

1 Running head: Multi-scale phenological niches

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

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59 syndrome, functional traits

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61

62 **Abstract**

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

81

## 82 INTRODUCTION

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

98 Co-occurring plant species with similar reproductive phenology might be more likely to  
99 compete for mutualist frugivores (Saracco et al. 2005) or other resources, given that reproduction  
100 is a resource-demanding activity (Karlsson and Méndez 2005). As a result, those species capable  
101 of coexisting might partition phenological space (i.e. temporally partition resource use).

102 Researchers have studied evidence for this axis of niche variation in tropical forests e.g. (Gentry  
103 1974, Stiles 1977, Wheelwright 1985, Ashton et al. 1988, Poulin et al. 1999, Jones and Comita  
104 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

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

136         We used wavelet analyses to characterize community-wide phenology, specifically to  
137 determine whether species exhibited synchronous seed rain or whether they exhibited  
138 compensatory (anti-synchronous) seed rain (Lasky et al. 2016). Wavelets are basis functions,  
139 linear combinations of which can be used to characterize signals in data (here, time series of seed  
140 rain). Wavelet transformations decompose signals into patterns at different scales, like other  
141 spectral analyses, but with the added advantage that wavelets can characterize time-localized and  
142 nonstationary patterns, i.e. patterns that are inconsistent over a time series (Terrence and Compo  
143 1998, Keitt 2008). In the wavelet transformation, the base wavelet is translated across the time  
144 series at varying scales/frequencies of the wavelet to identify the important time scales that  
145 contribute to the variability in the signal (Cazelles et al. 2008). By resolving non-stationary and  
146 scale-specific patterns, we may improve our ability to detect multiple opposing processes  
147 affecting seed rain dynamics at different temporal scales (scale-specific) or points in time (non-  
148 stationary). For example, while species may all increase reproduction during once-a-year seasons  
149 of high resource supply (annual-scale synchrony), species may peak in reproduction at different  
150 points within a favorable season (within-season-scale compensatory dynamics, Lasky et al.

151 2016). Here we used a statistic of wavelet-transformed seed rain dynamics (Keitt 2008) to  
152 identify locations in time and temporal scales of synchronous and compensatory seed rain  
153 patterns (illustrated in Figure 1).

154 We addressed the following questions:

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

169

## 170 **METHODS**

### 171 **Study sites**

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

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

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

### 191 **Seed rain data**

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



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

200 At Cocha Cashu, year-round fruit and seed fall were counted between 2002 and 2011  
201 within a 4-ha plot. A 17 × 17 array of 289 evenly spaced seed-fall traps was installed within the  
202 central 1.44 ha (120 × 120 m) of the plot at the beginning of the study. Seed traps consisted of  
203 0.49 m<sup>2</sup> (70 × 70 cm) open bags made of 1-mm nylon mesh sewn to wire frames with 0.5-mm  
204 monofilament line. Corners of the traps were attached to nearby trees with 1-mm monofilament  
205 line so that the traps were suspended approximately 1 m above the ground. The contents of the  
206 traps were collected every 2 weeks, and all seeds, fruit and fruit parts (capsules, valves, pods,  
207 etc.) were identified to species and recorded.

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

## 210 **Seed dispersal mechanisms**

211 At both sites, we grouped species into different dispersal syndromes. We conducted two separate  
212 classification efforts, one for all species, and another focused on tree species (excluding lianas,  
213 herbaceous, and woody shrub species). At Yasuní for all plants we focused our analysis on  
214 classifications as animal (N = 741) or wind (N = 139) dispersed. Next, for Yasuní trees with  
215 animal-dispersed seeds we followed (Harrison et al. 2013) and further classified them as  
216 dispersed by terrestrial animals (25 species), or with small (< 2cm, 230 species), medium (2-5  
217 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.

## 241 **Weather data**

242 We estimated monthly precipitation and minimum temperature at the plot level for each study  
243 site. Because local weather station data contained many missing observations, we used remotely  
244 sensed data. We used a ten-day precipitation time series estimated on a 0.05° grid by (Funk et al.  
245 2014) using both remote and locally-sensed data. We used ECMWF/ERA-Interim reanalysis 4-hr  
246 temperature data at 2 m height estimated on a N128 Gaussian (~2°) grid (European Centre for  
247 Medium-Range Weather Forecasts 2009) and calculated daily minimum temperatures and then  
248 monthly values.

249 To estimate the rough pattern of wind seasonality, we used weather station data. For  
250 Cocha Cashu, we calculated average monthly wind speed from a station 150 km away, within  
251 100 m elevation of Cocha Cashu, for the years 2004-2009  
252 ([http://atrium.andesamazon.org/meteo\\_station\\_display\\_info.php?id=12](http://atrium.andesamazon.org/meteo_station_display_info.php?id=12)). For Yasuní, we used a  
253 weather station (<http://www.serviciometeorologico.gob.ec/biblioteca/>) 115 km away within 70 m  
254 elevation of the Yasuní plot for the years 2005-2012.

## 255 *Statistical analysis*

### 256 **Wavelet transformation of seed rain data**

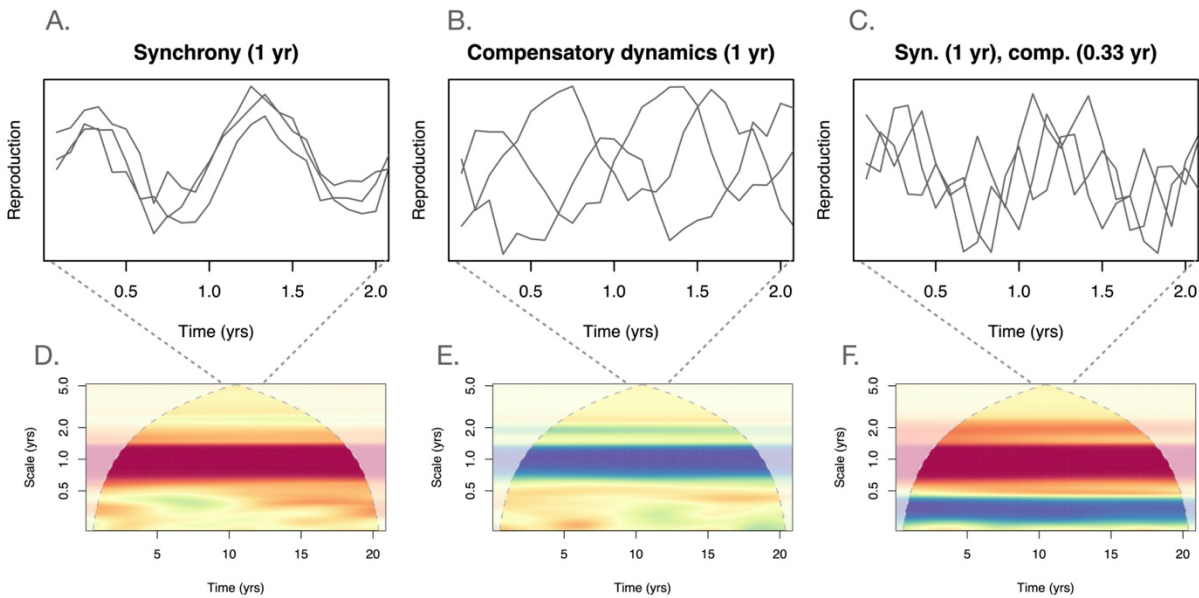
257 To characterize patterns of synchrony versus compensatory dynamics, we used wavelet analyses.  
258 Wavelet transformation, like the Fourier transformation, is a spectral analysis which can  
259 characterize information from multiple time scales across a time series, with the added flexibility 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

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

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

274

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



288

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

## 298 Taxonomic and seed dispersal groups

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

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

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

### 317 **Climatic association with synchrony vs compensatory dynamics**

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

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

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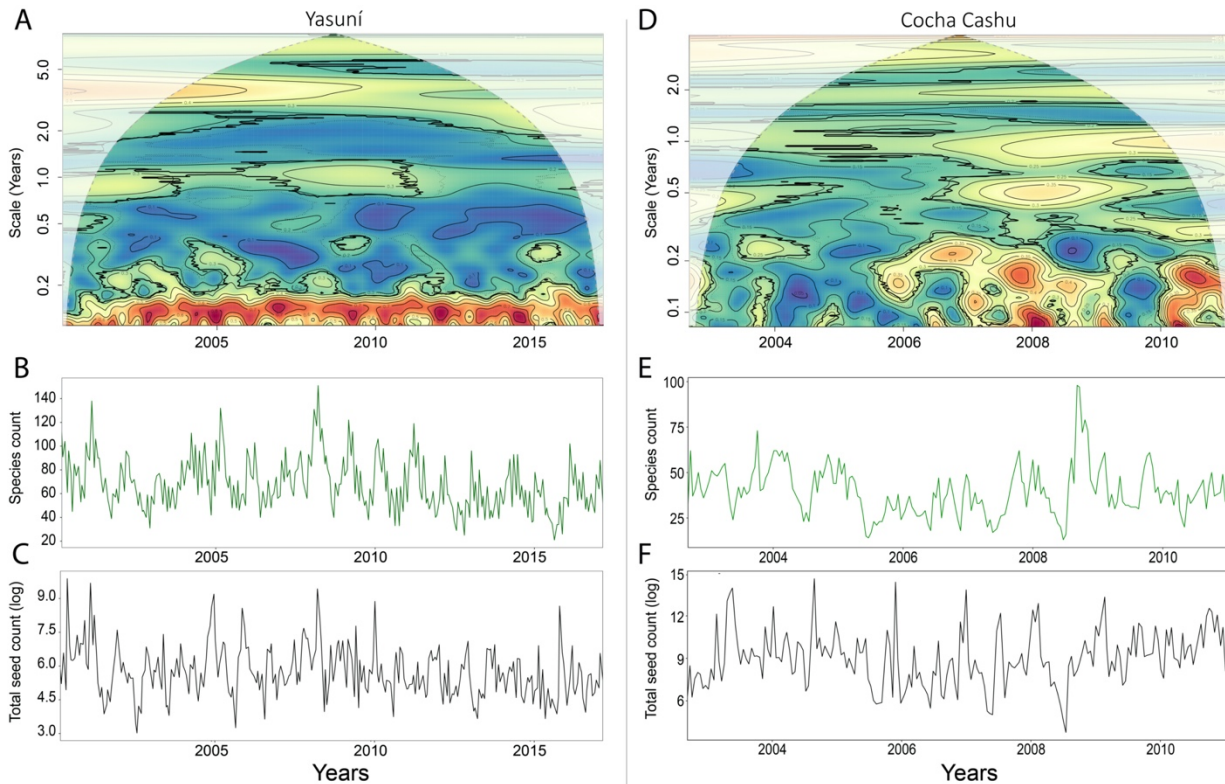
## 335 **RESULTS**

### 336 **Community-wide phenology**

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

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

349 **Figure 2:** The whole community wavelet modulus ratio (WMR) of seed rain (A,D) at Yasuní  
350 (1059 species) and Cocha Cashu (654 species), and time-series of the total species in traps (B,E)  
351 and total estimated seeds in traps (C,F, natural log) in each sampling period. In (A,D) red  
352 indicates synchronous dynamics (high WMR) while blue indicates compensatory dynamics (low  
353 WMR). The thin dashed contour lines bound the points in time and scale (years) when the WMR  
354 was nominally significant ( $p < 0.05$ ) based on bootstrapping, while thick black lines bound  
355 regions significant with a false discovery rate (FDR) = 0.05. Nearly all significant regions in the  
356 plot are high WMR (yellow to red). The cone of influence (white shading, A,D) marks the  
357 regions where the wavelet transforms are affected by the boundaries of the sampling period.  
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### 361 Phenology among confamilials

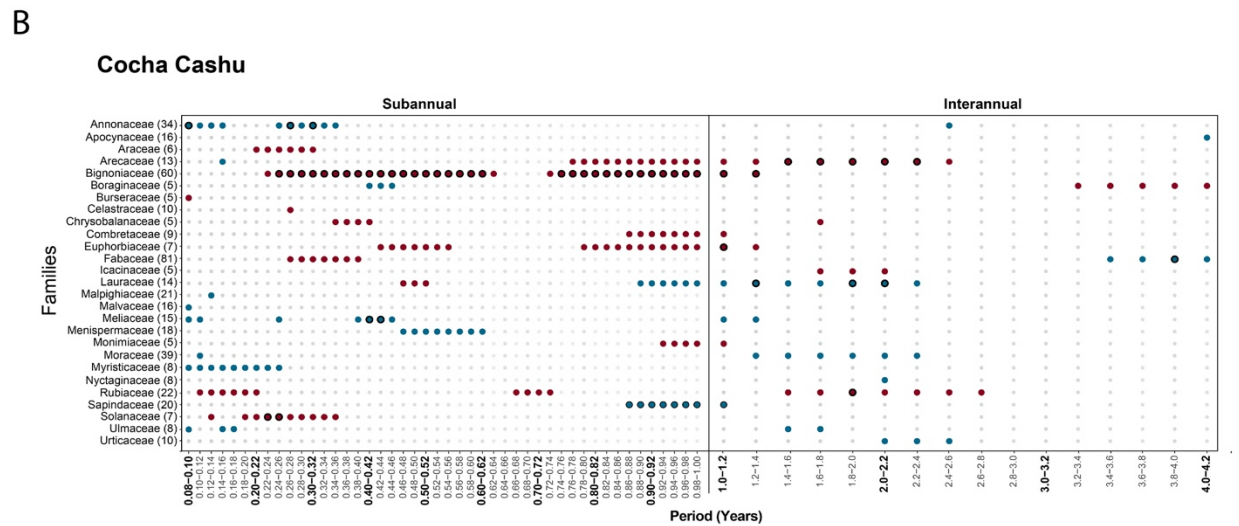
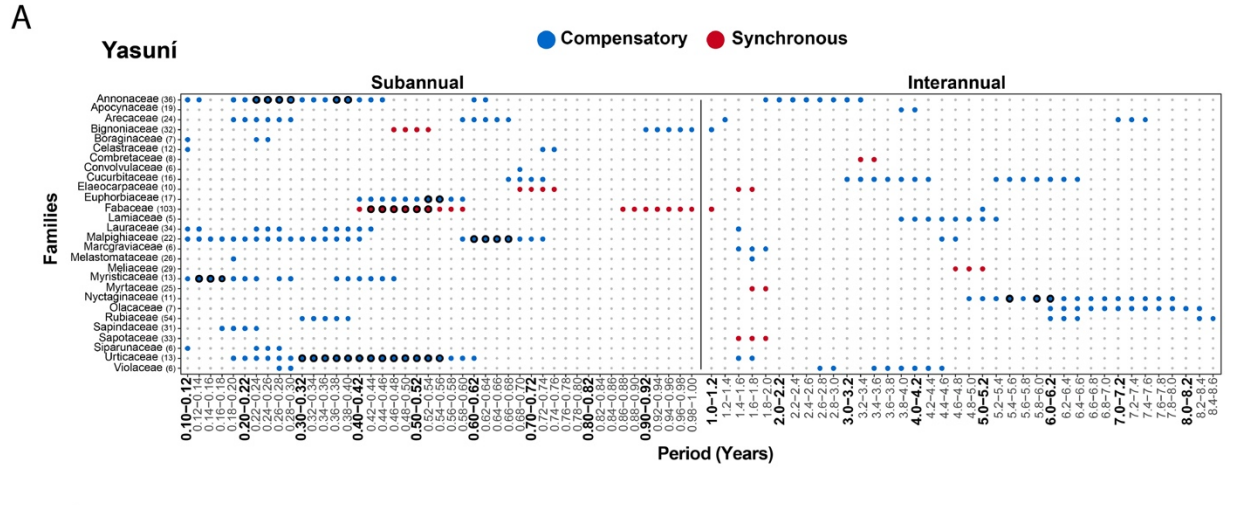
362 At Yasuní among the 28 families analyzed, we found that species of some families exhibited  
363 significant compensatory dynamics at sub-annual timescales (Figure 3A). In particular, species  
364 in the Annonaceae, Malpighiaceae, Myristicaceae, and Urticaceae families exhibited significant  
365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



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

371 We found some consistency of family patterns across sites. Annonaceae at Cocha Cashu  
372 exhibited significant compensatory dynamics at sub-annual timescales (1-4 mos) similar to at  
373 Yasuní. Additionally, Myristicaceae at both sites showed significant compensatory dynamics at  
374 1-3 mo scales (though these were not significant after FDR control at Cocha Cashu). By contrast,  
375 Bignoniaceae (a family of entirely wind-dispersed species) and Fabaceae species showed  
376 significant synchrony for sub-annual to annual time scales at both sites (though these were not  
377 significant after FDR control at Yasuní).

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



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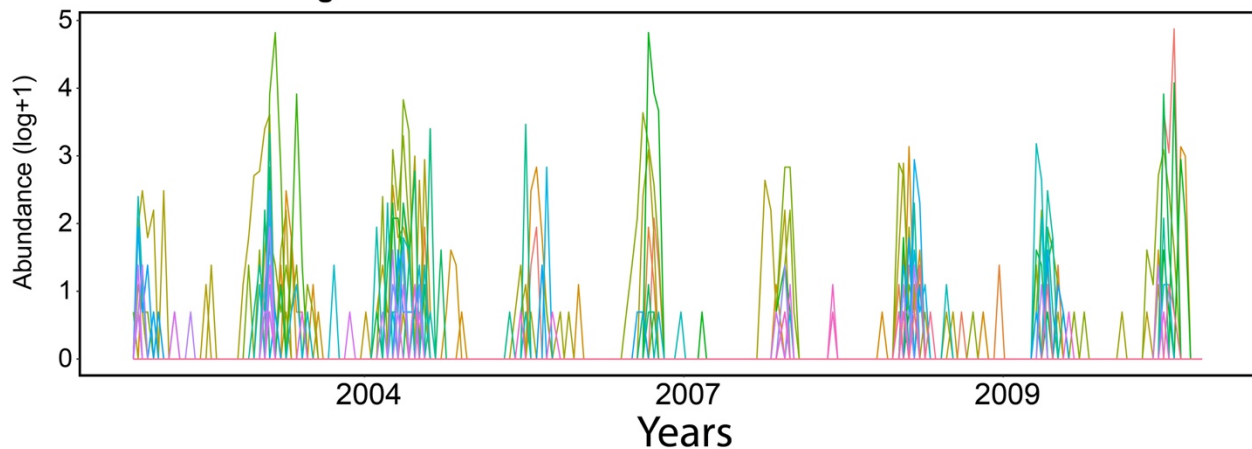
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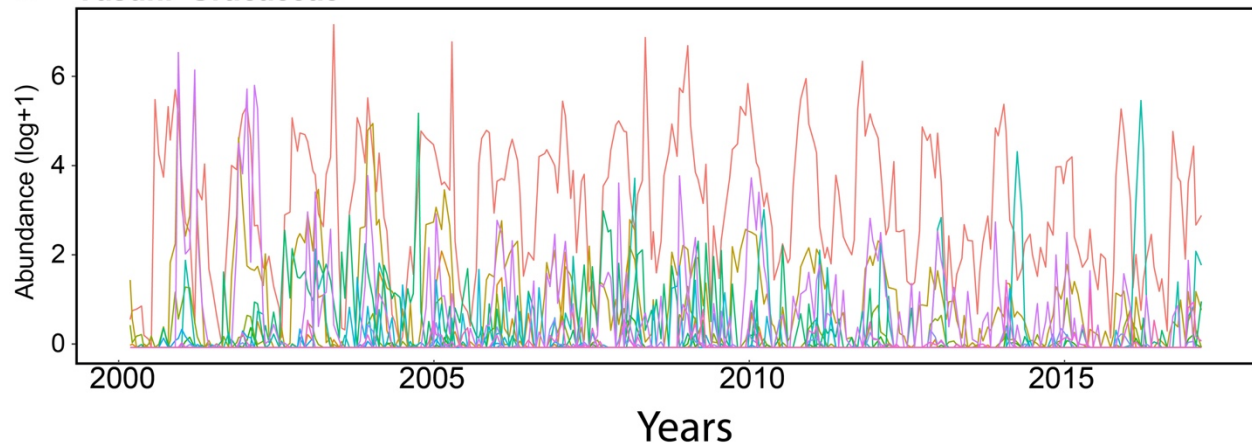
To help illustrate the patterns identified, we present two families with opposing patterns of synchrony or compensatory dynamics. At Cocha Cashu, Bignoniaceae shows strong synchrony at  $\sim 0.9$  year scales, which corresponds to a strong yearly peak in reproduction of multiple species (Figure 4A). At Yasuni, Urticaceae showed significant compensatory dynamics at scales of  $\sim 0.3$ - $0.54$  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).

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

A **Cocha Cashu-Bignoniaceae**



B **Yasuní-Urticaceae**



400

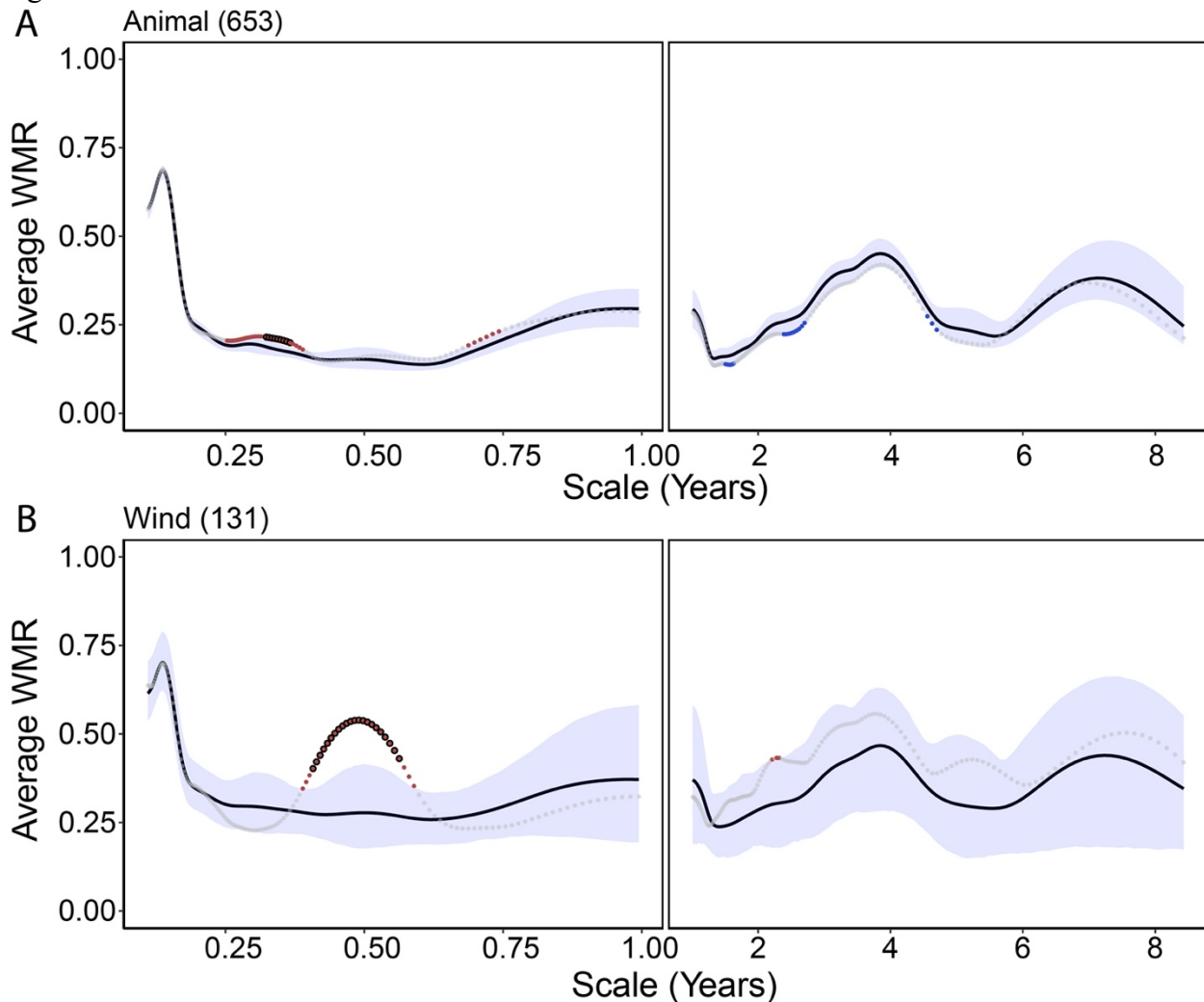
401 **Phenology among species sharing dispersal modes**

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

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

410

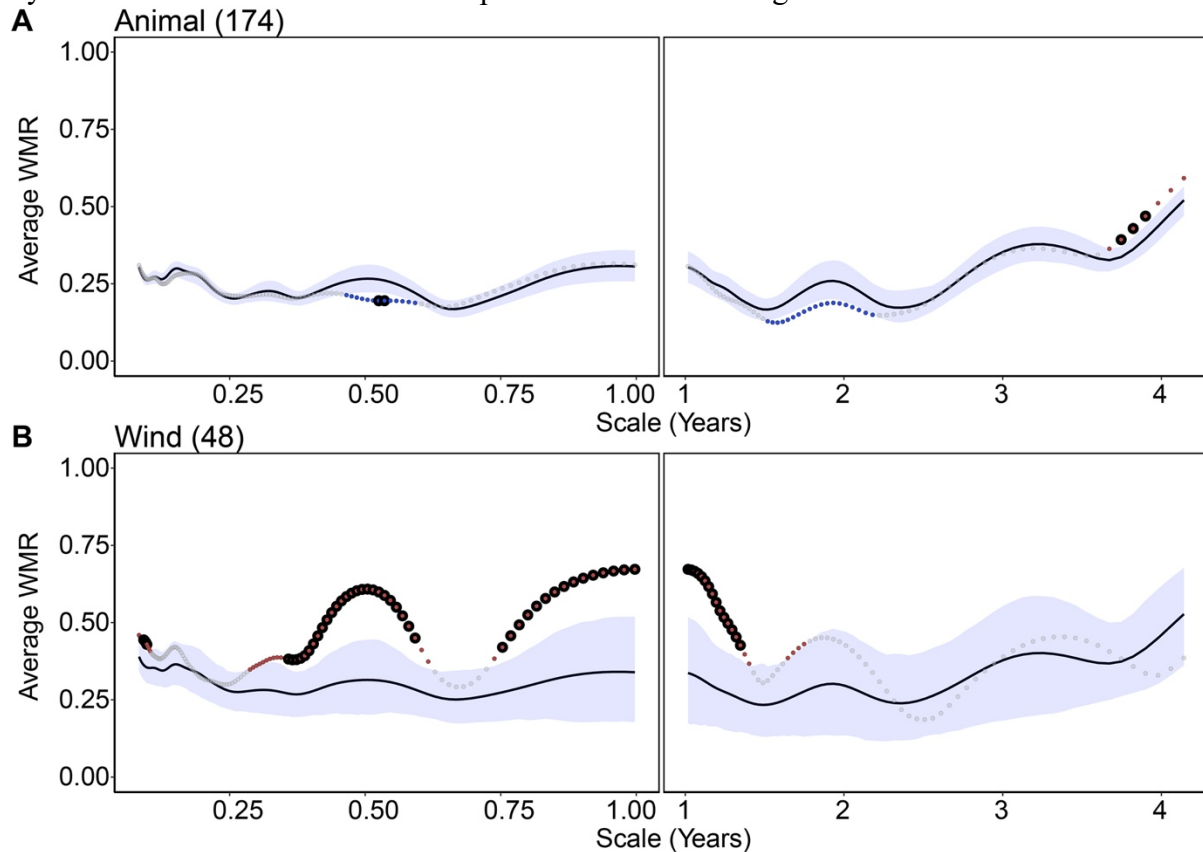
411 **Figure 5.** The averaged wavelet modulus ratio for all plant species in the ever-wet Yasuní based  
412 on dispersal syndrome. The number in parentheses represents the number of species within the  
413 animal and wind-dispersed groups. The light blue ribbon represents the 2.5-97.5<sup>th</sup>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



418

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

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



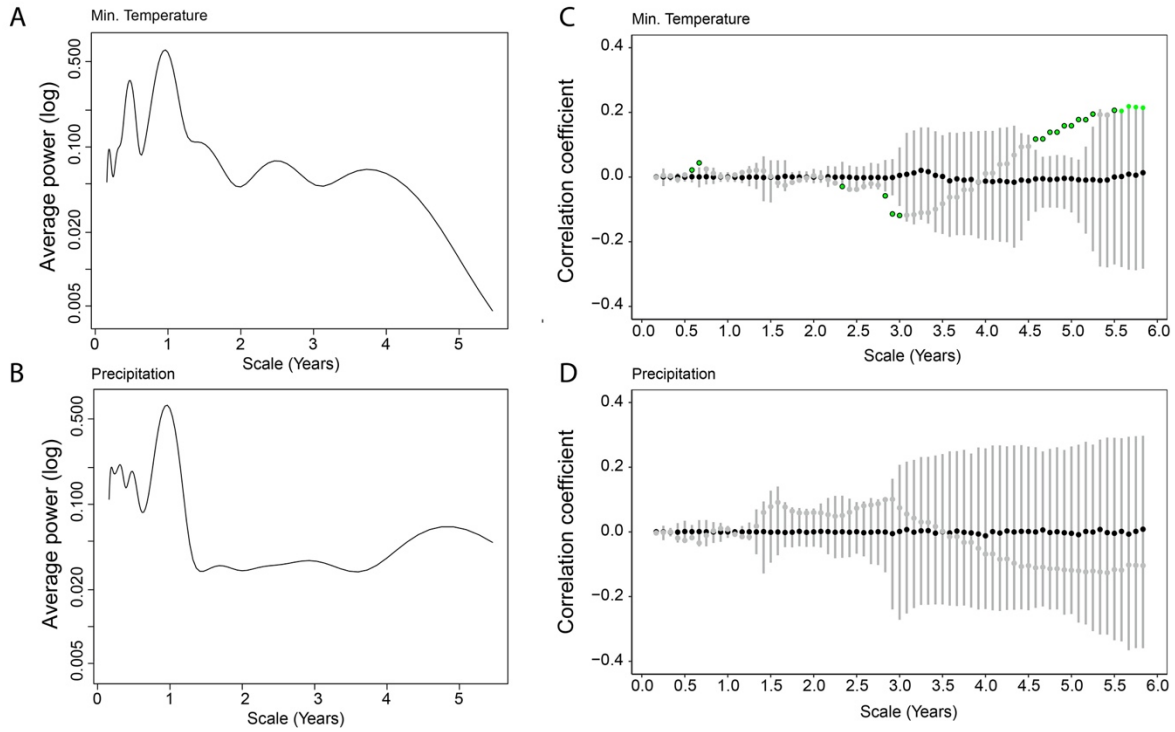
#### 434 **Temperature, precipitation, and community-wide phenology**

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

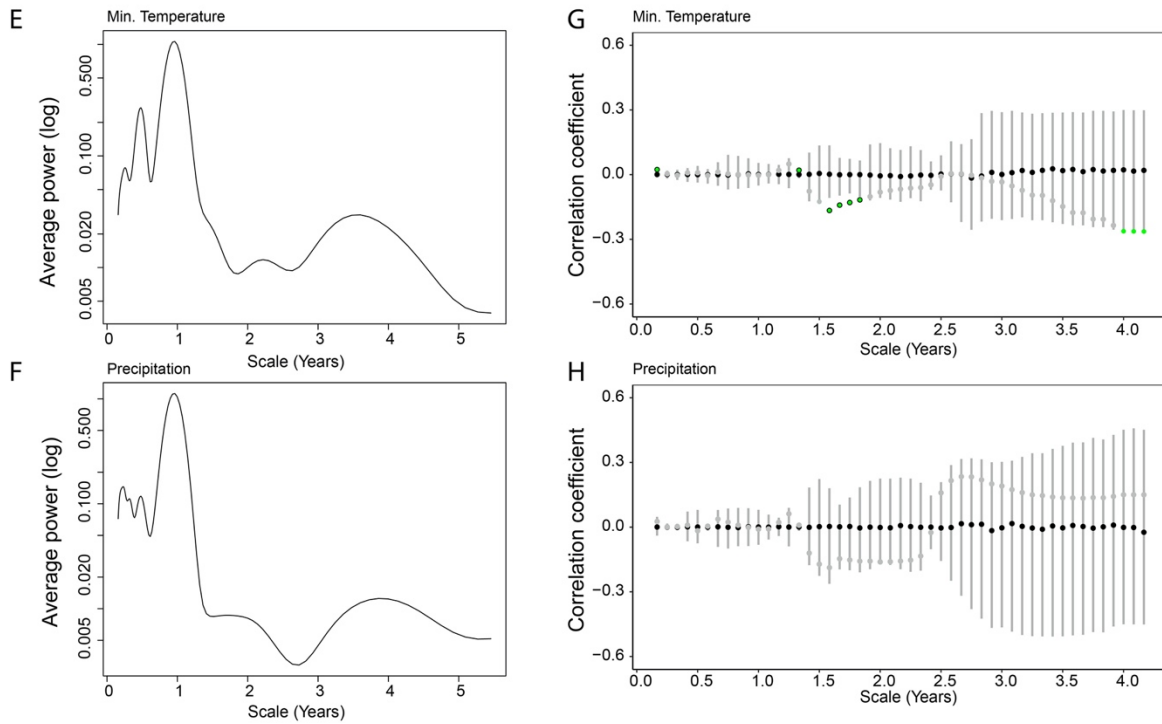
447

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

## Yasuní



## Cosha Cashu



457

458

459

## 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,

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

#### 541 **Synchrony among related species or species sharing dispersal mode**

542 We found that among all growth forms, wind-dispersed species exhibit strong synchrony of seed  
543 rain, particularly at time scales indicative of shared abiotic niches. At both sites we found  
544 significant ~6 mo synchrony among wind-dispersed species, consistent with the twice-yearly  
545 peaks in wind speed observed at nearby weather stations (Figures S2, S4, S5). Cocha Cashu has  
546 a strong peak in wind speed in September (Figure S5), also consistent with the synchrony at this  
547 site observed among wind-dispersed species at ~1 yr periods (Figures 6 & S4). Near Yasuní the  
548 wind had a broad peak in average speed from September to November with a small peak in April  
549 (Figure S2). The tendency for wind-dispersed species to synchronously release seed during  
550 windy seasons has been reported in the literature (Frankie et al. 1974, Janzen 1974, Detto et al.  
551 2018) and can be considered a positive control for our approach.

## 552 **Community phenology and abiotic fluctuations**

553 We found evidence that community-wide phenology was driven by climate fluctuations, with  
554 WMR being significantly associated with temperature at both sites at multiple scales. (Gentry  
555 1974) hypothesized that phenological diversity of communities was promoted by more  
556 permissive abiotic conditions and longer growing seasons compared to seasonally harsh  
557 environments, where the range of potential phenologies is narrower. We do not see evidence for  
558 this based on fluctuations in climate within our two tropical sites; the direction of the WMR-  
559 temperature associations contradicted this hypothesis. At both sites, sub-annual WMR was  
560 positively associated with temperature, indicating greater synchrony (as opposed to phenological  
561 diversity) at warmer times of the year. Our findings may signify that the community-wide trend  
562 is for a degree of synchrony to exploit favorable conditions during warmer parts of the year,  
563 potentially due to greater light resources (Detto et al. 2018).

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

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

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

## 577 **Conclusion**

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

585

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604

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## 770 **Supplementary Material**

### 771 *Seed rain data*

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

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

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

788

### 789 *Wavelet analyses*

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

793 
$$W_k(a, \tau) = \frac{1}{\sqrt{a}} \int_{-\infty}^{\infty} x_k(t) \varphi \frac{t-\tau}{a} d\tau \quad (\text{Equation 1}).$$

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

796 
$$\varphi(\tau) = \pi^{-\frac{1}{4}} \exp(2\pi i \tau - \frac{1}{2} \tau^2) \quad (\text{Equation 2}).$$

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

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

807 
$$WMR(t, s) = \frac{\Lambda_{t,a}(|\sum_k W_k(\tau, a)|)}{\Lambda_{t,a} \sum_k |W_k(\tau, a)|} \quad (\text{Equation 3})$$

808

809 where  $\Lambda_{t,a}(\cdot) = \int_{-\infty}^{\infty} e^{-\frac{1}{2}(\frac{t-\tau}{a})^2} (\cdot) d\tau$  and  $|\cdot|$  represents the complex norm (Keitt 2008, Keitt 2014,

810 Lasky et al. 2016) (Figure 1). When species seed rain dynamics through time perfectly cancel

811 each other out, the sum in the numerator of Eqn 3 is equal to zero (declining seed rain is

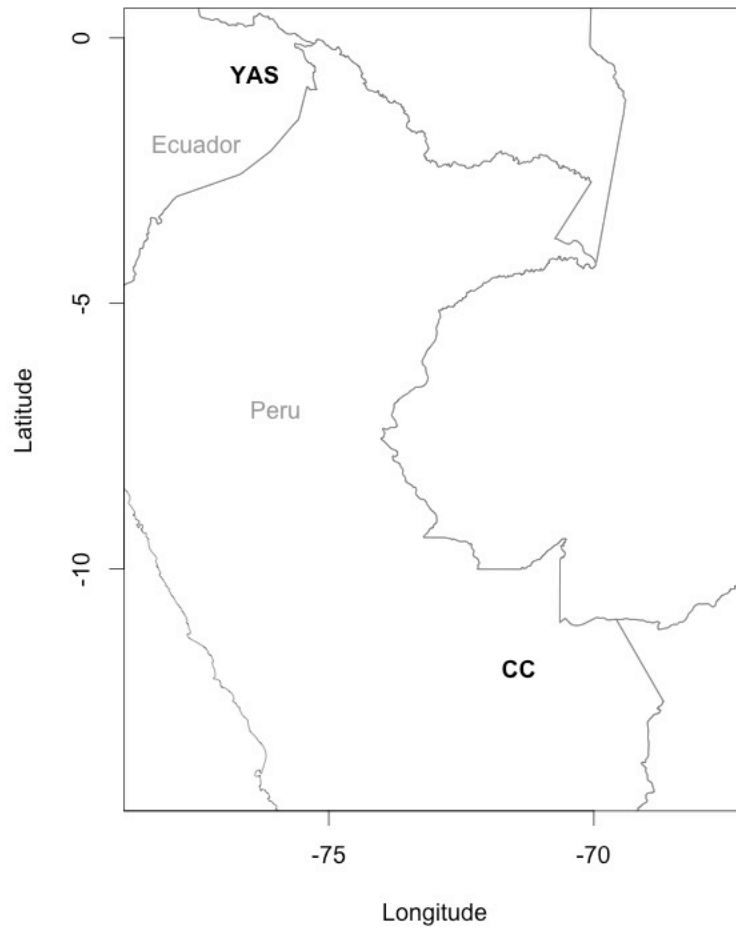
812 balanced by increasing seed rain). Thus at zero, the WMR indicates complete compensation or

813 anti-synchrony: all species-level dynamics are compensated so that community level

814 reproduction is constant. At unity, the WMR at the time period signifies complete phenological

815 synchrony among the species, as species-level phenological dynamics are completely reflected at  
816 the community level.  
817

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



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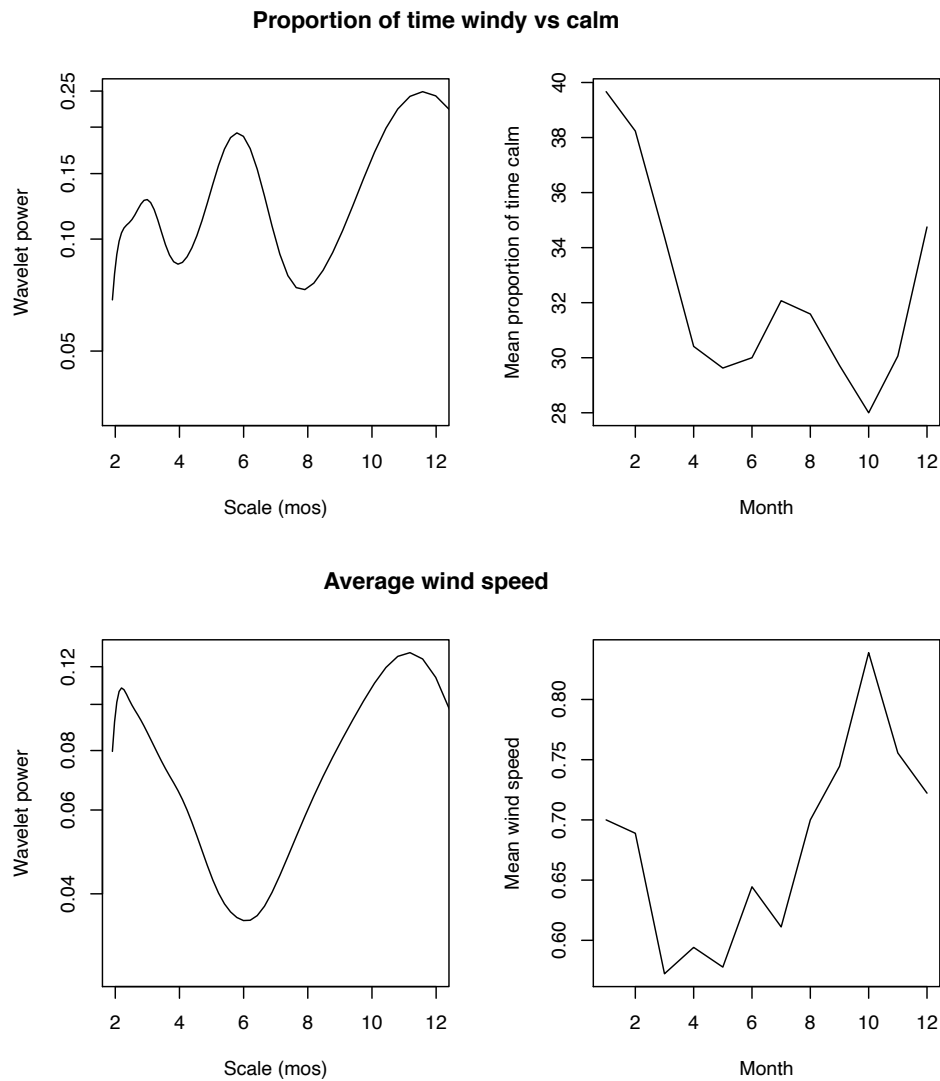
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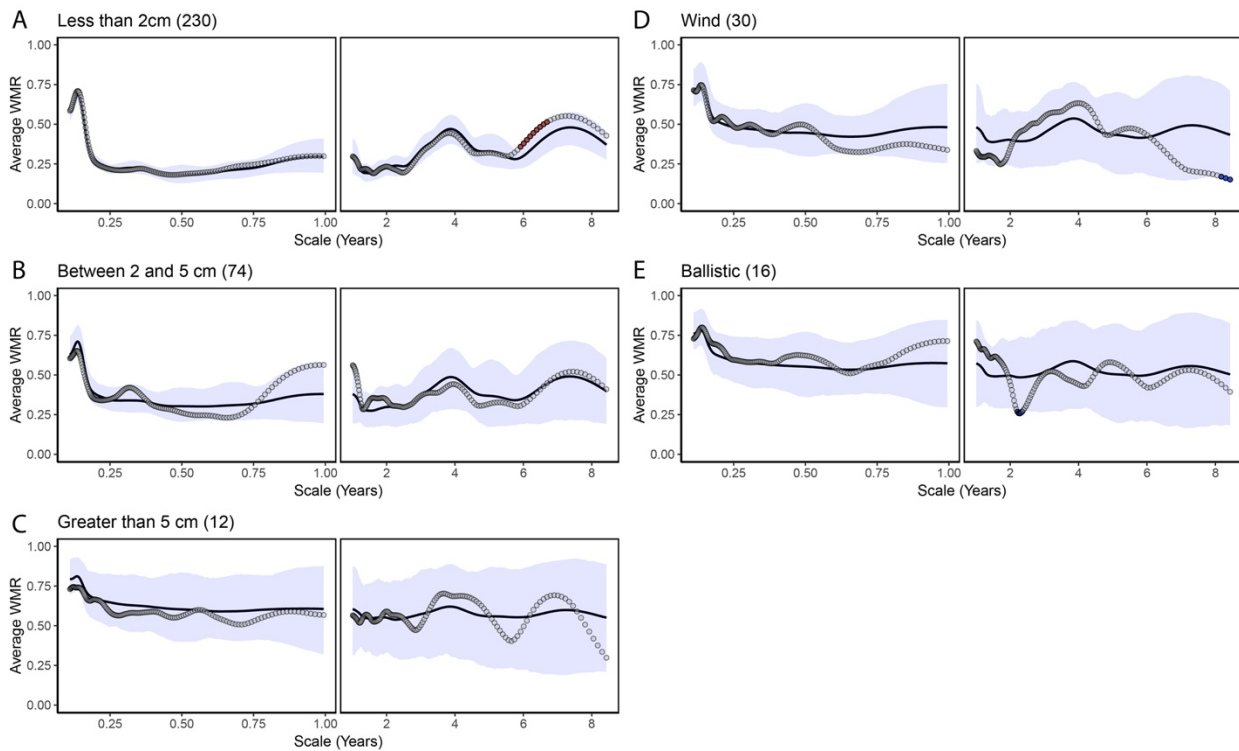
827 **Figure S2.** Wavelet power analysis (left panels) and average monthly wind (right panels) for the  
828 wind station data near Yasuní (1995-2012). Two wind parameters are shown: proportion of time  
829 calm (vs windy, top panels) and the average wind speed (bottom). Missing values were imputed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



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832

833 **Figure S3.** The averaged wavelet modulus ratio for tree species in Yasuní based on fruit size or  
834 dispersal syndrome. The number in parentheses represents the number of species within the  
835 dispersal group. The blue ribbon represents the null-distribution generated through bootstrapping  
836 ( $n=1000$ ). Any points that lie outside the ribbon were considered nominally significant ( $p<0.05$ )  
837 though no points were significant at  $FDR=0.05$ .  
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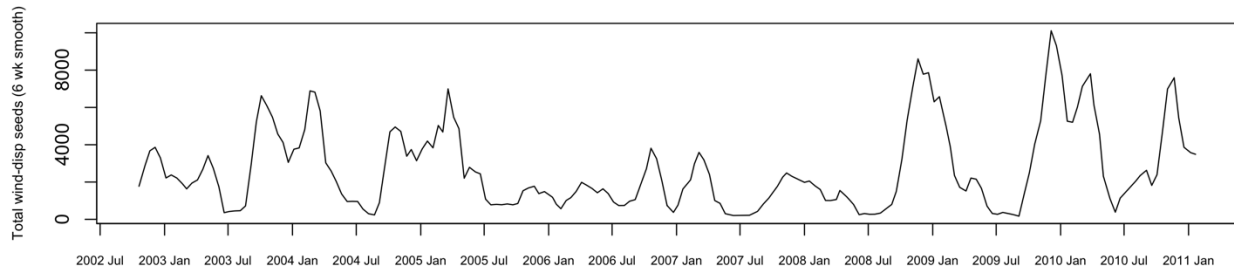
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844 **Figure S4.** Time series of wind-dispersed seed counts (with a 6 week smooth for visualization)  
845 at Cocha Cashu, highlighting the twice yearly peaks and 6 month scale synchrony.

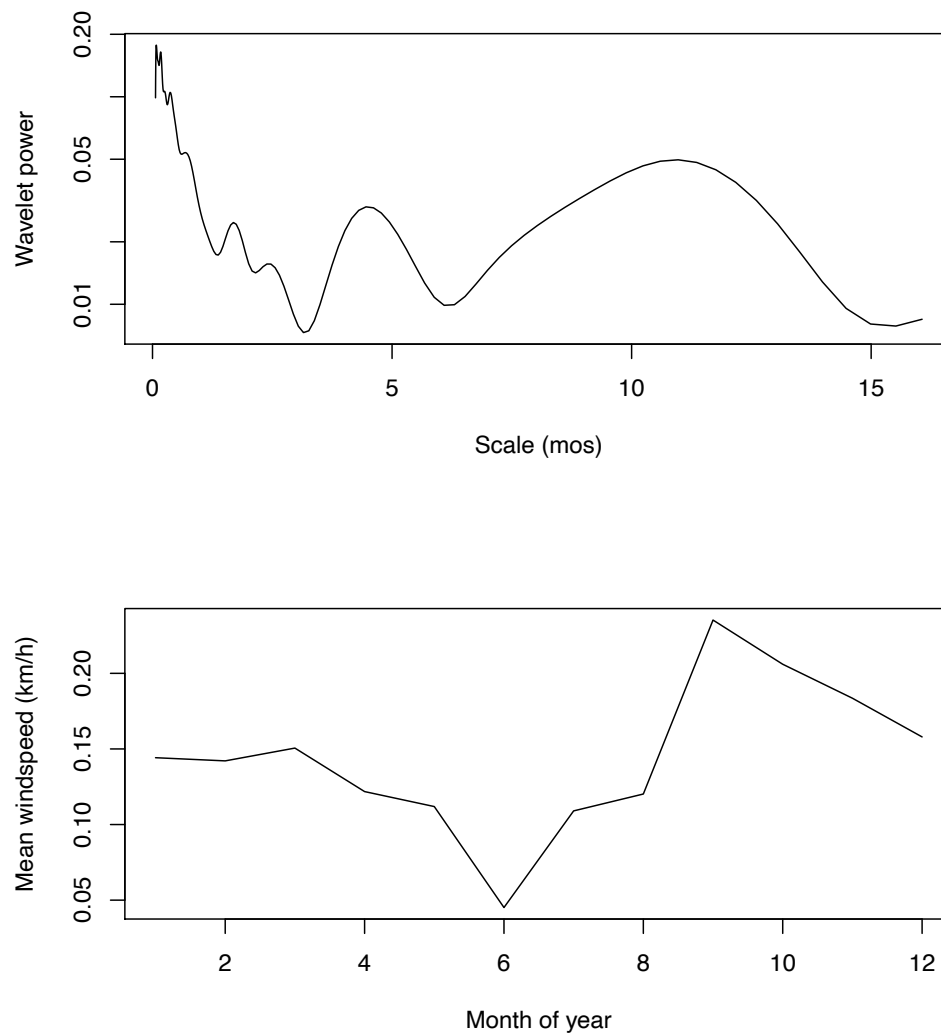


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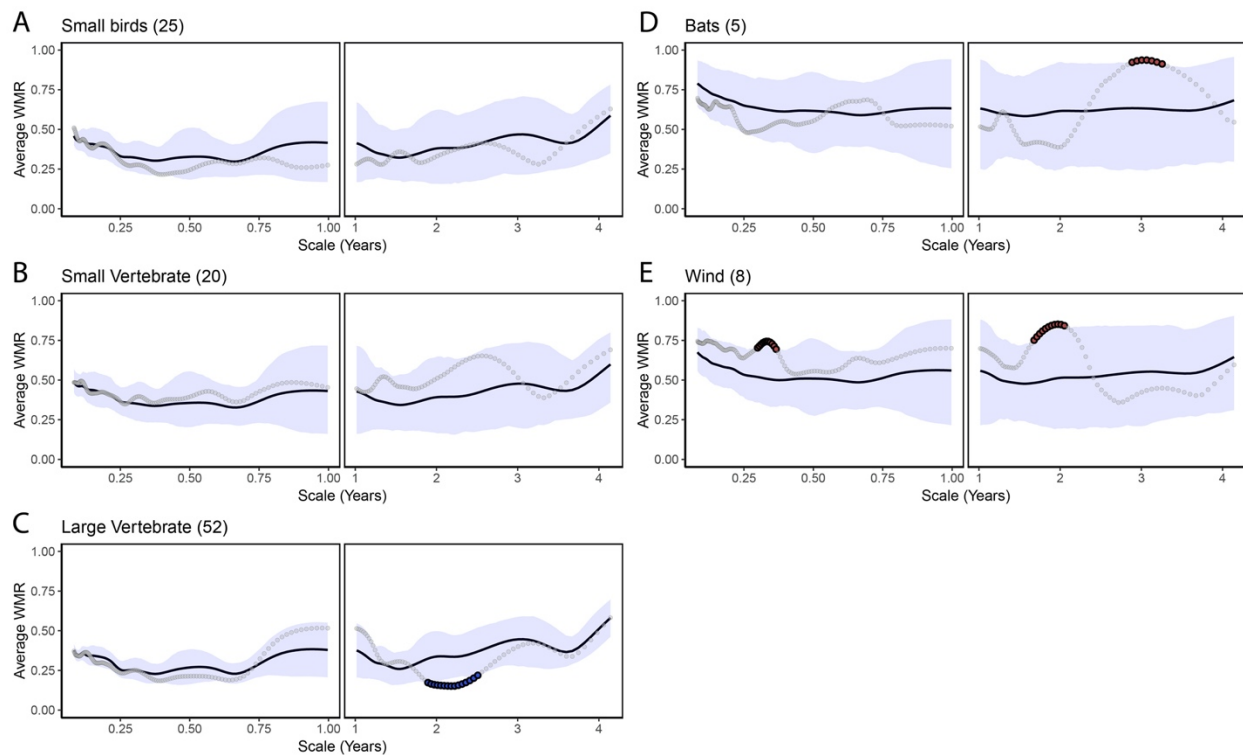
847 **Figure S5.** Wavelet power (top panel) and monthly averages (bottom panel) for average wind  
848 speed at a weather station near Cocha Cashu, 2004-2009.

849



850

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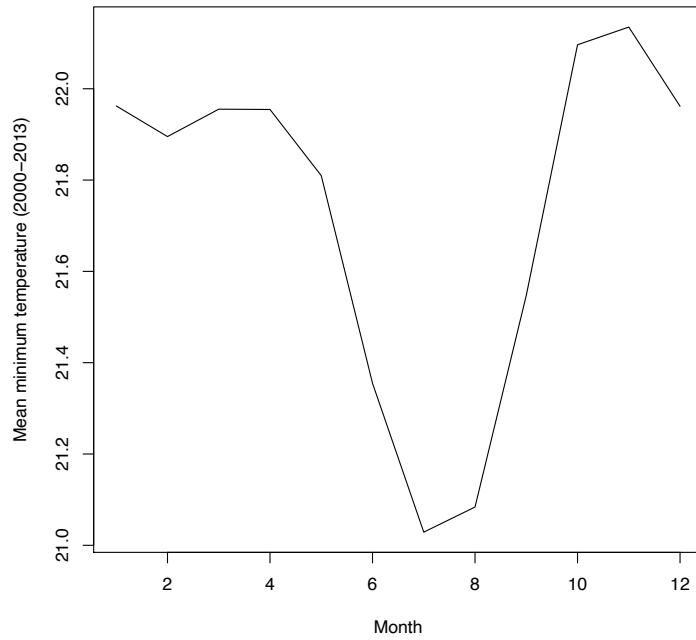


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862 **Figure S7.** Yasuní monthly minimum temperatures averaged over 2000-2013, using  
863 ECMWF/ERA-Interim reanalysis data.



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