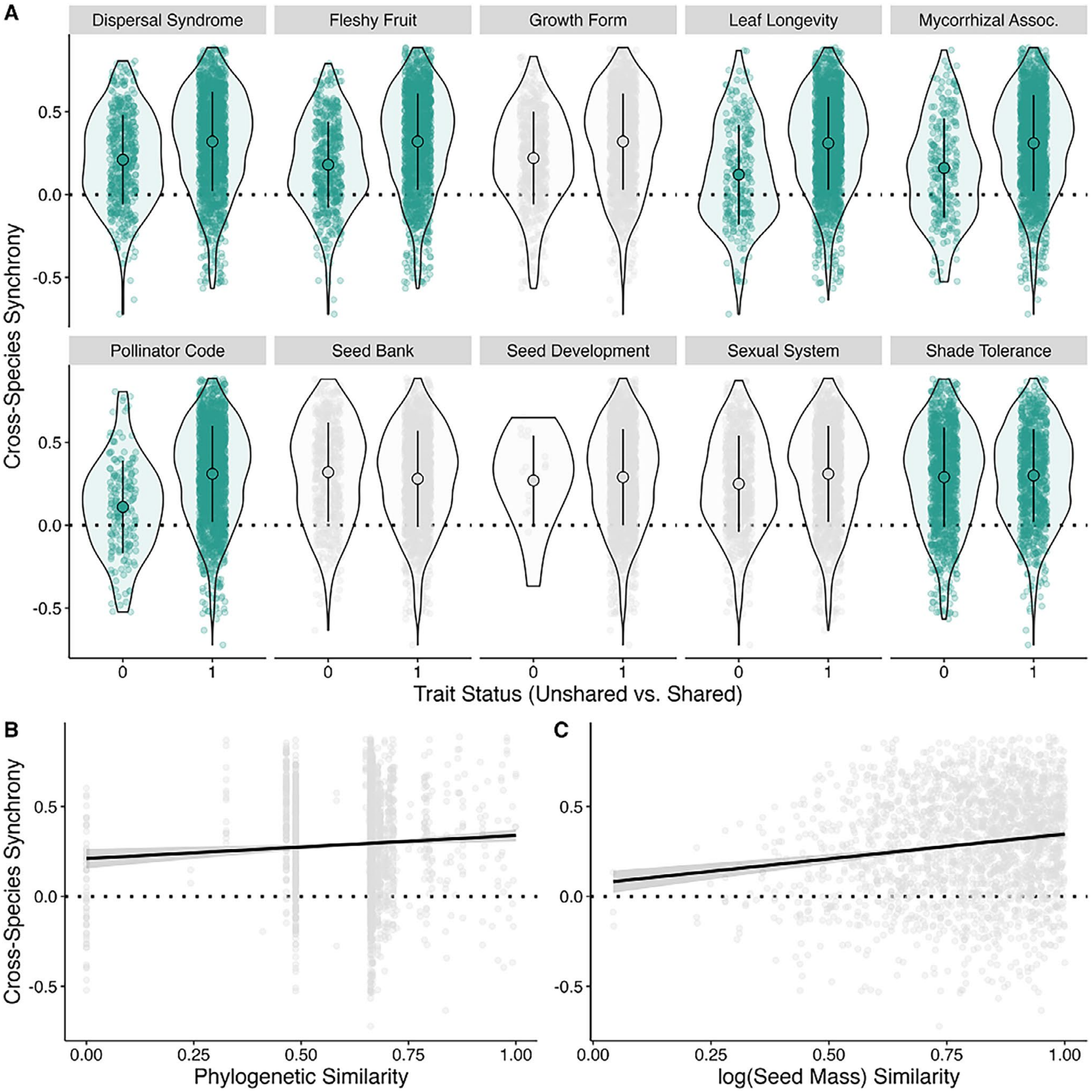

FIGURE 5 | Plots of Spearman correlations in reproductive cross-species synchrony of woody plants for: (A) pairs of species with same (1) or different (0) traits, showing data from all sites; raw data points are plotted with violin plots showing data distributions the mean values ± standard deviations shown, (B) phylogenetic similarity and (C) similarity of log seed mass; panels B and C have continuous axes and a solid best-fit line with standard error indicated by the grey envelope. Variables in the full multiple regression on distance matrices (MRM) that were statistically significant are shown in green, those that were not significant are shown in grey. Graphs for each Long-Term Ecological Research (LTER) site are available in Appendix S3.

Past mast-seeding studies examining cross-species synchrony have generally focused on closely-related species and have found a range of levels of synchrony. Among three species of *Quercus* in Florida, only one pair of species was significantly positively correlated ($r = 0.78$) (Pesendorfer et al. 2021) and pairwise synchrony at three sites in California and Iowa between three to five species of *Quercus* per site ranged between $r = -0.18$ and 0.43, with the negative correlations in temporal patterns of reproduction occurring between *Quercus* species with different seed-development times (Liebhold et al. 2004). In a more diverse tree community, Wang et al. (2017) found synchrony in 14 pairs of species (correlation range = 0.71–0.99) over 8 years among the 20 species in a 25-ha plot in China (out of a potential 190 cross-species comparisons). Synchrony within species in four genera (*Chionochloa*, *Nothofagus*, *Phormium* and *Dacrydium*) in New Zealand was high, of 171 within-genus comparisons they all had correlations >0.26 (median correlation = 0.71) (Schauber et al. 2002). A large number of species of Dipterocarpaceae in SE Asia demonstrate community-wide satiation in large reproductive 'mast year' events (Cannon et al. 2007; Curran and Leighton 2000; Janzen 1974),

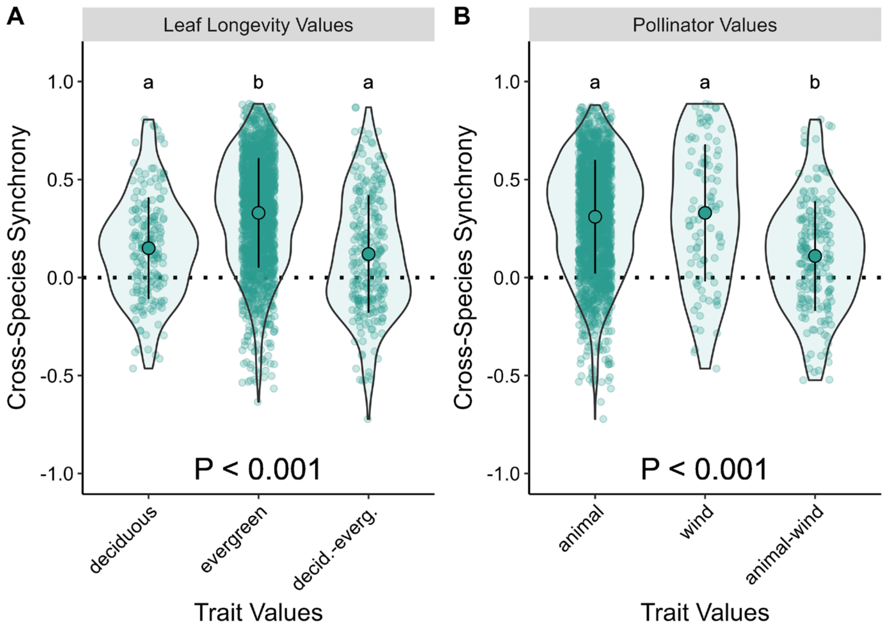

FIGURE 6 | Cross-species synchrony in woody plant reproduction depends on the actual trait values that are similar or different. When a single trait value is shown (e.g., 'deciduous') both species in the pair shared that value. Lowercase letters that are different for groups represent a significant difference in means based on pairwise comparisons. (A) A pair of evergreen species has greater cross-species synchrony than a species pair that includes a deciduous species. Conversely, (B) when both species are pollinated by either animals or both are pollinated by wind, there is greater synchrony compared to when one species is animal pollinated and the other is wind pollinated. See Appendix S3: Figure S1 for other traits.

TABLE 2 | Model coefficients for cross-species synchrony in woody plant reproduction over time based on similarity in species traits, phylogenetic similarity and climate.

Variable	Estimate	SE	*t*	*p*
Trait similarity	0.067	0.007	9.59	< 0.001
CWD	0.048	0.015	3.29	0.010
AET	0.029	0.023	1.26	0.273
Phylogenetic similarity	−0.004	0.007	−0.59	0.555

Note: Linear mixed models were conducted, with climate site and species pairs as random intercepts. Estimates are shown based on scaled variables.
Abbreviations: AET = actual evapotranspiration, CWD = log (climate water deficit).

but less is known about correlations in synchrony in reproduction between species that are variably-related across long time series. Patterns of seed rain in Amazonian forests have shown similarity in phenology of seedfall in confamilial species (Pak et al. 2023), while litterfall in five temperate species showed variation in their response to ENSO and leaf fall was more synchronous than seedfall (Zhu et al. 2022).

Similarity of individual traits between species pairs showed results that were broadly consistent with our hypothesis that shared traits between a pair of species was associated with higher synchrony. We examined 11 traits related to leaf and reproduction type, plus phylogenetic similarity, and we found that species pairs with greater overall trait similarity were more synchronous in their patterns of reproduction over time. Synchrony in the temporal fluctuations in population abundances of multiple species within communities have been of broad interest in ecology (Franzén et al. 2013; Rocha et al. 2021; Valencia et al. 2020; Van Klink et al. 2019), influencing the stability of ecological communities as related to food production and other ecosystem services, particularly when synchrony is low (Valencia et al. 2020). Our finding that species with higher trait similarity had greater synchrony has been observed in a range of taxa, including studies on fish population dynamics and trait-similarity (Rocha et al. 2021) and plants in New Zealand (Schauber et al. 2002). The degree of synchrony in seed production within plant populations has implications for predator satiation (Janzen 1971; Kelly and Sork 2002). We suggest that this extends to plant communities, particularly for generalist granivores that use multiple types of seeds as food sources, potentially influencing selection in plants (Yi, Yang, and Zhang 2011). Thus, predator satiation through cross-species synchrony may be more effective when there are fewer alternate resources for seed predators (Bogdziewicz, Zwolak, and Crone 2016; Kelly and Sork 2002), and where woody plant species diversity is low. Asynchrony in seed production across years should lead to higher local predation for all members of the plant community in those cases where the main predators are generalists because food would consistently be available—and is an area for future research.

There may be both costs and benefits for species associated with high levels of synchrony in reproduction. High synchrony in seed production between species may be due to trait similarity between species, or for example, because the benefits of predator satiation through reproductive synchrony extend to the community level (Curran and Leighton 2000; Janzen 1974). Asynchrony could be beneficial between species that share an insect defoliator, for instance, Eastern spruce budworm (*Choristoneura fumiferana*) feeds on reproductive buds of both white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*), and variation in the timing of large reproductive events where these species were co-located was related to the intensity of defoliation and mortality in these two host species (Corona, Leeper, and LaMontagne 2022). In this case, a mast-seeding event in white spruce coincided with a spruce budworm outbreak followed by high levels of defoliation and tree mortality, while co-occurring balsam fir trees (which did not share the mast-seeding event with white spruce) had no mortality (Corona, Leeper, and LaMontagne 2022). Greater reproductive synchrony between species that share plant mycorrhizal traits (Chaudhary et al. 2022) could indicate shared strategies to collaborate with fungi to not only access soil nutrients, but also store nutrients for future use in reproduction (Newbery 2005). Conversely, low synchrony or anti-synchrony between plant species might result from divergence in species attributes or competition for environmental resources.

The pollination efficiency hypothesis suggests there are benefits to synchronous reproductive events within a population (Kelly and Sork 2002; Norton and Kelly 1988). Indeed, insofar as stigmas or micropyles might be cluttered with nonconspecific anemophilous pollen, the effect of synchronous plant reproduction for the anemophilous species should be negative, however anemophilous pollination schedules across multiple species within communities of trees show a relatively small window for anemophilous pollination that can be as short as a matter of hours (Mckone, Thom, and Kelly 1997), suggest that pollen clogging is a minor issue (Bolmgren, Eriksson, and Linder 2003). In a grassland/herbaceous plant community, higher similarity in reproductive traits was associated with greater floral abundance that enhanced visits by generalist pollinators (Bergamo et al. 2020). Species pairs with the same pollination vectors were more synchronous with each other than pairs with different pollination vectors (wind vs. animals). While this may not be expected due to the potential for competition for pollinators, in Dipterocarps an adaptation to avoid competition for pollinators is to stagger flowering times within years (Ashton, Givnish, and Appanah 1988; Bolmgren, Eriksson, and Linder 2003). Furthermore, the costs of synchronous cross-species flowering can be moderated by spatial clustering of plants, which increases pollinator constancy within foraging bouts (Bruninga-Socolar, Winfree, and Crone 2022). Species with shared dispersal syndromes were more synchronous, particularly species that have endozoochorous dispersal. Pairs of species with fleshy fruits had significantly higher synchrony compared to species pairs that included at least one non-fleshy fruited species and could indicate that dispersers are not limiting in the study systems we examined. Alternatively, species with similar dispersal syndromes could produce fruits at different times within a year, similar to within-year partition of flowering to minimise competition for pollinators.

Synchrony among plant species could occur because they experience similar environmental conditions (Kelly and Sork 2002) and respond to the same weather cues for reproduction (Cleavitt and Fahey 2017; Kelly et al. 2013; Schauber et al. 2002). The effect of CWD on synchrony is evidence that indicates this patterns holds across our LTER sites, consistent with water deficit being an important driver of plant synchrony elsewhere (e.g. Qiu et al. 2023). We predicted higher synchrony between species with greater phylogenetic similarity; in contrast, we found that phylogenetic relatedness among species pairs was not a useful predictor of whether more closely related species were more synchronous in their reproduction. While we did not investigate weather conditions here, large-scale modes of climate variability such as El-Niño Southern Oscillation (ENSO) have been associated with mast seeding patterns over space and time and have been suggested to extend across taxa (Ascoli et al. 2021; Schauber et al. 2002), however the sensitivity of species to ENSO may vary (Wion et al. 2021). In our study, our analysis of synchrony was based on species that co-occurred at sites and therefore shared the same weather conditions, and we suggest that weather and trait similarity together may play a role in levels of synchrony. Veto events such as a strong frost can have a strong effect on within-species synchrony because all individuals are susceptible (Bogdziewicz et al. 2018; Schermer et al. 2020), but while some species respond similarly to temperature and/or precipitation cues and have similar windows of time during which they are sensitive, other species co-occurring in the same region have different periods of time when they are receptive to cues (Bogdziewicz et al. 2023) which could affect levels of cross-species synchrony. Vetos affecting a whole community are more likely to be large disturbances or long climatic events such as drought that make conditions poor for reproduction for all plant species, and thus rarer as a selective process. Also consistent with our finding that phylogenetic relatedness was not a driver of synchrony is that for 20 species of trees at their study plot, Wang et al. (2017) found that levels of synchrony in mast seeding varied across congeneric species, with their two *Tilia* species being synchronous, but not the two *Populus* species, and for seven species of *Acer*, out of 21 species pairs only five showed cross-species synchrony. For cross-species synchrony, we suggest there is likely some interaction occurring between weather and shared traits, and overall climate at the site; these interactions are an area for future study to clarify the extent to which the Moran effect drives synchrony, and to what degree positive synchrony between species as a result of shared cues to environmental stochasticity (Massie et al. 2015) constitutes a null hypothesis versus a selective effect for strong synchrony. We focused on 11 traits and phylogenetic similarity among species, and suggest that future studies examine other potential traits that could influence cross-species synchrony.

Our study included a synthesis of seven LTER sites spanning a range of biomes and woody-plant communities that greatly varied in the diversity of species that were present and for which we had data. Advantages of this synthesis across a broad range of sites includes the broad range of trait space for species that were included in this study, and the sensitivity analysis removing individual sites showed that the findings of significance for individual traits were largely robust. However, in a synthesis study spanning a breadth of sites and biomes, analysing any site alone may show variation in the predictors across sites. In some cases, this was due to limited trait space captured by the species. For example, in cases of low species diversity sites, trait variation was confounded with phylogenetic variation (i.e., the variation is the same). Lack of significant influence in the full MRM model across all sites for a trait such as seed-development time likely resulted from the small proportion of species pairs with variation in this trait, given that it was significant at individual sites where there was variation in this trait. For example, only three woody plant species occur at SEV, a semi-arid woodland site, and thus multiple traits varied consistently across species, reducing the power to identify key traits that may drive variation across species because any one of several traits could account for the variability in cross-species synchrony.

5 | Concluding Remarks and Future Research

Mast-seeding is a population-level phenomenon, with consequences that may extend to the community level. Here, we show that cross-species synchrony in reproduction occurs across a range of biomes across North America. A natural future direction would be to extend these findings to understand environmental drivers of synchrony, which could aid in forecasting community-wide mast seeding events (Journé et al. 2023; Pearse et al. 2021). Future investigation of this pattern would require site-specific models, tuned to the conditions needed for pollination in each region and for each species (Satake and Kelly 2021). Similarly, the consequences of the levels of mast seeding synchrony between species as they cascade across trophic levels, and further investigations into the roles of specific traits such as mycorrhizal associations, sexual systems and levels of synchrony are open for further study to identify the levels of synchrony that constitute or go beyond what would be expected from the Moran effect alone. In addition, the LTER plant reproduction data used in this synthesis provide a rich resource for examining environmental pressures on the range of biomes represented, from hurricanes in Puerto Rico, to wildfires in the west and warming climates in the boreal.

Author Contributions

J.M.L. formulated the original idea. J.K.Z., N.L.C., K.M.N., D.M., T.E.X.M., M.D.R., W.D.K. and J.F.J. provided, compiled and/or consulted on LTER data. J.K.Z., N.J.L., J.M.L., A.C., N.L.C., D.M., V.B.C., R.S.S., D.F.G. and J.H.B. compiled trait data. I.S.P. compiled the phylogeny data. N.J.L., E.P.H., R.S.S., T.E.X.M., M.D.R. and J.M.L. conducted data analysis. J.M.L., M.D.R. and E.E.C. obtained funding for the project. J.M.L., E.P.H., J.K.Z., N.J.L., D.M., D.F.G. and J.F.J. wrote the first draft and all authors contributed substantial feedback throughout the project and to manuscript revisions.

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Data Availability Statement

Data and code used for analyses and the generation of figures are publicly available on Figshare at https://doi.org/10.6084/m9.figshare.25112972.

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.