Running head: Multi-scale phenological niches

Title: **Multi-scale phenological niches in diverse Amazonian plant communities**

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Abstract

Phenology has long been hypothesized as an avenue for niche partitioning or interspecific facilitation, both promoting species coexistence. Tropical plant communities exhibit striking diversity in reproductive phenology, including seasonal patterns of fruit production. Here we study whether this phenological diversity is non-random, what are the temporal scales of phenological patterns, and ecological factors that drive reproductive phenology. We applied multivariate wavelet analyses to test for phenological synchrony versus compensatory dynamics (*i.e*. anti-synchronous patterns where one species' decline is compensated by the rise of another) among species and across temporal scales. We used data from long-term seed rain monitoring of hyperdiverse plant communities in the western Amazon. We found significant synchronous whole-community phenology at a wide range of time scales, consistent with shared environmental responses or positive interactions among species. We also observed both compensatory and synchronous phenology within groups of species likely to share traits (confamilials) and seed dispersal mechanisms. Wind-dispersed species exhibited significant synchrony at ~6 mo scales, suggesting these species share phenological niches to match seasonality of wind. Our results indicate that community phenology is shaped by shared environmental responses but that the diversity of tropical plant phenology partly results from temporal niche partitioning. The scale-specificity and time-localized nature of community phenology patterns highlights the importance of multiple and shifting drivers of phenology.

INTRODUCTION

Species within ecological communities often exhibit interspecific diversity in the phenology of key life events. This diversity may represent an axis of niche partitioning that reflects mechanisms of community assembly as well as evolutionary processes (Ashton et al. 1988, Gonzalez and Loreau 2009, Wolkovich and Cleland 2011, Bernard-Verdier et al. 2012, Godoy and Levine 2013). Species differences in phenology may limit interspecific competition and promote species coexistence by causing niche complementarity through time in resource use or interactions with mutualists like pollinators, or in apparent competition mediated by natural enemies (Robertson 1895, Rathcke and Lacey 1985). Alternatively, periodically harsh environmental conditions may limit the possible phenological options, or pulses in resource supply may promote phenological synchrony (Gentry 1974, Rathcke and Lacey 1985, Vasseur et al. 2014, Usinowicz et al. 2017, Detto et al. 2018). Additionally, facilitation due to enhanced attraction of mutualist animals or predator satiation may promote synchronous reproduction (Janzen 1974). However, phenology remains a relatively poorly characterized dimension of functional diversity in many communities, owing to a lack of long-term monitoring and the multi-scale complexity of phenology (Wolkovich et al. 2014).

Co-occurring plant species with similar reproductive phenology might be more likely to compete for mutualist frugivores (Saracco et al. 2005) or other resources, given that reproduction is a resource-demanding activity (Karlsson and Méndez 2005). As a result, those species capable of coexisting might partition phenological space (i.e. temporally partition resource use). Researchers have studied evidence for this axis of niche variation in tropical forests e.g. (Gentry 1974, Stiles 1977, Wheelwright 1985, Ashton et al. 1988, Poulin et al. 1999, Jones and Comita 2010) and other communities (Elzinga et al. 2007, Botes et al. 2008, Albrecht et al. 2015).

105 Within a diverse community, phenological niche partitioning might be strongest among species
106 with shared mutualists (e.g. animal seed dispersers) or resource requirements (Encinas-Viso et al.
107 2012) as is often the case among species that are phylogenetically related (Robertson 1895,
108 Prinzing et al. 2001, Donoghue 2008, Davies et al. 2013). However, some past studies have
109 found little evidence for temporal niche partitioning in mutualist interactions. Part of the
110 challenge of detecting such partitioning is that there are simultaneous and opposing processes
111 acting on phenology, such as seasonally harsh abiotic conditions versus resource competition. As
112 a result, phenological patterns indicative of shared temporal niches (interspecific synchrony)
113 versus temporal niche partitioning (interspecific compensation, or anti-synchrony) may only
114 emerge at certain time scales or over certain periods of time (Baird 1980, Vasseur et al. 2005,
115 Keitt 2008, Lasky et al. 2016).

116 Tropical plant communities have highly varied phenology and there are often multiple
117 species reproducing at any given time of the year (Frankie et al. 1974, Gentry 1974, van Schaik
118 et al. 1993), including for the specific reproductive stage that we study here: seed fall (Smythe
119 1970, Chang-Yang et al. 2016, Detto et al. 2018). The phenological diversity of tropical plants
120 may be made possible by favorable temperature and (in rainforests) moisture for much of the
121 year (Gentry 1974, Usinowicz et al. 2017). Without strong abiotic constraints, phenology may be
122 free to evolve neutrally across the year. Alternatively, different species may be limited by
123 different conditions fluctuating across the year (e.g. light, moisture, heat), thus diversity in the
124 phenology of seed fall may be a consequence of distinct strategies or sensitivities to seasonality
125 in resources (Lasky et al. 2016). Furthermore, despite the year-round reproduction of some
126 species, tropical plant communities often exhibit synchrony among a subset of the community,
127 perhaps due to shared responses to abiotic seasonality and the role of environmental filtering in

community assembly (van Schaik et al. 1993, Detto et al. 2018) or seasonality in frugivory and seed dispersal (Poulin et al. 1999). Additionally, positive density dependent interactions among species may promote synchrony, for example when greater reproductive output among plants decreases rates of seed predation (Ashton et al. 1988, Jones and Comita 2010) or when reproduction by one species facilitates frugivory on a neighboring species (Carlo 2005). Community patterns of synchronous versus compensatory reproduction might occur during periods with specific abiotic conditions, suggesting that abiotic conditions constrain species interactions (Vasseur et al. 2005).

We used wavelet analyses to characterize community-wide phenology, specifically to determine whether species exhibited synchronous seed rain or whether they exhibited compensatory (anti-synchronous) seed rain (Lasky et al. 2016). Wavelets are basis functions, linear combinations of which can be used to characterize signals in data (here, time series of seed rain). Wavelet transformations decompose signals into patterns at different scales, like other spectral analyses, but with the added advantage that wavelets can characterize time-localized and nonstationary patterns, i.e. patterns that are inconsistent over a time series (Terrence and Compo 1998, Keitt 2008). In the wavelet transformation, the base wavelet is translated across the time series at varying scales/frequencies of the wavelet to identify the important time scales that contribute to the variability in the signal (Cazelles et al. 2008). By resolving non-stationary and scale-specific patterns, we may improve our ability to detect multiple opposing processes affecting seed rain dynamics at different temporal scales (scale-specific) or points in time (non-stationary). For example, while species may all increase reproduction during once-a-year seasons of high resource supply (annual-scale synchrony), species may peak in reproduction at different points within a favorable season (within-season-scale compensatory dynamics, Lasky et al.

2016). Here we used a statistic of wavelet-transformed seed rain dynamics (Keitt 2008) to identify locations in time and temporal scales of synchronous and compensatory seed rain patterns (illustrated in Figure 1).

We addressed the following questions:

1. Do communities exhibit compensatory patterns or synchronous patterns of seed fall through time compared to a null model where species' phenologies are random with respect to each other?
2. Is evidence for compensatory and synchronous dynamics scale-specific or non-stationary?
3. Is evidence for niche partitioning of seed fall phenology strongest among functionally similar species, potentially those with the greatest likelihood of interspecific competition? Specifically, do species with similar fruit morphology exhibit stronger compensatory dynamics? Do related species exhibit stronger compensatory dynamics? Or alternatively do morphologically similar or related species exhibit synchrony?
4. Does community phenology differ between two sites, one with more seasonality of rainfall (Cocha Cashu) than the other site (Yasuní)? Are phenological niches mediated by fluctuations in environment, e.g. such that wetter periods allow more diversity in phenology, or such that drier periods induce synchronous reproduction?

METHODS

Study sites

We studied two forest plots in the western Amazon basin, in Cocha Cashu, Peru and Yasuní, Ecuador (Figure S1). These plots were monitored continuously for different intervals, from February 2000–February 2017 in Yasuní and September 2002–January 2011 in Cocha Cashu.

The study plot in Ecuador was located in Yasuní National Park at the Estación Científica Yasuní (0° 41’ S, 76° 24’ W), a research station maintained by Pontificia Universidad Católica del Ecuador. The Yasuní lowland rainforest is in the wettest and least seasonal region of the Amazon (Xiao et al. 2006, Silman 2007). Mean annual rainfall is 2826 mm, with no months having <100 mm rainfall on average (Valencia et al. 2004b, 2004a). Seed traps were placed within the 50-ha Yasuní Forest Dynamics Plot (YFDP, established in 1995), where elevation ranged from 216 to 248 m. This is a hyperdiverse forest, with 1104 tree species recorded in 25 ha of the YFDP (Valencia et al. 2004b, 2004a).

The study plot in Peru is located at Cocha Cashu Biological Station (11°54'S, 71°22'W), which is situated at 360m mean elevation within the core area of Manu National Park, at the western margin of the Madre de Dios river basin. The study plot is located in mature floodplain forest habitat, which comprises over 700 tree species (Pitman et al. 2002). Annual precipitation ranges between 2000–2500 mm, with a pronounced dry season from June to October with typically less than 100 mm monthly rainfall (Gentry 1993). In the period from September and April there is an excess of fruit available for frugivorous vertebrates (Terborgh 1986b), which may indicate plants compete to attract frugivores during this period.

Seed rain data

In each plot, an array of seed traps was established. At Yasuní we followed the methods of (Wright and Calderon 1995). In February 2000, 200 seed traps were placed in the 50-ha YFDP along trails but >50 m from the plot border. Every 13.5 m along the trails, a trap was placed a

random distance between 4 and 10 m perpendicular from the trail, alternating left and right. Traps were constructed of PVC tubes and 1-mm fiberglass mesh, positioned 0.75 m above ground, with an area of 0.57 m^2. Twice monthly from February 2000 to February 2017 all reproductive parts in each trap were counted and identified to species or morphospecies using a reference collection of seeds and fruits maintained on site.

At Cocha Cashu, year-round fruit and seed fall were counted between 2002 and 2011 within a 4-ha plot. A 17 × 17 array of 289 evenly spaced seed-fall traps was installed within the central 1.44 ha (120 × 120 m) of the plot at the beginning of the study. Seed traps consisted of 0.49 m^2 (70 × 70 cm) open bags made of 1-mm nylon mesh sewn to wire frames with 0.5-mm monofilament line. Corners of the traps were attached to nearby trees with 1-mm monofilament line so that the traps were suspended approximately 1 m above the ground. The contents of the traps were collected every 2 weeks, and all seeds, fruit and fruit parts (capsules, valves, pods, etc.) were identified to species and recorded.

For fruit counts at both sites we estimated number of seeds collected by multiplying by the average number of seeds per fruit. Further detail is available in the Supplemental Material.

Seed dispersal mechanisms

At both sites, we grouped species into different dispersal syndromes. We conducted two separate classification efforts, one for all species, and another focused on tree species (excluding lianas, herbaceous, and woody shrub species). At Yasuní for all plants we focused our analysis on classifications as animal (N = 741) or wind (N = 139) dispersed. Next, for Yasuní trees with animal-dispersed seeds we followed (Harrison et al. 2013) and further classified them as dispersed by terrestrial animals (25 species), or with small (< 2cm, 230 species), medium (2-5 cm long, 74 species), and large (> 5 cm, 12 species) seeds dispersed by canopy animals (groups

218 are mutually exclusive). For trees with seeds dispersed abiotically, we included ballistically
219 dispersed seeds (16 species) and wind dispersed seeds (30 species).
220 We classified species of all growth forms at Cocha Cashu as one of three dispersal
221 syndromes: animal, wind or ballistic. Species with fruit that contain pulp or aril were considered
222 animal-dispersed, while those with fruits or seeds adapted for flight were considered wind-
223 dispersed. A small number of species with dehiscent fruit lacking pulp or aril that explosively
224 release seeds upon dehiscence were assigned to the ballistic syndrome. For trees, dispersal
225 mechanism was assigned in a prior study using information from published studies conducted in
226 the Madre de Dios basin and other long-term Neotropical rainforest sites (Bagchi et al. 2018).
227 Tree species were classified based on their proportional dispersal by members of seven dispersal
228 groups: 1) large- and medium- bodied vertebrates (e.g. tapirs, spider monkeys, capuchins, guans,
229 toucans, trumpeters), 2) small bodied non-volant arboreal mammals (e.g. tamarins, night
230 monkeys, kinkajous), 3) small birds (e.g. manakins, cotingas and tanagers), 4) bats (*Artibeus*
231 spp.) (5 species), 6) ballistic, 7) wind dispersal, and 8) those with unknown dispersal mechanism
232 (two species of *Calatola,* Icacinaceae) (Bagchi et al. 2018). We took these published estimates
233 and performed k-means clustering to produce six mutually exclusive groups of species with
234 similar dispersal modes. These approximately correspond (based on cluster means) to groups
235 dispersed mostly by large vertebrates (52 species), small birds (25 species), small vertebrates (20
236 species), wind (8), and bats (5), ordered by decreasing number of plant species in each group.
237 For all analyses on the taxonomic and dispersal groups, we only included groups that had
238 at least 5 species. We did not use a lower threshold on number of records for inclusion of a
239 species, as species contributions to group-wide phenological dynamics are weighted by number
240 of seeds in the analyses below.

Weather data

We estimated monthly precipitation and minimum temperature at the plot level for each study site. Because local weather station data contained many missing observations, we used remotely sensed data. We used a ten-day precipitation time series estimated on a 0.05º grid by (Funk et al. 2014) using both remote and locally-sensed data. We used ECMWF/ERA-Interim reanalysis 4-hr temperature data at 2 m height estimated on a N128 Gaussian (~2º) grid (European Centre for Medium-Range Weather Forecasts 2009) and calculated daily minimum temperatures and then monthly values.

To estimate the rough pattern of wind seasonality, we used weather station data. For Cocha Cashu, we calculated average monthly wind speed from a station 150 km away, within 100 m elevation of Cocha Cashu, for the years 2004-2009 (http://atrium.andesamazon.org/meteo_station_display_info.php?id=12). For Yasuní, we used a weather station (http://www.serviciometeorologico.gob.ec/biblioteca/) 115 km away within 70 m elevation of the Yasuní plot for the years 2005-2012.

Statistical analysis

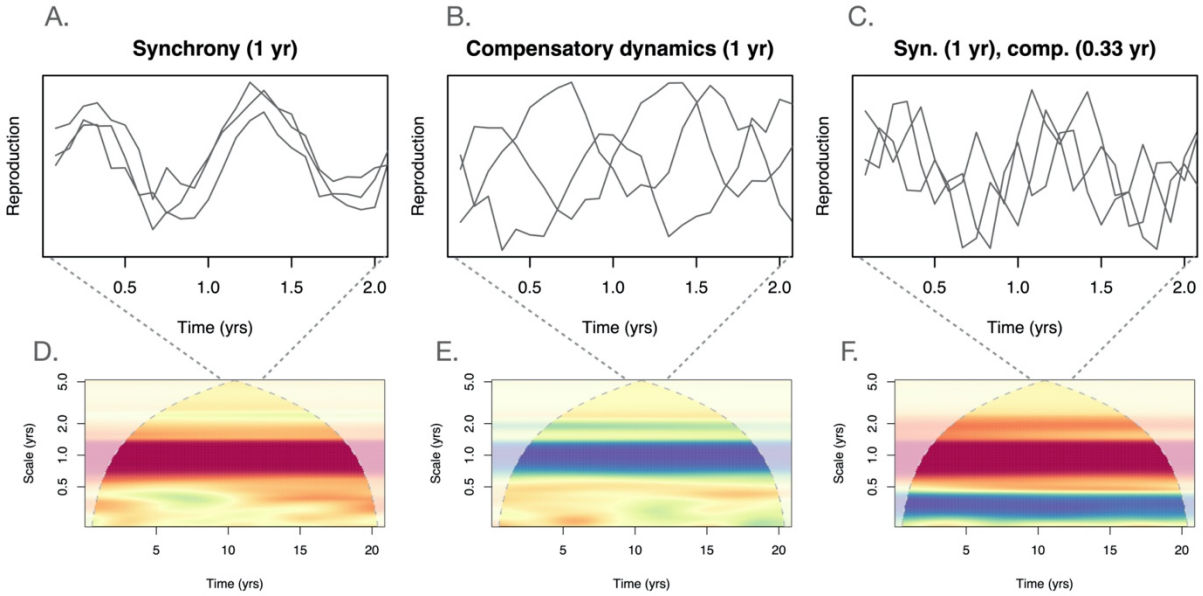
Wavelet transformation of seed rain data

To characterize patterns of synchrony versus compensatory dynamics, we used wavelet analyses. Wavelet transformation, like the Fourier transformation, is a spectral analysis which can characterize information from multiple time scales across a time series, with the added flexibility that wavelets can characterize localized, non-stationary patterns (i.e. patterns that change over time) (Keitt and Urban 2005, Cazelles et al. 2008).

For each species, we summed seed rain for each time point across traps and then log-transformed the count + 1, resulting in a single time series for each species. We then applied a

continuous Morlet wavelet transformation to each species' time series (see greater detail in the Online Supplement). To characterize individual species' phenology in relation to the community or group of species, we calculated the wavelet modulus ratio (WMR). WMR quantifies the relationship between the variation in the aggregate community-wide reproduction (numerator of Eqn. S3) relative to variation in species-level reproduction. When species seed rain dynamics through time perfectly cancel each other out, aggregate variation is zero (declining seed rain is balanced by increasing seed rain). Thus at zero, the WMR indicates complete compensation: all species-level dynamics are compensated so that community level reproduction is constant. At unity, the WMR signifies complete phenological synchrony among the species, as species-level phenological dynamics are completely reflected at the community level.

Figure 1. Illustration of wavelet modulus ratio (WMR) as a measure of multi-species patterns in reproduction. (A-C) Shows two-year time series of reproduction (excerpted from a 20-year series) for three different scenarios for a 3-species community. (D-F) Demonstrates WMR for these scenarios across a whole 20-year time series, where WMR is determined by the variation in total aggregate community reproduction relative to the variation in individual species reproduction. When there is synchrony (A), the aggregate community variation is similar to the individual species variation, and WMR is high at the relevant scale (1 yr). When there are compensatory dynamics (B), the aggregate community variation is low but the individual species variation is high, and WMR is low at the relevant scale (1 yr). Both synchrony and compensatory dynamics can occur at different scales (C), in this case long-scale synchrony and short scale compensation. A small amount of noise was added to each scenario. The cone of influence (white shading in D-F) marks the regions where the wavelet transforms are affected by the boundaries of the sampling period.



To answer Questions 1 and 2 above, we calculated the whole community WMR for all species in Yasuní (0.10 to 8.5 yr periods) and Cocha Cashu (0.08 to 4.2 yr periods). The periods differed between sites because of the frequency of trap collection and duration. The minimum scales were twice the median distance between successive dates and the maximum scales were calculated as half the total duration. We tested statistical significance of whole community WMR using bootstrapping where each species had the phase of their wavelet at a given scale randomly shifted (Keitt 2008). This shift in phase has the effect of shifting where a wave is located in time, resulting in random patterns of among-species phenology. All analyses were run in R (v 3.3.2). WMR was calculated using the package 'mvcwt' (Keitt 2014, https://github.com/thk686/mvcwt).

Taxonomic and seed dispersal groups

To investigate if species that are closely related share similar phenological niches or partition phenological niches (Question 3 above), we focused on taxonomic groups. Our analyses were done at the family-level to ensure sufficient sample size. Confamilials often share characteristics making them likely to exhibit evolutionary niche conservation or character displacement.

Similarly, groups with shared dispersal mechanisms might be more likely to exhibit non-random phenology (Question 3) so we separately grouped species based on their dispersal syndromes.

For these grouped analyses (family or dispersal syndrome), we first calculated WMR (as with the whole-community analyses above) for each taxonomic or dispersal group. To test the hypothesis that species within a group exhibited synchronous reproduction or compensatory reproduction, we generated a null distribution of each group's WMR using permutations. We permuted species labels over the entire community while maintaining the number of species in each group, calculated WMR for the members of the permuted group, and then repeated this permutation 1000 times. If the observed WMR of a group averaged across time points was above the 97.5th percentile of the permutation-based null distribution, we considered it as significant synchrony, if the observed WMR of a group averaged across time points was below the 2.5th percentile of the null distribution, we considered it as significant compensatory dynamics. We calculated two-tailed p-values from permutations and implemented false discovery rate (FDR) control across the multiple hypothesis tests using the method of (Benjamini and Yekutieli 2001).

Climatic association with synchrony vs compensatory dynamics

To determine whether climatic fluctuations might influence phenology among community members (Question 4 above), we investigated the association of local temperature and precipitation on whole community WMR calculated above. We calculated monthly average climate data and we aggregated seed rain data to monthly average seed counts. We then calculated WMR for Yasuní (2-70 mo scales) and Cocha Cashu (2-50 mo scales). We used wavelet transformation of the climate variables at the specific scales so that we could calculate their relationship with community WMR. Specifically, at each scale, we calculated the Pearson correlation coefficient between the community WMR and the wavelet-transformed minimum

temperature or precipitation. The significance of the relationship was verified by comparing it to a null distribution of the Pearson correlation coefficients. Null distributions were generated by permuting the starting point of the wavelet transformed climate time series while maintaining periodic boundaries (i.e., adding climate values from before the randomly chosen staring points to the end of the permuted climate series) and calculating the Pearson correlation between the randomized climate wavelet and the WMR (n=1000, but with only 70 or 50 unique possible values for Yasuní and Cocha Cashu, respectively). The wavelet transform of climate was done in the R package "WaveletComp" (Rösch and Schmidbauer 2016).

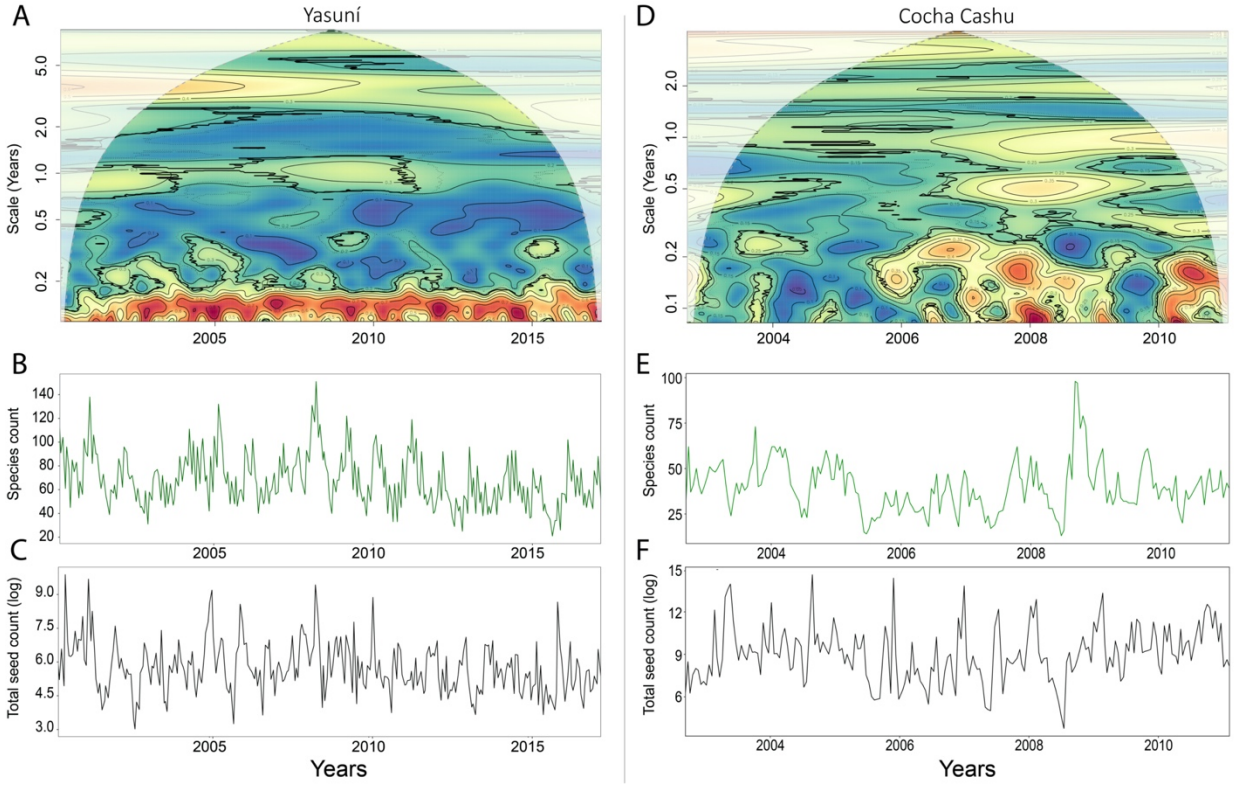
RESULTS

Community-wide phenology

At the ever-wet site Yasuní we found a general trend of strong whole community synchrony in seed rain at scales of less than ~50 days, while larger sub-annual periods were typically non-significant (Figure 2A). At the annual scale we also found significant synchrony for most of the study, and we found significant synchrony at scales greater than ~2 yrs, strongest at ~3.85 yrs. These patterns were largely stationary (consistent) across the time period of the study, especially the pattern of strong synchrony at ~50 days. However, there was a weakening to non-significance of annual-scale synchrony from 2012-2015.

By contrast, we found little evidence for synchrony at the sub-annual time scales at the seasonally dry Cocha Cashu before 2006 (Figure 2D). From 2006 into early 2008, we found community-wide synchrony across a wide range of temporal scales. Additionally, there was consistent significant synchrony at the ~1 year, ~2 year, and >3 year scales across the duration of the study, indicating some shared annual, biannual, and multi-year dynamics among species.

Figure 2: The whole community wavelet modulus ratio (WMR) of seed rain (A,D) at Yasuní (1059 species) and Cocha Cashu (654 species), and time-series of the total species in traps (B,E) and total estimated seeds in traps (C,F, natural log) in each sampling period. In (A,D) red indicates synchronous dynamics (high WMR) while blue indicates compensatory dynamics (low WMR). The thin dashed contour lines bound the points in time and scale (years) when the WMR was nominally significant ($p<0.05$) based on bootstrapping, while thick black lines bound regions significant with a false discovery rate (FDR) = 0.05. Nearly all significant regions in the plot are high WMR (yellow to red). The cone of influence (white shading, A,D) marks the regions where the wavelet transforms are affected by the boundaries of the sampling period.



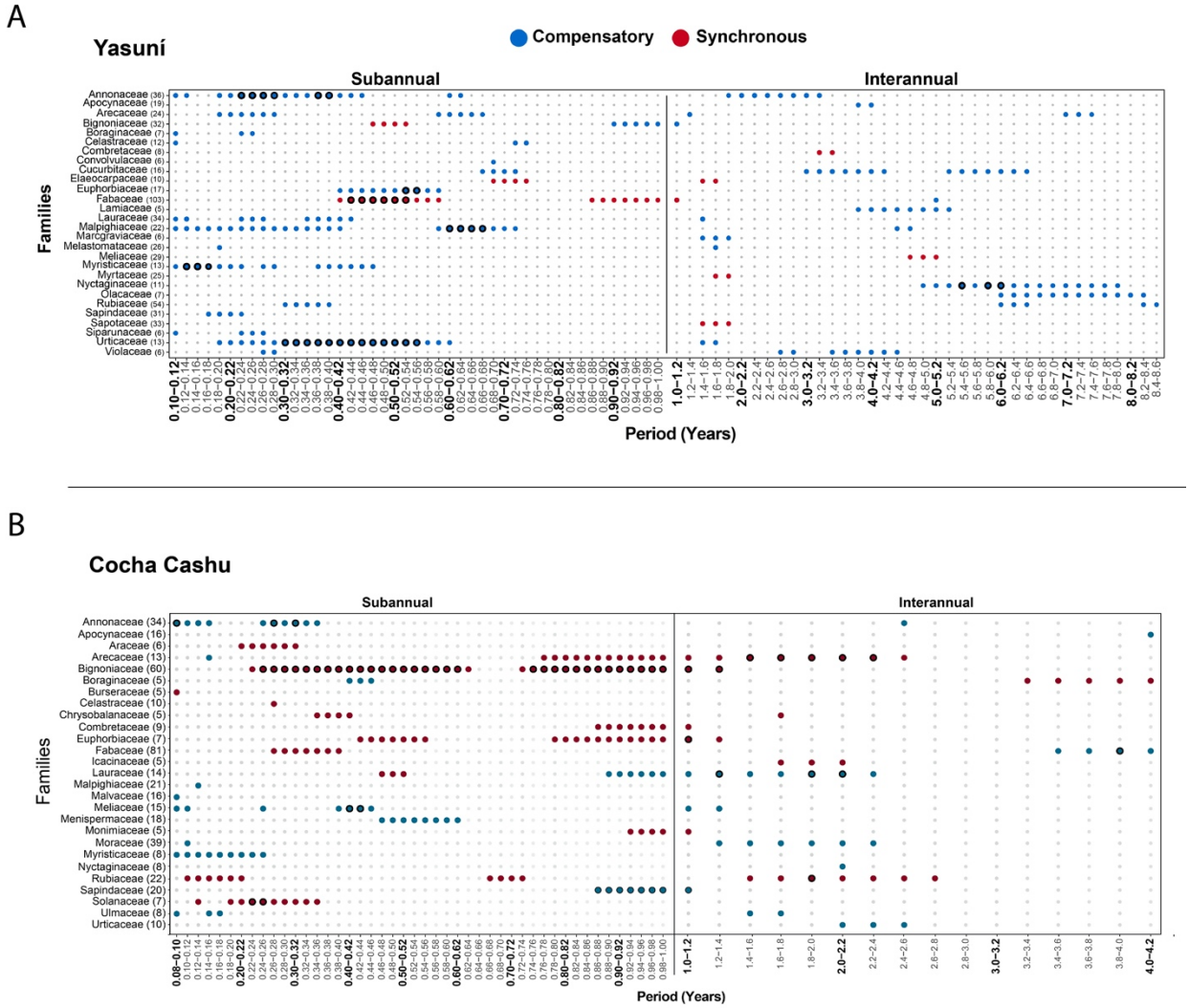
Phenology among confamilials

At Yasuní among the 28 families analyzed, we found that species of some families exhibited significant compensatory dynamics at sub-annual timescales (Figure 3A). In particular, species in the Annonaceae, Malpighiaceae, Myristicaceae, and Urticaceae families exhibited significant compensatory dynamics at the 2-5 month timescales (FDR = 0.05). That is, species that declined in reproduction over a few months scale tended to be replaced by other species in the same family increasing in reproduction over that timescale. Additionally, we found evidence of strong

compensatory dynamics at the longer time scales (e.g. 5-8 yrs) for Nyctaginaceae. By contrast, at Cocha Cashu among the 27 studied families, members of the same family exhibited a mix of significant synchrony or compensation, especially at sub-annual time scales (Figure 3B).

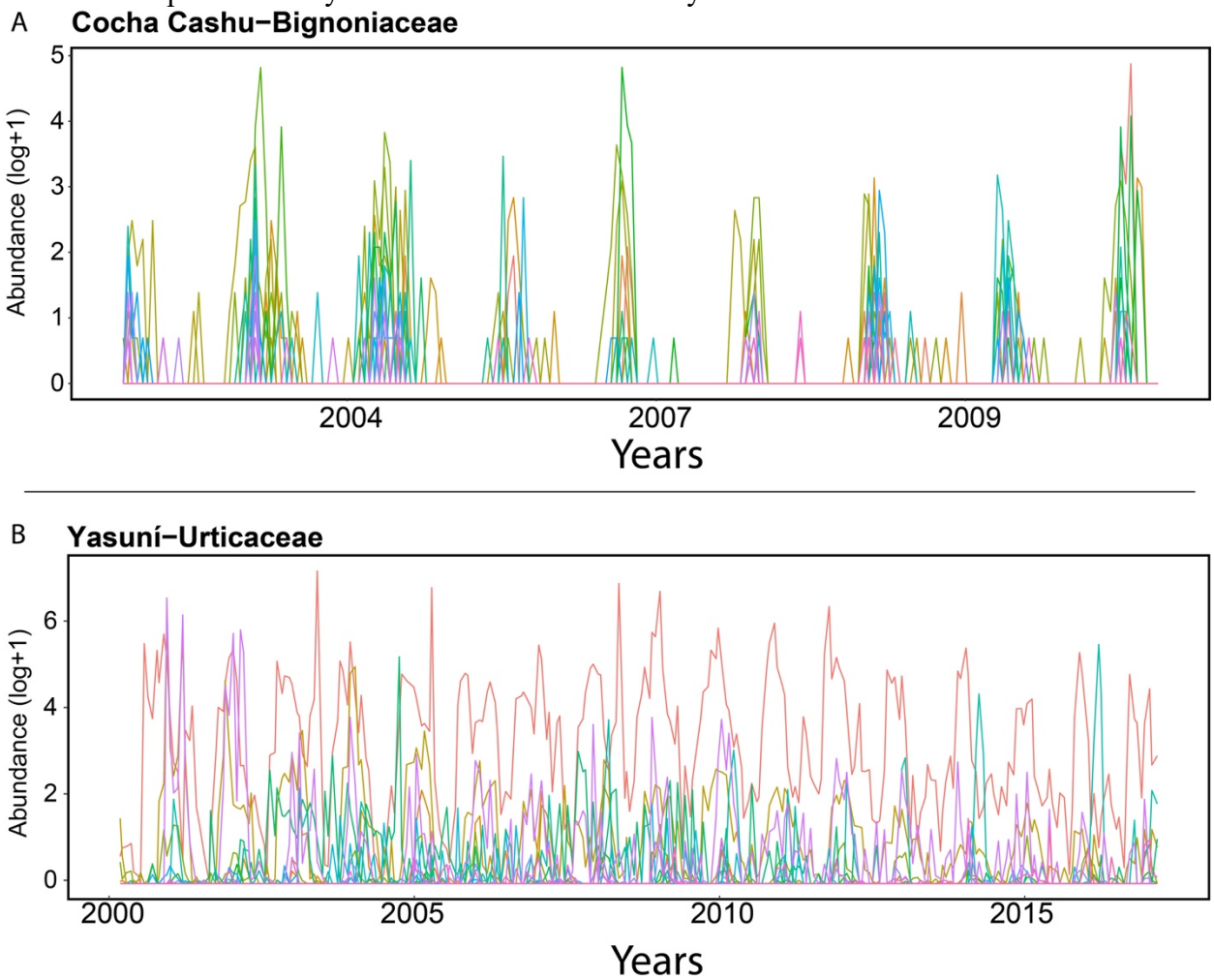
We found some consistency of family patterns across sites. Annonaceae at Cocha Cashu exhibited significant compensatory dynamics at sub-annual timescales (1-4 mos) similar to at Yasuní. Additionally, Myristicaceae at both sites showed significant compensatory dynamics at 1-3 mo scales (though these were not significant after FDR control at Cocha Cashu). By contrast, Bignoniaceae (a family of entirely wind-dispersed species) and Fabaceae species showed significant synchrony for sub-annual to annual time scales at both sites (though these were not significant after FDR control at Yasuní).

Figure 3: The averaged wavelet modulus ratio of families at Yasuní (A) and Cocha Cashu (B) at the sub-annual (left) and interannual (right) scales. The number in parenthesis represents the number of species analyzed within the family. Colored points represent either nominally significant synchronous (red) or compensatory (blue) dynamics at the time scale ($p < 0.05$). Thick borders around the points indicate significant points at false discovery rate (FDR) = 0.05.



To help illustrate the patterns identified, we present two families with opposing patterns of synchrony or compensatory dynamics. At Cocha Cashu, Bignoniaceae shows strong synchrony at ~0.9 year scales, which corresponds to a strong yearly peak in reproduction of multiple species (Figure 4A). At Yasuní, Urticaceae showed significant compensatory dynamics at scales of ~0.3-0.54 years, which corresponds to a family-wide pattern where multiple species are typically releasing seed at any given point in time, and different species are often reproductive at different times of year (Figure 4B).

Figure 4. Two families at each site with opposing patterns of phenology, with each species' time series of estimated seed counts in traps shown as a different colored line. Bignoniaceae (A) at Cocha Cashu (60 species) shows synchrony especially at ~0.9 year scales, with multiple species rising and falling in reproduction together in concert at these scales. By contrast, Urticaeae (B) at Yasuní (13 species) shows significant compensatory dynamics at ~0.3-0.54 year scales. The most abundant Urticaeae species peak at distinctly different parts of the year, and even as some species decline in reproduction over these scales, others replace them, so that there is always substantial reproduction by some members of the family.

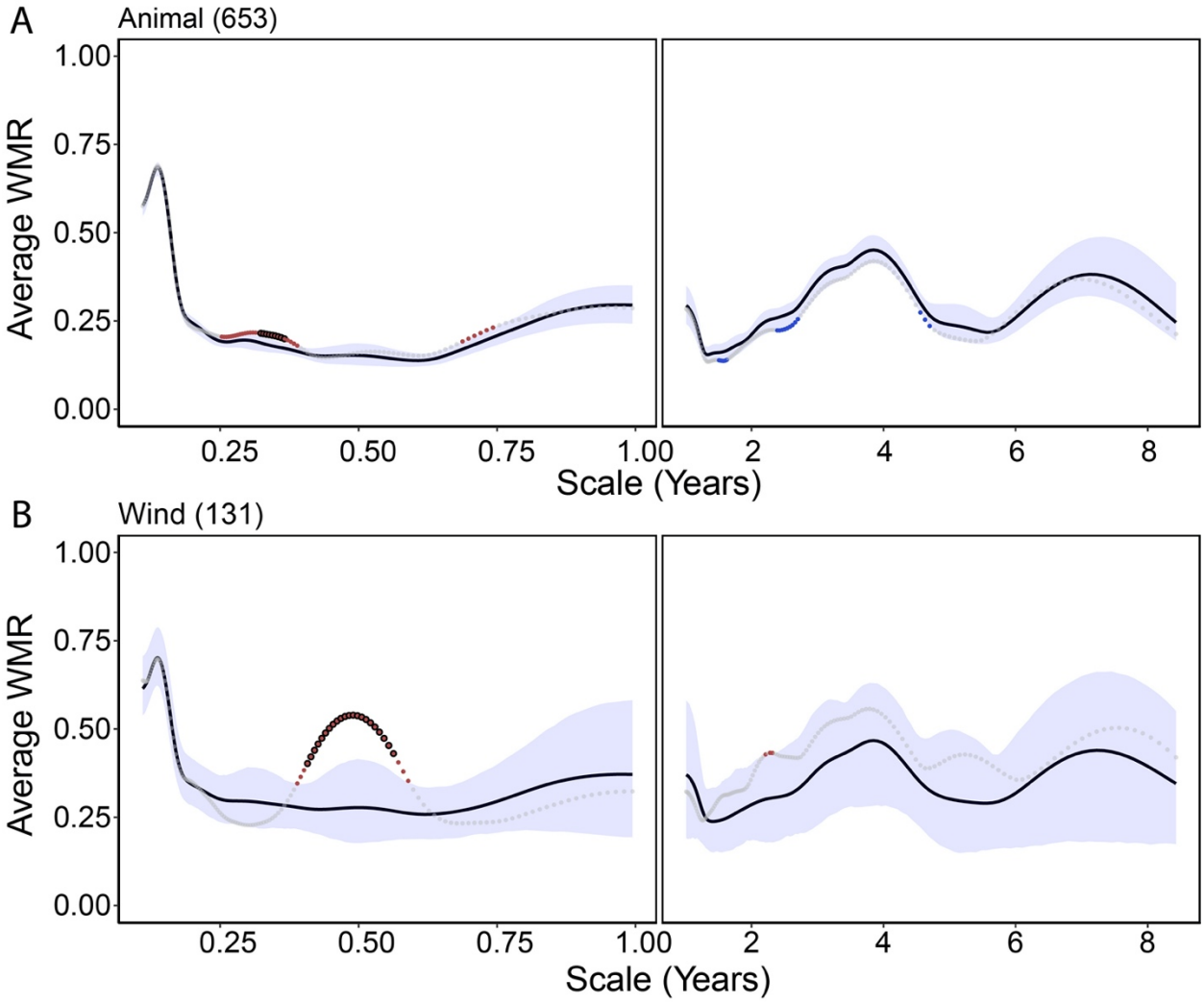


Phenology among species sharing dispersal modes

Among the species with putatively similar dispersal mechanisms, we found significant synchrony at multiple scales at the ever-wet Yasuní (Figure 5). When considering all growth forms, we found animal dispersed species (N=653) exhibit significant synchrony at ~3 month scales but no significant compensatory dynamics (FDR = 0.05). For wind-dispersed species

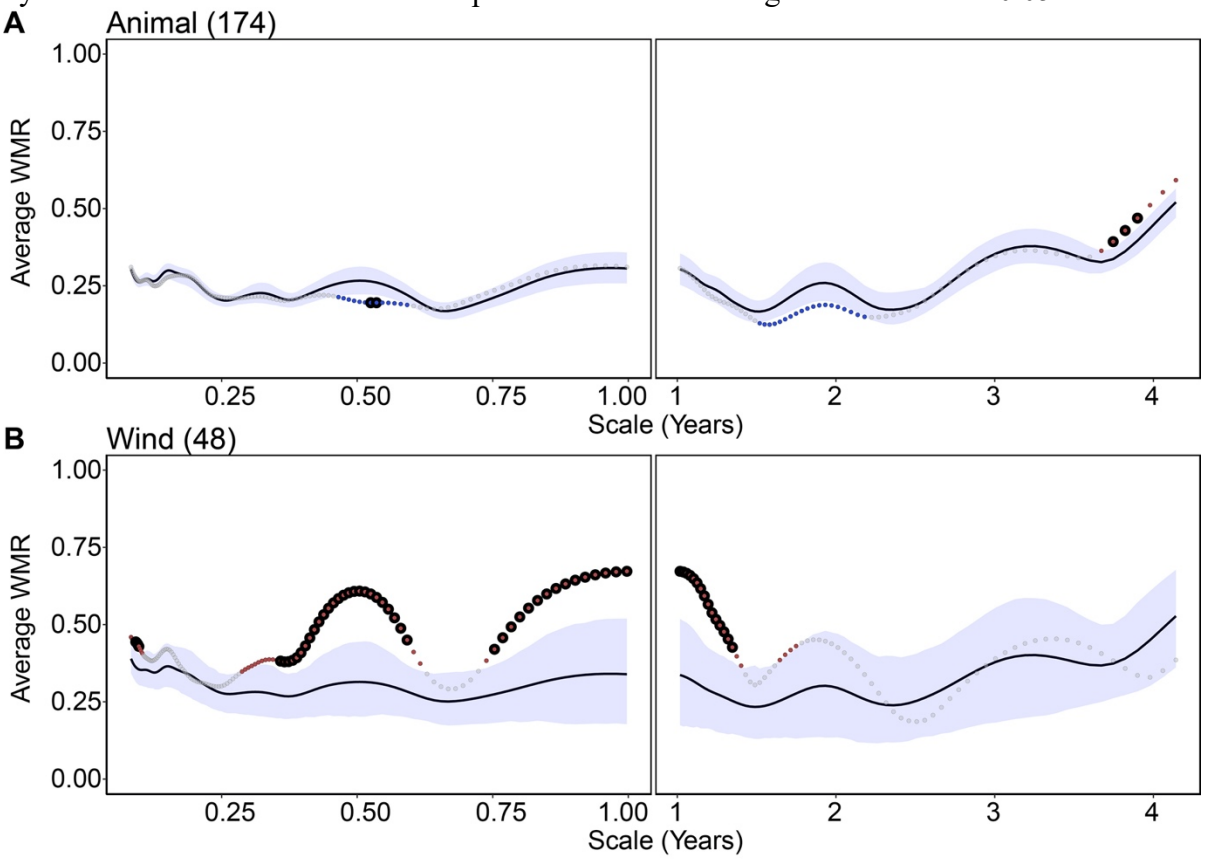
(N=131), we found significant synchrony at ~6 month scales, consistent with the peak in wind variability at ~6 and 12 month scales (Figure S2). For only trees, we did not find significantly non-random phenology for groups of species with similar size fruits or similar abiotic dispersal mechanisms (though some were nominally significant $p < 0.05$, Figure S3).

Figure 5. The averaged wavelet modulus ratio for all plant species in the ever-wet Yasuní based on dispersal syndrome. The number in parentheses represents the number of species within the animal and wind-dispersed groups. The light blue ribbon represents the 2.5-97.5th percentiles of the null-distribution generated through bootstrapping. Any points that lie above the ribbon were considered nominally significant and synchronous while any points below the ribbon indicated nominally significant, compensatory dynamics. Thick borders around the points indicate significant at FDR = 0.05.



At seasonally dry Cocha Cashu, we found significant synchrony and compensatory dynamics (Figure 6). Among all growth forms, wind-dispersed species exhibited strong synchrony at ~6 and ~12 month timescales (Figure S4). Wind variation also showed a peak in variability at ~12 month scales (and ~6 month, depending on the metric, Figure S5). Animal-dispersed species showed significant compensatory dynamics at ~6 month timescales and significant synchrony at ~4 year timescales (FDR 0.05). For only tree species, we did not find non-random phenology for groups of species with similar dispersal syndromes or similar abiotic dispersal mechanisms (though some were nominally significant, Figure S6).

Figure 6: The averaged wavelet modulus ratio for all plant species in seasonally dry Cochu Cashu based on dispersal syndrome. The number in parentheses represents the number of species within the animal and wind-dispersed groups. The ribbon represents the null distribution generated through bootstrapping. Any points that lie above the ribbon was considered significant and synchronous while any points below the ribbon indicated significant, compensatory dynamics. Thick borders around the points indicate those significant at FDR=0.05.

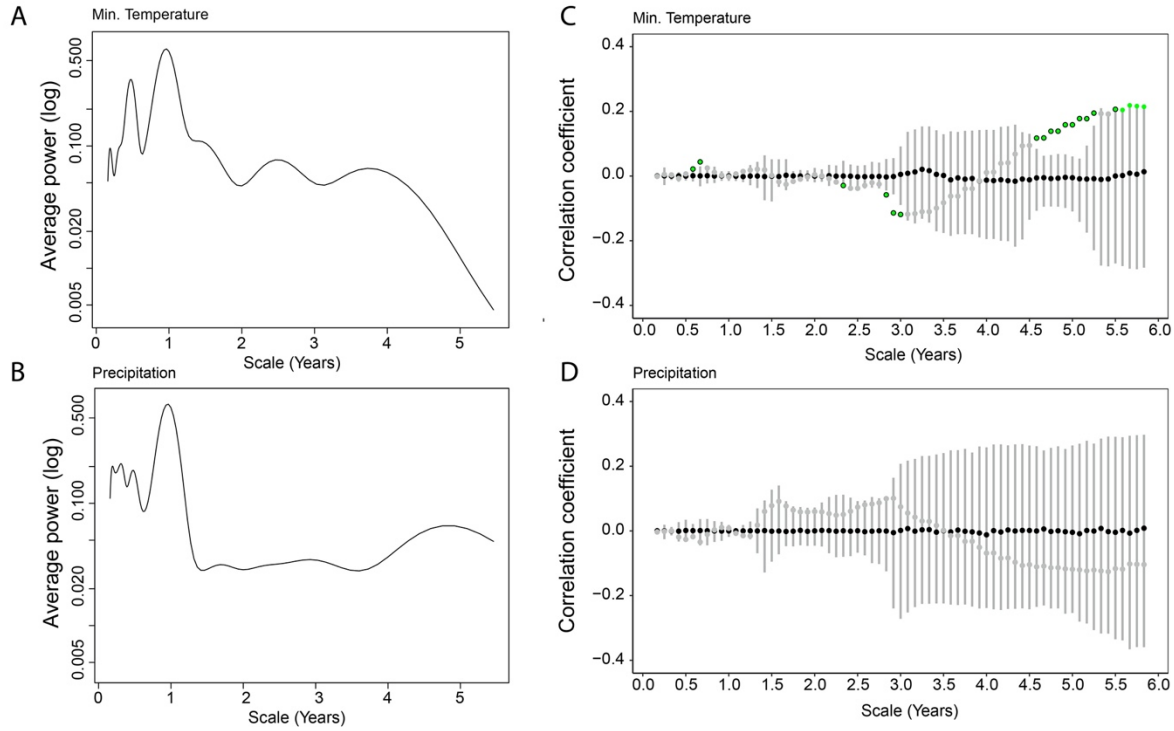


Temperature, precipitation, and community-wide phenology

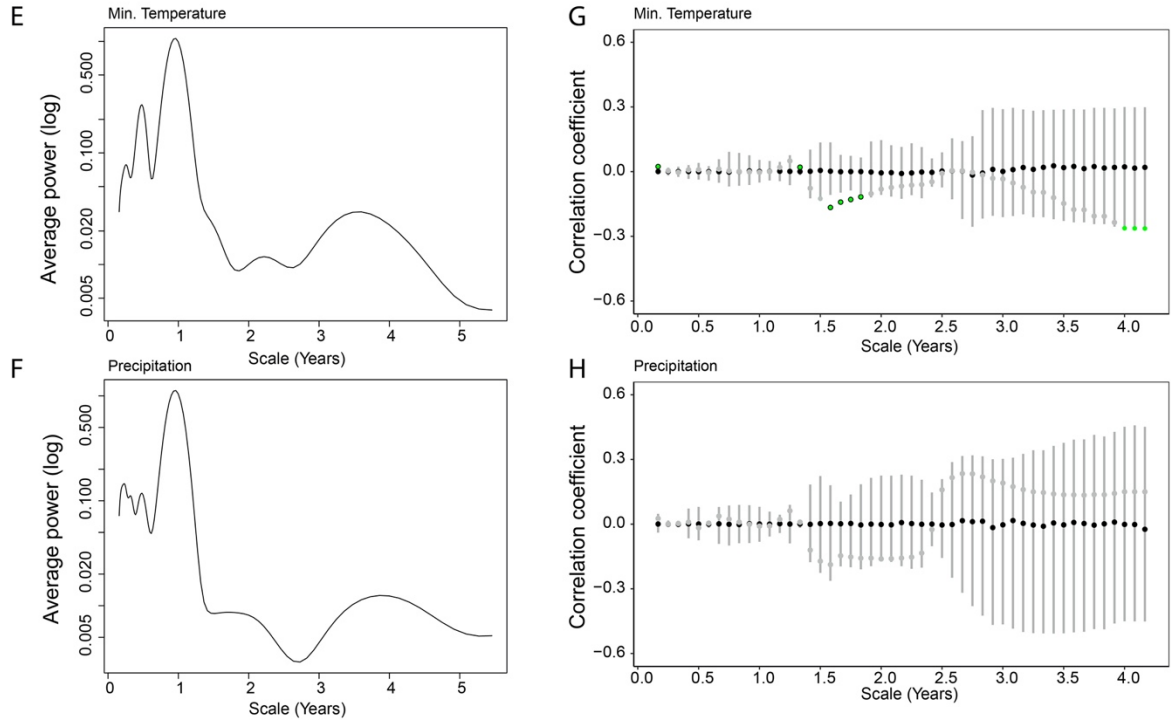
There was a significant relationship between the temperature, but not precipitation, and community-wide WMR (Figure 7). The ever-wet site, Yasuní, had a positive temperature-WMR relationship at ~6-7 mo scales, indicating twice yearly increases in among-species seed rain synchrony with warming temperatures. Relatedly, there is a ~6 mo scale variation in minimum temperature at Yasuní associated with a peak in warmth in April, a 1ºC cooler period in June-September followed by warming up again in October (Figure S7). At Yasuní, there was also a significant positive correlation between WMR and minimum temperature at the ~4-6 yr scale. The positive coefficients indicate that warmer periods were correlated with increases in the WMR, i.e. community synchrony. At the seasonally dry Cocha Cashu at the ~1.5 yr scale, there was a significant negative correlation between the WMR and the minimum temperature, indicating that cooler periods were associated with greater WMR and synchronous seed rain. Unexpectedly, there was no increase in synchrony at Cocha Cashu during wet or dry periods.

Figure 7: (A,B,E,F) Wavelet power across time scales for each climate variable, with higher power for a given scale indicating greater variability. (C,D,G,H) The Pearson correlation coefficient at varying scales (months) between the wavelet modulus ratio (WMR) and wavelet-transformed minimum temperature or precipitation. Positive correlations indicate that increases in the climate variable are associated with greater whole community synchrony, while negative correlations indicate the climate variable is associated with weaker whole community synchrony (or greater compensatory dynamics). The vertical lines represent the 2.5-97.5th percentiles of the null distribution (black circle shows mean of null) through phase-randomization permutation. Any points outside the distribution are considered nominally significant (colored in green).

Yasuní



Cosha Cashu



460 **DISCUSSION**

461 Communities harbor extensive phenological diversity among member species, especially in
462 tropical wet forests (Frankie et al. 1974). This phenological diversity might help explain species
463 coexistence within communities if phenology is a key axis of niche partitioning among species.
464 That is, if phenological differences reduce competition among species for mutualists involved in
465 reproduction (e.g. frugivores) or reduce competition for the resources required for reproduction
466 or seedling survival (Usinowicz et al. 2017), then these species might be more likely to coexist
467 (Godoy and Levine 2013). However, temporal traits (e.g. aspects of phenology) remain lesser
468 known dimensions of diversity in ecological communities. In particular, in hyperdiverse
469 communities, most pairs of species likely have weak interactions, making it challenging to infer
470 how species interactions structure communities.

471 We used flexible spectral analyses to show evidence that Amazonian plant communities
472 frequently exhibit significant reproductive synchrony at the whole community level, suggesting
473 shared response to environment or positive interactions among species structure community
474 phenology. However, groups of species sharing dispersal mechanisms or related groups of
475 species sometimes exhibited significant compensatory (anti-synchronous) dynamics.

476 **Do communities exhibit synchronous or compensatory reproduction?**

477 Overall, we found many cases of strong synchronous dynamics in seed rain at the whole
478 community level, and almost no significant whole-community compensatory dynamics. This
479 synchrony suggests whole-community dynamics are driven by shared responses to fluctuations
480 in environmental (abiotic or biotic) conditions such as rainfall or frugivore abundance, or by
481 positive heterospecific interactions such as enhanced frugivore attraction or natural enemy
482 satiation (van Schaik et al. 1993). When interpreting our results, note that ecological forces

483 shaping phenology of fruiting and seed release are also tied to other developmental stages.
484 Flowering, leaf emergence and senescence, and seed germination all can interact with abiotic and
485 biotic conditions. Future research will benefit from an integrative understanding of how full life
486 cycle phenology interacts with environment (Borchert 1996).

487 Note that in our study we were only able to observe patterns deviating from our
488 permutation-based null. Processes that influence the shape (but not the phase, which we
489 randomized to generate our null) of the phenology of the pool of species present are outside our
490 scope of detection (Case et al. 1983).

491 **Are compensatory and synchronous dynamics scale-specific or non-stationary?**

492 At both sites, synchronous seed fall was strongest and most consistent across sites at scales of
493 approximately 1-2 mos, 1 yr, and >3 yrs. The fastest scale of synchrony at ever-wet Yasuní may
494 represent shared and rapid community responses to relatively brief cloudless periods of high
495 radiation alternating with cloudy periods, similar to what was observed in response to rainfall in
496 a seasonally dry forest (Lasky et al. 2016). However, we did not find a correlation between
497 temperature or rainfall and WMR at the ~1 mo scale. Additionally, the synchrony at 1 and >3 yr
498 periods at both sites might reflect shared responses to annual or longer scale oscillations of
499 environmental conditions, given that we found WMR associated with temperature fluctuations at
500 these scales. At both sites, the yearly and super-annual patterns of synchrony were fairly
501 consistent throughout the study. Clear yearly fluctuations were visible even in the raw species or
502 seed counts over time, highlighting the strength of synchrony at this scale, despite the presence
503 of many reproductive species year-round (Figure 2 B,C,E,F).

504 At seasonally dry Cocha Cashu, we observed strong non-stationarity. We observed a shift
505 from essentially random among-species phenology to synchronous dynamics, across all time

506 scales <1 yr in 2007 (Figure 2D). The ecological explanation for this shift is unclear, but many
507 species decreased reproduction in this period and then subsequently increased to a high level of
508 reproduction (Figure 2 E&F). The deep decrease followed by a high peak in reproduction might
509 indicate multiple species were accumulating resources synchronously (reducing reproduction) in
510 order to subsequently invest a large amount in reproduction, akin to, but not as dramatic as,
511 bursts of reproduction in masting species (Janzen 1974, Ashton et al. 1988).

512 **Is evidence for phenological partitioning strongest among ecologically similar species?**

513 In contrast to our findings at the whole community level, which lacked compensatory dynamics,
514 we found significant compensatory dynamics within focal groups of species (confamilials and
515 species with similar animal seed dispersers). These compensatory dynamics are evidence for
516 phenological niche partitioning; where one species increases in reproduction at times when
517 others are decreasing, allowing partitioning of resources.

518 Whole community patterns may obscure phenological niche partitioning that occurs
519 within groups of closely interacting species. Previous studies that have shown evidence for such
520 partitioning have been largely focused on groups of closely related species hypothesized to be
521 closely interacting due to shared pollinators or mutualists (Gentry 1974, Ashton et al. 1988,
522 Botes et al. 2008). Future efforts might use our approach to identify these species based on non-
523 random phenological patterns instead of relying on prior knowledge. Annonaceae species
524 showed similar patterns of compensatory reproduction for within-year timescales at both sites,
525 perhaps indicating consistency in phenological niche partitioning among species in this family.

526 The ultimate mechanisms leading to compensatory reproduction among species may be
527 due to divergent responses to environmental fluctuations, or due to community assembly or
528 coevolution leading to cooccurrence of species with distinct phenology (Robertson 1895,

Rathcke and Lacey 1985). It is challenging to determine from our approach whether compensation is due to phenological niche partitioning with respect to abiotic or biotic components of environment. An example potentially misleading scenario is where a group of species share dispersal mechanisms but also other traits, the latter of which lead to competition that is ameliorated by phenological niche partitioning. To conclusively identify niche partitioning requires additional evidence. For example, (Botes et al. 2008) showed how species that deposit pollen on the same location on pollinators' bodies (suggesting competition or interference in pollination) exhibited compensatory flowering, but species depositing pollen on different locations did not. (Wheelwright 1985) observed fruit removal to test whether overlapping phenology indicated competition for frugivores (it did not). If compensatory phenology of seed rain does reflect biotic interactions, it will require additional study to determine if compensation is due to seed dispersal or processes affecting other stages (e.g. seedling survival).

Synchrony among related species or species sharing dispersal mode

We found that among all growth forms, wind-dispersed species exhibit strong synchrony of seed rain, particularly at time scales indicative of shared abiotic niches. At both sites we found significant ~6 mo synchrony among wind-dispersed species, consistent with the twice-yearly peaks in wind speed observed at nearby weather stations (Figures S2, S4, S5). Cocha Cashu has a strong peak in wind speed in September (Figure S5), also consistent with the synchrony at this site observed among wind-dispersed species at ~1 yr periods (Figures 6 & S4). Near Yasuní the wind had a broad peak in average speed from September to November with a small peak in April (Figure S2). The tendency for wind-dispersed species to synchronously release seed during windy seasons has been reported in the literature (Frankie et al. 1974, Janzen 1974, Detto et al. 2018) and can be considered a positive control for our approach.

Community phenology and abiotic fluctuations

We found evidence that community-wide phenology was driven by climate fluctuations, with WMR being significantly associated with temperature at both sites at multiple scales. (Gentry 1974) hypothesized that phenological diversity of communities was promoted by more permissive abiotic conditions and longer growing seasons compared to seasonally harsh enviornments, where the range of potential phenologies is narrower. We do not see evidence for this based on fluctuations in climate within our two tropical sites; the direction of the WMR-temperature associations contradicted this hypothesis. At both sites, sub-annual WMR was positively associated with temperature, indicating greater synchrony (as opposed to phenological diversity) at warmer times of the year. Our findings may signify that the community-wide trend is for a degree of synchrony to exploit favorable conditions during warmer parts of the year, potentially due to greater light resources (Detto et al. 2018).

We did not observe differences between ever-wet Yasuní and seasonally dry Cocha Cashu that can easily be explained by the sites' precipitation seasonality. Even though Yasuní may represent the most climatically favorable site, the whole community still showed strong synchrony. By contrast, (Lasky et al. 2016) previously found whole-community compensatory dynamics of seed rain at sub-annual scales and synchrony at other scales in a much less diverse Puerto Rican tropical dry forest. Furthermore, there was no link between the strength of synchrony at our seasonally dry site (Cocha Cashu) and precipitation (Figure 6).

Super-annual WMR showed strong associations with temperature at some scales. In particular, at Yasuní at >5 yr scales we found higher synchrony in warmer periods, perhaps corresponding to enhanced community synchrony driven by longer range climatic oscillations like the El Niño Southern Oscillation. At Barro Colorado Island in Panama, community-wide

peaks in seed rain occur during ENSO events (Detto et al. 2018), presumably as trees had shared responses to increased light during these dry and warm periods (Wright and Calderón 2006).

Conclusion

Here we showed how whole-community phenology in diverse plant communities is largely characterized by synchrony, and to a certain degree in association with warmer temperatures. However, we also uncovered evidence that groups of related or ecologically similar species often show compensatory patterns of seed rain, indicating potential phenological axes of niche partitioning that might promote species coexistence. Our results highlight the scale-specific and sometimes non-stationary characteristics of community phenology. Flexible multi-scale analyses may reveal evidence of scale-specific niche partitioning and environmental filtering.

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References

Albrecht, J., V. Bohle, D. G. Berens, B. Jaroszewicz, N. Selva, and N. Farwig. 2015. Variation in neighbourhood context shapes frugivore-mediated facilitation and competition among co-dispersed plant species. Journal of Ecology 103:526–536.

Alvarez-Buylla, E. R., and M. Martinez-Ramos. 1992. Demography and Allometry of Cecropia Obtusifolia, a Neotropical Pioneer Tree - An Evaluation of the Climax-Pioneer Paradigm for Tropical Rain Forests. Journal of Ecology 80:275–290.

Ashton, P. S., T. J. Givnish, and S. Appanah. 1988. Staggered Flowering in the Dipterocarpaceae: New Insights Into Floral Induction and the Evolution of Mast Fruiting in the Aseasonal Tropics. The American Naturalist 132:44–66.

Bagchi, R., V. Swamy, J.-P. L. Farfan, J. Terborgh, C. I. A. Vela, N. C. A. Pitman, and W. G. Sanchez. 2018. Defaunation increases the spatial clustering of lowland Western Amazonian tree communities. Journal of Ecology 106:1470–1482.

Baird, J. W. 1980. The Selection and Use of Fruit by Birds in an Eastern Forest. The Wilson Bulletin 92:63–73.

Benjamini, Y., and D. Yekutieli. 2001. The control of the false discovery rate in multiple testing under dependency. Annals of Statistics 29:1165–1188.

Bernard-Verdier, M., M.-L. Navas, M. Vellend, C. Violle, A. Fayolle, and E. Garnier. 2012. Community assembly along a soil depth gradient: contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology 100:1422–1433.

Borchert, R. 1996. Phenology and flowering periodicity of Neotropical dry forest species: evidence from herbarium collections. Journal of Tropical Ecology 12:65–80.

Botes, C., S. D. Johnson, and R. M. Cowling. 2008. Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology. Oikos 117:875–882.

Carlo, T. A. 2005. Interspecific Neighbors Change Seed Dispersal Pattern of an Avian-Dispersed Plant. Ecology 86:2440–2449.

Case, T. J., J. Faaborg, and R. Sidell. 1983. THE ROLE OF BODY SIZE IN THE ASSEMBLY OF WEST INDIAN BIRD COMMUNITIES. Evolution; International Journal of Organic Evolution 37:1062–1074.

Cazelles, B., M. Chavez, D. Berteaux, F. Ménard, J. O. Vik, S. Jenouvrier, and N. C. Stenseth. 2008. Wavelet analysis of ecological time series. Oecologia 156:287–304.

Chang-Yang, C.-H., I.-F. Sun, C.-H. Tsai, C.-L. Lu, and C.-F. Hsieh. 2016. ENSO and frost codetermine decade-long temporal variation in flower and seed production in a subtropical rain forest. Journal of Ecology 104:44–54.

Cornejo, F., and J. Janovec. 2010. Seeds of Amazonian plants. Princeton University Press.

Davies, T. J., E. M. Wolkovich, N. J. B. Kraft, N. Salamin, J. M. Allen, T. R. Ault, J. L. Betancourt, K. Bolmgren, E. E. Cleland, B. I. Cook, T. M. Crimmins, S. J. Mazer, G. J. McCabe, S. Pau, J. Regetz, M. D. Schwartz, and S. E. Travers. 2013. Phylogenetic conservatism in plant phenology. Journal of Ecology 101:1520–1530.

Detto, M., S. J. Wright, O. Calderón, and H. C. Muller-Landau. 2018. Resource acquisition and reproductive strategies of tropical forest in response to the El Niño–Southern Oscillation. Nature Communications 9:1–8.

Donoghue, M. J. 2008. A phylogenetic perspective on the distribution of plant diversity. Proceedings of the National Academy of Sciences of the United States of America 105:11549–11555.

Elzinga, J. A., A. Atlan, A. Biere, L. Gigord, A. E. Weis, and G. Bernasconi. 2007. Time after time: flowering phenology and biotic interactions. Trends in Ecology & Evolution 22:432–439.

Encinas-Viso, F., T. A. Revilla, and R. S. Etienne. 2012. Phenology drives mutualistic network structure and diversity. Ecology Letters 15:198–208.

European Centre for Medium-Range Weather Forecasts. 2009. ERA-Interim Project. Research Data Archive at the National Center for Atmospheric Research, Computational and Information Systems Laboratory.

Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. The Journal of Ecology:881–919.

Funk, C. C., P. J. Peterson, M. F. Landsfeld, D. H. Pedreros, J. P. Verdin, J. D. Rowland, B. E. Romero, G. J. Husak, J. C. Michaelsen, and A. P. Verdin. 2014. A Quasi-Global Precipitation Time Series for Drought Monitoring.

Gentry, A. H. 1974. Flowering Phenology and Diversity in Tropical Bignoniaceae. Biotropica 6:64–68.

Gentry, A. H. 1993. Four neotropical rainforests. Yale University Press.

Gentry, A. H. 1996. A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru): With Supplementary Notes on Herbaceous Taxa. University of Chicago Press.

Godoy, O., and J. M. Levine. 2013. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. Ecology 95:726–736.

Gonzalez, A., and M. Loreau. 2009. The Causes and Consequences of Compensatory Dynamics in Ecological Communities. Annual Review of Ecology, Evolution, and Systematics 40:393–414.

Harrison, R. D., S. Tan, J. B. Plotkin, F. Slik, M. Detto, T. Brenes, A. Itoh, and S. J. Davies. 2013. Consequences of defaunation for a tropical tree community. Ecology Letters 16:687–694.

Janzen, D. H. 1974. Tropical Blackwater Rivers, Animals, and Mast Fruiting by the Dipterocarpaceae. Biotropica 6:69–103.

Jones, F. A., and L. S. Comita. 2010. Density-dependent pre-dispersal seed predation and fruit set in a tropical tree. Oikos 119:1841–1847.

Kalko, E. K. V., and M. A. Condon. 1998. Echolocation, Olfaction and Fruit Display: How Bats Find Fruit of Flagellichorous cucurbits. Functional Ecology 12:364–372.

Karlsson, P. S., and M. Méndez. 2005. 1 - The Resource Economy of Plant Reproduction. Pages 1–49 *in* E. G. Reekie and F. A. Bazzaz, editors. Reproductive Allocation in Plants. Academic Press, Burlington.

Keitt, T. H. 2008. Coherent ecological dynamics induced by large-scale disturbance. Nature 454:331–334.

Keitt, T. H., and D. L. Urban. 2005. Scale-Specific Inference Using Wavelets. Ecology 86:2497–2504.

Lasky, J. R., M. Uriarte, and R. Muscarella. 2016. Synchrony, compensatory dynamics, and the functional trait basis of phenological diversity in a tropical dry forest tree community: effects of rainfall seasonality. Environmental Research Letters 11:115003.

Pitman, N. C. A., J. W. Terborgh, M. R. Silman, P. Núñez V., D. A. Neill, C. E. Cerón, W. A. Palacios, and M. Aulestia. 2002. A comparison of tree species diversity in two upper amazonian forests. Ecology 83:3210–3224.

Poulin, B., S. J. Wright, G. Lefebvre, and O. Calderón. 1999. Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. Journal of Tropical Ecology 15:213–227.

Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2001. The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:2383–2389.

Rathcke, B., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics:179–214.

Robertson, C. 1895. The Philosophy of Flower Seasons, and the Phaenological Relations of the Entomophilous Flora and the Anthophilous Insect Fauna. The American Naturalist 29:97–117.

Rösch, A., and H. Schmidbauer. 2016. WaveletComp 1.1: A guided tour through the R package. URL: http://www. hsstat. com/projects/WaveletComp/WaveletComp_guided_tour. pdf.

Russo, S. E. 2003. Responses of dispersal agents to tree and fruit traits in Virola calophylla (Myristicaceae): implications for selection. Oecologia 136:80–87.

Saracco, J. F., J. A. Collazo, M. J. Groom, and T. A. Carlo. 2005. Crop Size and Fruit Neighborhood Effects on Bird Visitation to Fruiting Schefflera morototoni Trees in Puerto Rico. Biotropica 37:81–87.

van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. Annual Review of Ecology and Systematics 24:353–377.

Silman, M. R. 2007. Plant species diversity in Amazonian forests. Pages 269–294 *in* M. B. Bush and J. R. Flenley, editors. Tropical Rainforest Responses to Climatic Change. Springer Berlin Heidelberg, Berlin, Heidelberg.

Smythe, N. 1970. Relationships between Fruiting Seasons and Seed Dispersal Methods in a Neotropical Forest. The American Naturalist 104:25–35.

Stevenson, P. R., M. C. Castellanos, J. C. Pizarro, and M. Garavito. 2002. Effects of Seed Dispersal by Three Ateline Monkey Species on Seed Germination at Tinigua National Park, Colombia. International Journal of Primatology 23:1187–1204.

Stiles, F. G. 1977. Coadapted Competitors: The Flowering Seasons of Hummingbird-Pollinated Plants in a Tropical Forest. Science 198:1177–1178.

Usinowicz, J., C.-H. Chang-Yang, Y.-Y. Chen, J. S. Clark, C. Fletcher, N. C. Garwood, Z. Hao, J. Johnstone, Y. Lin, M. R. Metz, T. Masaki, T. Nakashizuka, I.-F. Sun, R. Valencia, Y. Wang, J. K. Zimmerman, A. R. Ives, and S. J. Wright. 2017. Temporal coexistence mechanisms contribute to the latitudinal gradient in forest diversity. Nature 550:105–108.

Valencia, R., R. Condit, R. B. Foster, K. Romoleroux, G. Villa Munoz, J.-C. Svenning, E. Magård, M. S. Bass, E. C. Losos, and H. Balslev. 2004a. Yasuni forest dynamics plot, Ecuador. Tropical forest diversity and dynamism: findings from a large-scale plot network:609–620.

Valencia, R., R. B. Foster, G. Villa, R. Condit, J.-C. Svenning, C. Hernández, K. Romoleroux, E. Losos, E. Magård, and H. Balslev. 2004b. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. Journal of Ecology 92:214–229.

Vasseur, D. A., J. W. Fox, A. Gonzalez, R. Adrian, B. E. Beisner, M. R. Helmus, C. Johnson, P. Kratina, C. Kremer, C. de Mazancourt, E. Miller, W. A. Nelson, M. Paterson, J. A. Rusak, J. B. Shurin, and C. F. Steiner. 2014. Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems. Proceedings of the Royal Society B: Biological Sciences 281.

Vasseur, D. A., U. Gaedke, and K. S. McCann. 2005. A seasonal alternation of coherent and compensatory dynamics occurs in phytoplankton. Oikos 110:507–514.

Wheelwright, N. T. 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. Oikos:465–477.

Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment 9:287–294.

Wolkovich, E. M., B. I. Cook, and T. J. Davies. 2014. Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. New Phytologist 201:1156–1162.

Wright, S. J., and O. Calderon. 1995. Phylogenetic Patterns among Tropical Flowering Phenologies. Journal of Ecology 83:937–948.

Wright, S. J., and O. Calderón. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. Ecology Letters 9:35–44.

Xiao, X., S. Hagen, Q. Zhang, M. Keller, and B. M. Iii. 2006. Detecting leaf phenology of seasonally moist tropical forests in South America with multi-temporal MODIS images. Remote Sensing of Environment 103 :465–473.

Supplementary Material

Seed rain data

Some species at Yasuní were not well separated in earlier years and thus these species were excluded from some analyses. For the family-level analyses, we censored Clusiaceae (due to issues with *Clusia* identification) and Solanaceae before 1/1/2007. For the family-level analyses of Moraceae, time series were censored before 1/1/2008 (due to issues with *Ficus* identification). Species without identification issues in these families were included in whole-community analyses.

At Yasuní, seeds and whole mature fruits were counted individually; fruit segments (such as capsule values) were aggregated and counted as the equivalent number of whole fruit. The number of seeds per fruit was counted directly from fresh specimens, our reference collection or photographs, or estimated from generic or familial data. These estimates of seeds per fruit were used to impute seed number from counted fruits.

For fruits collected at Cocha Cashu, fruit counts were converted to seed counts by multiplying by the average number of seeds per fruit for that species. Data on seeds per fruit were obtained from the literature (Alvarez-Buylla and Martinez-Ramos 1992, Gentry 1996, Kalko and Condon 1998, Stevenson et al. 2002, Russo 2003, Cornejo and Janovec 2010). For both sites, unidentified seeds not counted as specific morphospecies were excluded.

Wavelet analyses

For each species, we summed seed rain for each time point across traps and then log-transformed the count, resulting in a single time series for each species. We then applied the continuous wavelet transformation to each species' time series using the Morlet wavelet

$$W_k\,(a,\tau) \;=\; \frac{1}{\sqrt{a}}\int_{-\infty}^{\infty} x_k(t)\varphi\,\frac{t-\tau}{a}\,d\tau \qquad \text{(Equation 1).}$$

Here, the wavelet coefficient W_x is the cross-correlation between species' k seed rain time series, x_k(t), and the complex-valued Morlet wavelet φ,

$$\varphi(\tau) = \pi^{-\frac{1}{4}}\exp\,(2\pi i\tau - \frac{1}{2}\tau^2) \qquad \text{(Equation 2).}$$

A complex Morlet wavelet is a Gaussian-tapered complex sine wave, where the tapering allows one to capture localized patterns. The wavelet is stretched to different scales, a, such that the Gaussian taper occurs over different scales, and translated across the different points in time of the study, τ.

After each species' seed rain time series was wavelet transformed, we then sought to characterize each species' phenology in relation to the entire community of species, or taxonomic/dispersal group of species. To do so, we calculated the wavelet modulus ratio (WMR). This quantifies the relationship between the variation in the aggregate community-wide reproduction (numerator of Eqn. 3) relative to variation in species-level reproduction (denominator of Eqn. 3) at scale a and centered on time t,

$$WMR(t,s) = \frac{\Lambda_{\mathrm{t,a}}(|\sum_k W_k(\tau,a)|)}{\Lambda_{\mathrm{t,a}}\;\sum_k |W_k(\tau,a)|} \qquad \text{(Equation 3)}$$

where $\Lambda_{t,a}(.) = \int_{-\infty}^{\infty} e^{-\frac{1}{2}\left(\frac{t-\tau}{a}\right)^2}(\cdot)d\tau$ and $|\cdot|$ represents the complex norm (Keitt 2008, Keitt 2014, Lasky et al. 2016) (Figure 1). When species seed rain dynamics through time perfectly cancel each other out, the sum in the numerator of Eqn 3 is equal to zero (declining seed rain is balanced by increasing seed rain). Thus at zero, the WMR indicates complete compensation or anti-synchrony: all species-level dynamics are compensated so that community level reproduction is constant. At unity, the WMR at the time period signifies complete phenological

synchrony among the species, as species-level phenological dynamics are completely reflected at the community level.

Figure S1. Map showing locations of the Yasuní (YAS) and Cocha Cashu (CC) plots.

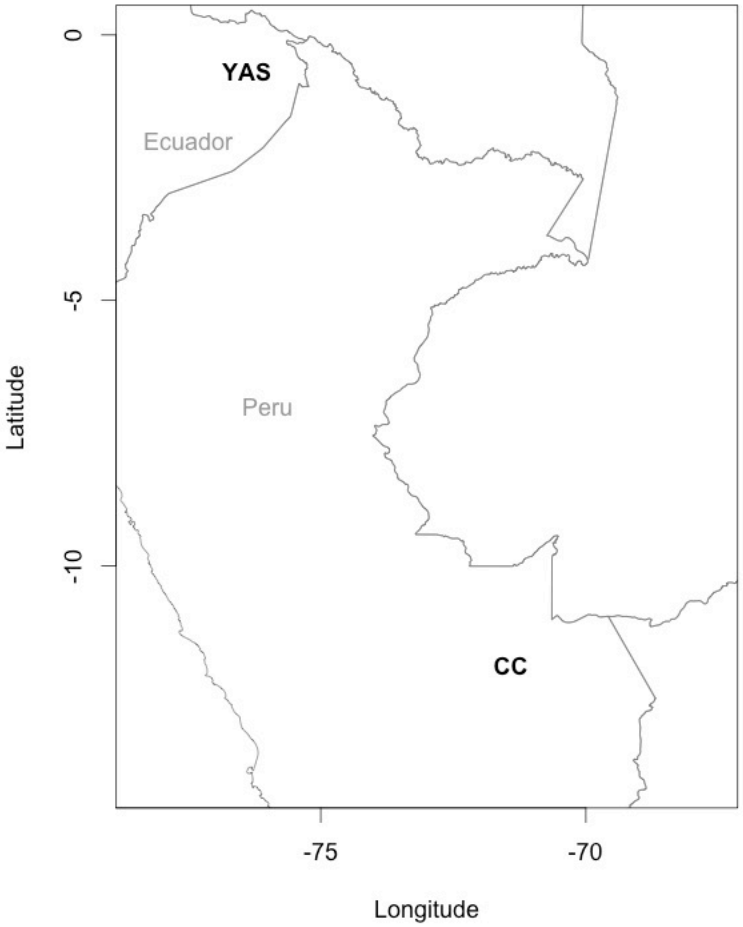

Figure S2. Wavelet power analysis (left panels) and average monthly wind (right panels) for the wind station data near Yasuní (1995-2012). Two wind parameters are shown: proportion of time calm (vs windy, top panels) and the average wind speed (bottom). Missing values were imputed using a weighted moving average with k = 2 in the imputeTS package in R.

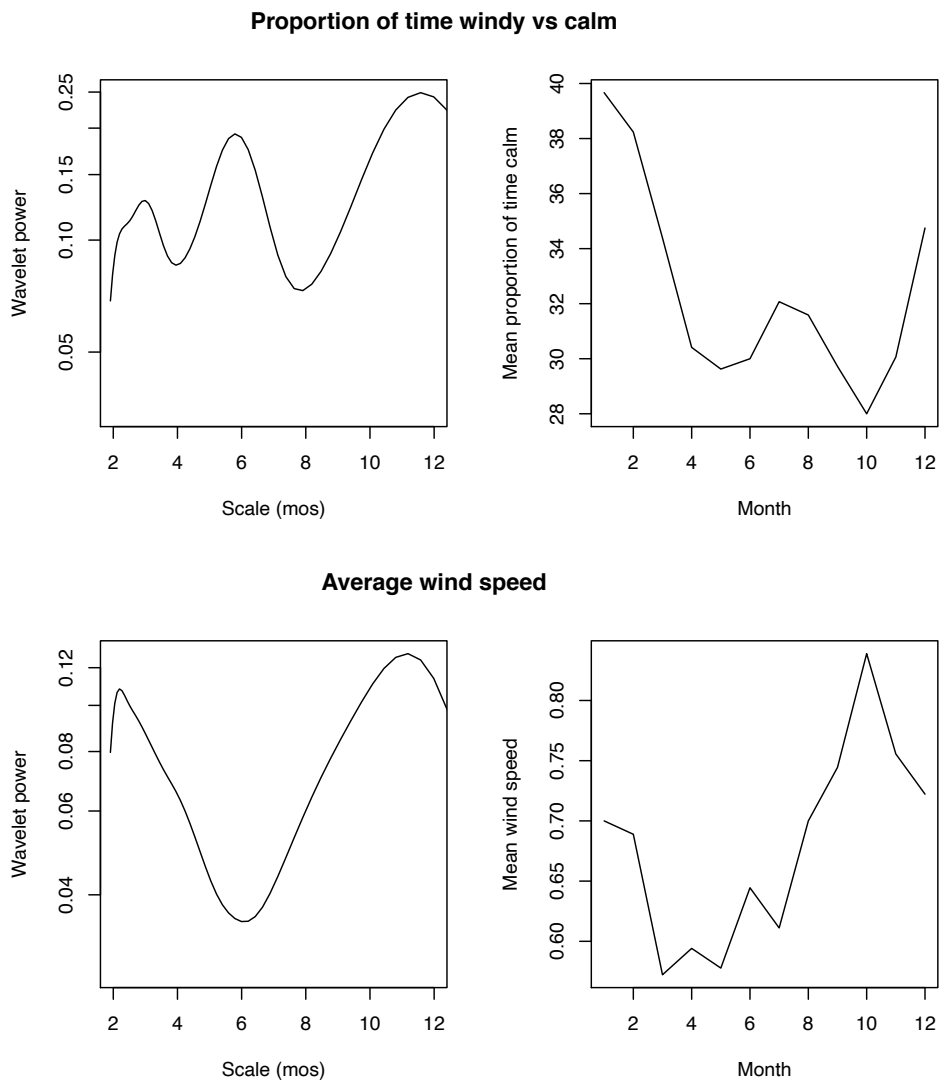

Figure S3. The averaged wavelet modulus ratio for tree species in Yasuní based on fruit size or dispersal syndrome. The number in parentheses represents the number of species within the dispersal group. The blue ribbon represents the null-distribution generated through bootstrapping (n=1000). Any points that lie outside the ribbon were considered nominally significant ($p<0.05$) though no points were significant at FDR=0.05.

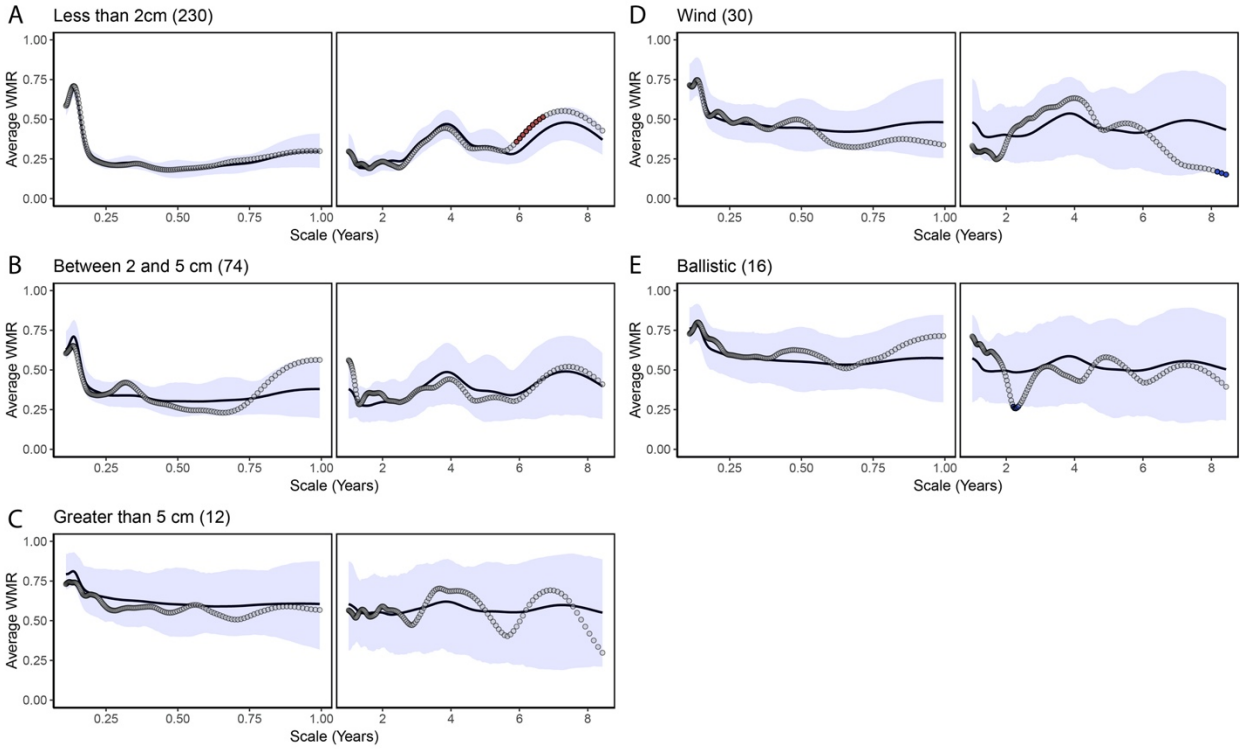

Figure S4. Time series of wind-dispersed seed counts (with a 6 week smooth for visualization) at Cocha Cashu, highlighting the twice yearly peaks and 6 month scale synchrony.

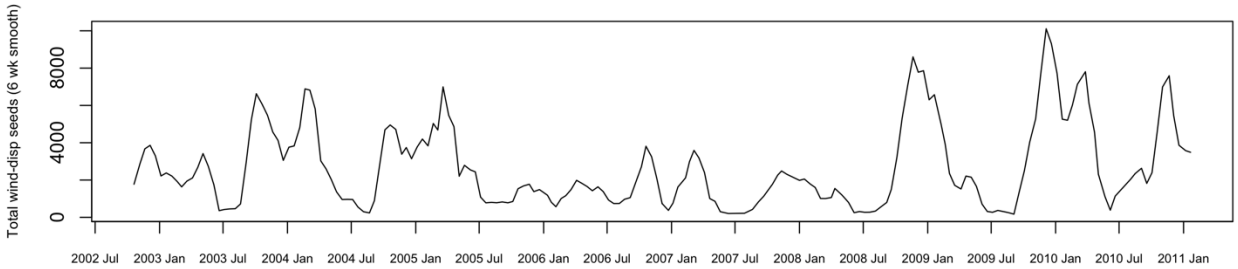

Figure S5. Wavelet power (top panel) and monthly averages (bottom panel) for average wind speed at a weather station near Cocha Cashu, 2004-2009.

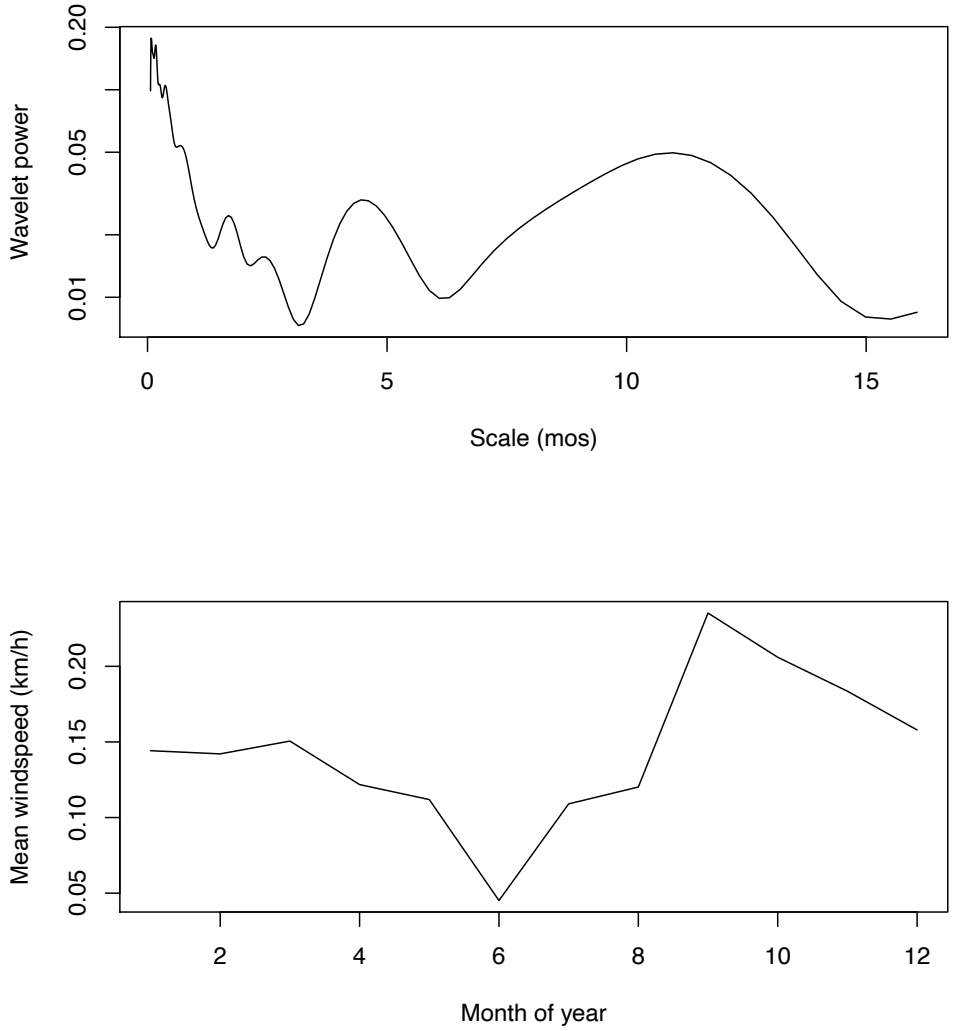

Figure S6. The averaged wavelet modulus ratio for tree species in Cochu Cashu based on dispersal syndrome. The number in parentheses represents the number of species within each group. The blue ribbon represents the null distribution generated through bootstrapping (n=1000). Any points that lie above the ribbon was considered significant and synchronous while any points below the ribbon indicated significant, compensatory dynamics. Any points that lie outside the ribbon were considered nominally significant ($p<0.05$) though no points were significant at FDR=0.05.

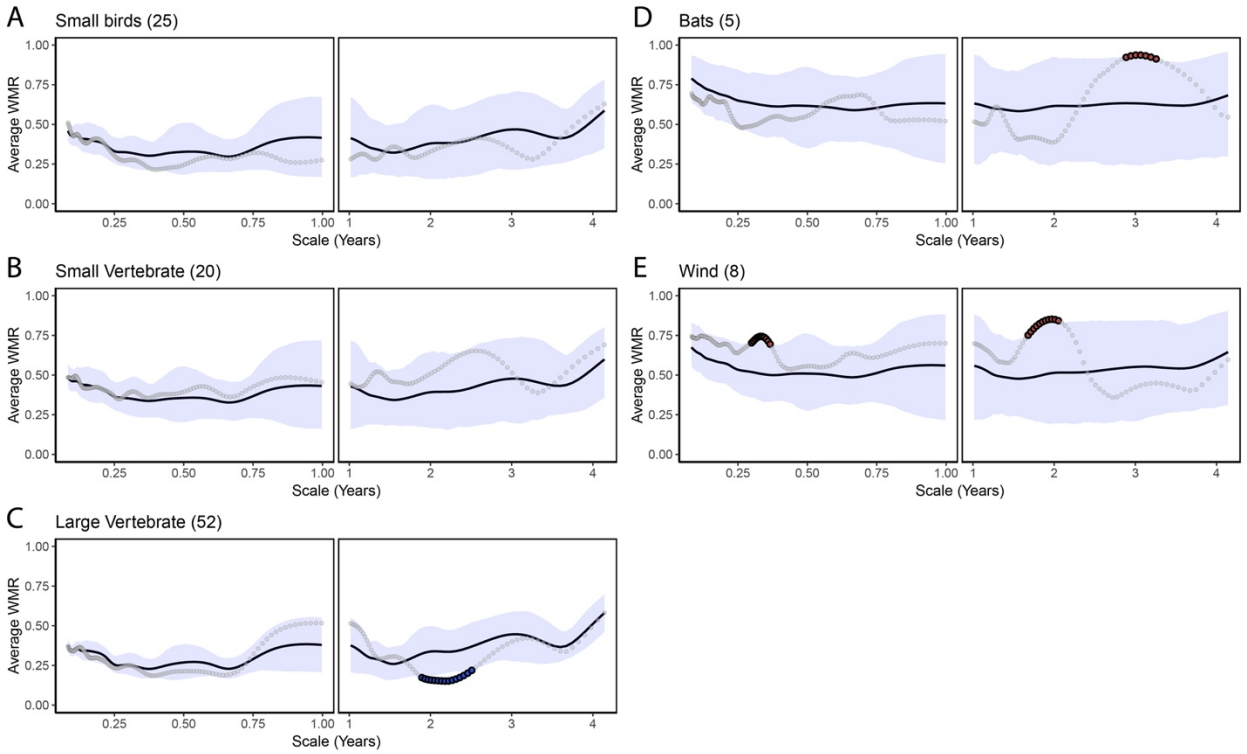
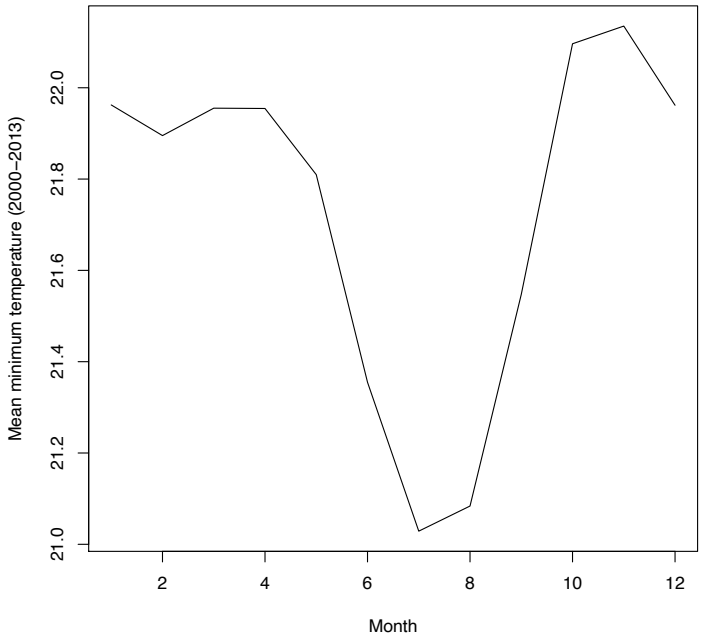
Figure S7. Yasuní monthly minimum temperatures averaged over 2000-2013, using ECMWF/ERA-Interim reanalysis data.