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# Masting is uncommon in trees that depend on mutualist dispersers in the context of global climate and fertility gradients

Tong Qiu<sup>1</sup>, Marie-Claire Aravena<sup>2</sup>, Davide Ascoli<sup>3</sup>, Yves Bergeron<sup>4</sup>, Michal Bogdziewicz<sup>5</sup>, Thomas Boivin<sup>6</sup>, Raul Bonal<sup>7</sup>, Thomas Caignard<sup>8</sup>, Maxime Cailleret<sup>9</sup>, Rafael Calama<sup>10</sup>, Sergio Donoso Calderon<sup>2</sup>, J. Julio Camarero<sup>11</sup>, Chia-Hao Chang-Yang<sup>12</sup>, Jerome Chave<sup>13</sup>, Francesco Chianucci<sup>14</sup>, Benoit Courbaud<sup>15</sup>, Andrea Cutini<sup>16</sup>, Adrian J. Das<sup>17</sup>, Nicolas Delpierre<sup>18</sup>, Sylvain Delzon<sup>8</sup>, Michael Dietze<sup>19</sup>, Laurent Dormont<sup>20</sup>, Josep Maria Espelta<sup>21</sup>, Timothy J. Fahey<sup>22</sup>, William Farfan-Rios<sup>23</sup>, Jerry F. Franklin<sup>24</sup>, Catherine A. Gehring<sup>25</sup>, Gregory S. Gilbert<sup>26</sup>, Georg Gratzer<sup>27</sup>, Cathryn H. Greenberg<sup>28</sup>, Arthur Guignabert<sup>29</sup>, Qinfeng Guo<sup>30</sup>, Andrew Hacket-Pain<sup>31</sup>, Arndt Hampe<sup>8</sup>, Qingmin Han<sup>32</sup>, Jan Holik<sup>33</sup>, Kazuhiko Hoshizaki<sup>34</sup>, Ines Ibanez<sup>35</sup>, Jill F. Johnstone<sup>36</sup>, Valentin Journe<sup>15</sup>, Thomas Kitzberger<sup>37</sup>, Johannes M.H. Knops<sup>38</sup>, Georges Kunstler<sup>15</sup>, Hiroko Kurokawa<sup>39</sup>, Jonathan G.A. Lageard<sup>40</sup>, Jalene M. LaMontagne<sup>41</sup>, Francois Lefevre<sup>6</sup>, Theodor Leininger<sup>42</sup>, Jean-Marc Limousin<sup>43</sup>, James A. Lutz<sup>44</sup>, Diana Macias<sup>45</sup>, Anders Marell<sup>46</sup>, Eliot J.B. McIntire<sup>47</sup>, Christopher M. Moore<sup>48</sup>, Emily Moran<sup>49</sup>, Renzo Motta<sup>3</sup>, Jonathan A. Myers<sup>50</sup>, Thomas A. Nagel<sup>51</sup>, Shoji Naoe<sup>52</sup>, Mahoko Noguchi<sup>52</sup>, Michio Oguro<sup>53</sup>, Robert Parmenter<sup>54</sup>, Ian S. Pearse<sup>55</sup>, Ignacio M. Perez-Ramos<sup>56</sup>, Lukasz Piechnik<sup>57</sup>, Tomasz Podgorski<sup>58</sup>, John Poulsen<sup>59</sup>, Miranda D. Redmond<sup>60</sup>, Chantal D. Reid<sup>59</sup>, Kyle C. Rodman<sup>61</sup>, Francisco Rodriguez-Sanchez<sup>62</sup>, Pavel Samonil<sup>33</sup>, Javier D. Sanguinetti<sup>63</sup>, C. Lane Scher<sup>59</sup>, Barbara Seget<sup>57</sup>, Shubhi Sharma<sup>59</sup>, Mitsue Shibata<sup>53</sup>, Miles Silman<sup>64</sup>, Michael A. Steele<sup>65</sup>, Nathan L. Stephenson<sup>17</sup>, Jacob N. Straub<sup>66</sup>, Samantha Sutton<sup>59</sup>, Jennifer J. Swenson<sup>59</sup>, Margaret Swift<sup>59</sup>, Peter A. Thomas<sup>67</sup>, Maria Uriarte<sup>68</sup>, Giorgio Vacchiano<sup>69</sup>, Amy V. Whipple<sup>70</sup>, Thomas G. Whitham<sup>70</sup>, Andreas P. Wion<sup>71</sup>, S. Joseph Wright<sup>72</sup>, Kai Zhu<sup>35</sup>, Jess K. Zimmerman<sup>73</sup>, Magdalena Zywiec<sup>57</sup>, James S. Clark<sup>15,59</sup>

- <sup>1</sup>Department of Ecosystem Science and Management, Pennsylvania State University, University Park, PA 16802 USA.  
<sup>2</sup>Universidad de Chile, Facultad de Ciencias Forestales y de la Conservacion de la Naturaleza (FCFCN), La Pintana, 8820808 Santiago, Chile.  
<sup>3</sup>Department of Agriculture, Forest and Food Sciences, University of Torino, 10095 Grugliasco, TO, Italy.  
<sup>4</sup>Forest Research Institute, University of Quebec in Abitibi-Temiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada.  
<sup>5</sup>Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznan, Poland.  
<sup>6</sup>Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), Ecologie des Forets Mediteranennes, 84000 Avignon, France.  
<sup>7</sup>Department of Biodiversity, Ecology and Evolution, Complutense University of Madrid, 28040 Madrid, Spain.  
<sup>8</sup>Universite Bordeaux, Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), Biodiversity, Genes, and Communities (BIOGECO), 33615 Pessac, France.  
<sup>9</sup>INRAE, Aix-Marseille University, UMR RECOVER, 3275 Route de Cezanne, CS 40061, Aix-en-Provence Cedex 5, France.  
<sup>10</sup>Centro de Investigacion Forestal (INIA-CSIC), 28040 Madrid, Spain .  
<sup>11</sup>Instituto Pirenaico de Ecologia, Consejo Superior de Investigaciones Cientificas (IPE-CSIC), 50059 Zaragoza, Spain.  
<sup>12</sup>Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung 80424, Taiwan.  
<sup>13</sup>Laboratoire Evolution et Diversite Biologique, UMR 5174 (CNRS/IRD/UPS), 31062 Toulouse Cedex 9, France.  
<sup>14</sup>CREA - Research Centre for Forestry and Wood, Viale S. Margherita 80, 52100 Arezzo, Italy.  
<sup>15</sup>Universite Grenoble Alpes, Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), Laboratoire EcoSystemes et Societes En Montagne (LESSEM), 38402 St. Martin-d'Herès, France.  
<sup>16</sup>Research Centre for Forestry and Wood, Arezzo, Italy.  
<sup>17</sup>U.S. Geological Survey Western Ecological Research Center, Three Rivers, CA, 93271 USA.  
<sup>18</sup>Universite Paris-Saclay, Centre national de la recherche scientifique, AgroParisTech, Ecologie Systematique et Evolution, 91405 Orsay, France.  
<sup>19</sup>Earth and Environment, Boston University, Boston, MA, 02215 USA.  
<sup>20</sup>Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), Centre National de la Recherche Scientifique (CNRS), 34293 Montpellier, France..  
<sup>21</sup>Centre de Recerca Ecologica i Aplicacions Forestals (CREAF), Bellaterra, Catalunya 08193, Spain.  
<sup>22</sup>Natural Resources, Cornell University, Ithaca, NY, 14853 USA.

- <sup>23</sup>Washington University in Saint Louis, Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, MO 63110 USA.
- <sup>24</sup>Forest Resources, University of Washington, Seattle, WA 98195 USA.
- <sup>25</sup>Department of Biological Sciences and Center for Adaptive Western Landscapes.
- <sup>26</sup>Department of Environmental Studies, University of California, Santa Cruz, CA 95064 USA.
- <sup>27</sup>Institute of Forest Ecology, Peter-Jordan-Strasse 82, 1190 Wien, Austria.
- <sup>28</sup>Bent Creek Experimental Forest, USDA Forest Service, Asheville, NC 28801 USA.
- <sup>29</sup>INRAE, Bordeaux Sciences Agro, UMR 1391 ISPA, Villenave d'Ornon, France.
- <sup>30</sup>Eastern Forest Environmental Threat Assessment Center, USDA Forest Service, Southern Research Station, Research Triangle Park, NC 27709 USA.
- <sup>31</sup>Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom.
- <sup>32</sup>Department of Plant Ecology Forestry and Forest Products Research Institute (FFPRI), Tsukuba, Ibaraki, 305-8687 Japan.
- <sup>33</sup>Department of Forest Ecology, Silva Tarouca Research Institute, 60200 Brno, Czech Republic.
- <sup>34</sup>Department of Biological Environment, Akita Prefectural University, Akita 010-0195, Japan.
- <sup>35</sup>School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109.
- <sup>36</sup>Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99700, USA.
- <sup>37</sup>Department of Ecology, Instituto de Investigaciones en Biodiversidad y Medioambiente (Consejo Nacional de Investigaciones Científicas y Técnicas - Universidad Nacional del Comahue), Quintral 1250, 8400 Bariloche, Argentina.
- <sup>38</sup>Health and Environmental Sciences Department, Xian Jiaotong-Liverpool University, Suzhou, China, 215123.
- <sup>39</sup>address Kurokawa.
- <sup>40</sup>Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK.
- <sup>41</sup>Department of Biological Sciences, DePaul University, Chicago, IL 60614 USA.
- <sup>42</sup>USDA, Forest Service, Southern Research Station, PO Box 227, Stoneville, MS 38776.
- <sup>43</sup>CEFE, Univ Montpellier, CNRS, EPHE, IRD, 1919 route de Mende, 34293 Montpellier Cedex 5, France.
- <sup>44</sup>Department of Wildland Resources, and the Ecology Center, Utah State University, Logan, UT 84322 USA.
- <sup>45</sup>Department of Biology, University of New Mexico, Albuquerque, NM 87131 USA.
- <sup>46</sup>INRAE, UR EFNO, FR-45290 Nogent-sur-Vernisson, France.
- <sup>47</sup>Pacific Forestry Centre, Victoria, British Columbia, V8Z 1M5 Canada.
- <sup>48</sup>Department of Biology, Colby College, Waterville, ME 04901 USA.
- <sup>49</sup>School of Natural Sciences, UC Merced, Merced, CA 95343 USA.
- <sup>50</sup>Department of Biology, Washington University in St. Louis, St. Louis, MO.
- <sup>51</sup>Department of forestry and renewable forest resources, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia.
- <sup>52</sup>Tohoku Research Center, Forestry and Forest Products Research Institute, Morioka, Iwate, 020-0123, Japan.
- <sup>53</sup>Department of Forest vegetation, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki, 305-8687, Japan.
- <sup>54</sup>Valles Caldera National Preserve, National Park Service, Jemez Springs, NM 87025 USA.
- <sup>55</sup>U.S. Geological Survey Fort Collins Science Center, 2150 Centre Avenue, Bldg C, Fort Collins, CO 80526 USA.
- <sup>56</sup>Inst. de Recursos Naturales y Agrobiología de Sevilla, Consejo Superior de Investigaciones Científicas (IRNAS-CSIC), Seville, Andalucía, Spain.
- <sup>57</sup>W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Krakow, Poland.
- <sup>58</sup>Mammal Research Institute, Polish Academy of Sciences, Ul. Stoczek 1, 17-230, Bialowieza, Poland, Mammal Research Institute, Polish Academy of Sciences, Bialowieza, Poland.
- <sup>59</sup>Nicholas School of the Environment, Duke University, Durham, NC 27708 USA.
- <sup>60</sup>Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO, USA.
- <sup>61</sup>Ecological Restoration Institute, Northern Arizona University, Flagstaff AZ 86011, USA.
- <sup>62</sup>Department of Biología Vegetal y Ecología, Universidad de Sevilla, 41012 Sevilla, Spain.
- <sup>63</sup>Bilogo Dpto. Conservacin y Manejo Parque Nacional Lanin Elordi y Perito Moreno 8370, San Marten de los Andes Neuquén Argentina.
- <sup>64</sup>Department of Biology, Wake Forest University, 1834 Wake Forest Rd, Winston-Salem, NC 27106 USA.
- <sup>65</sup>Department of Biology, Wilkes University, 84 West South Street, Wilkes-Barre, PA 18766 USA.
- <sup>66</sup>Department of Environmental Science and Ecology, State University of New York-Brockport, Brockport, NY 14420 USA.
- <sup>67</sup>School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK.
- <sup>68</sup>Department of Ecology, Evolution and Environmental Biology, Columbia University, 1113 Schermerhorn Ext., 1200 Amsterdam Ave., New York, NY 10027.
- <sup>69</sup>Department of Agricultural and Environmental Sciences - Production, Territory, Agroenergy (DISAA), University of Milan, 20133 Milano, Italy.
- <sup>70</sup>Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011 USA.

<sup>71</sup>Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA.

<sup>72</sup>Smithsonian Tropical Research Institute, Apartado 0843n03092, Balboa, Republic of Panama.

<sup>73</sup>Department of Environmental Sciences, University of Puerto Rico, Rio Piedras, PR 00936 USA

## **corresponding author:**

Tong Qiu, tvq5043@psu.edu

## Abstract

The benefits of masting (volatile, quasi-synchronous seed production at lagged intervals) include satiation of seed predators, but these benefits come with the cost to mutualist pollen and seed dispersers. If the evolution of masting represents a balance between these benefits and costs, we expect mast avoidance in the species that are heavily reliant on mutualist dispersers. These effects play out in the context of variable climate and site fertility among species that vary widely in nutrient demand. Meta-analyses of published data have focused on variation at the population scale, thus omitting periodicity within trees and synchronicity between trees. From raw data on 12 million tree-years worldwide, we quantified three components of masting that have not previously been analyzed together: 1) volatility (frequency-weighted year-to-year variation); 2) periodicity (lag between high-seed years); and 3) synchronicity (tree-to-tree correlation). Results show that mast avoidance (low volatility, low synchronicity) by species dependent on mutualist dispersers explains more variation than any other effect. Nutrient-demanding species, species that are most common on nutrient-rich and warm/wet sites, have low volatility and short periods. The prevalence of masting in cold/dry sites coincides with the climatic conditions where dependence on vertebrate dispersers is less common compared to the wet tropics. Mutualist dispersers neutralize the benefits of masting for predator satiation, further balancing the effects of climate, fertility, and nutrient demands.

**Keywords:** *masting, periodicity, pollination, synchronicity, seed production, seed dispersal, traits, volatility*

# 1 Introduction

2 Unpredictable reproduction in trees (“masting”) could be an evolved response to thwart seed con-  
3 sumers<sup>(1,2,3)</sup>, but then there is a conundrum: the volatility that limits seed predators could be just as  
4 deleterious to mutualist pollen and seed dispersers<sup>(4,2,5,6)</sup>, while also concentrating competition within  
5 offspring<sup>(7,8)</sup>. For natural enemies and mutualists alike, masting effects depend on three elements (fig.  
6 1), i) year-to-year *volatility*, or the time-dependent magnitude of variation, ii) *quasi-periodicity*, the lag  
7 between high seed-production years, and iii) *quasi-synchronicity*, the tendency for individuals to produce  
8 large seed crops in the same years<sup>(9)</sup>. Explanations for forest diversity invoke combinations of these  
9 three elements<sup>(10,11,12)</sup>, but they operate together: the costs and benefits of masting depend on the  
10 interactions between them and the foraging ranges of consumers and dispersers<sup>(13,9)</sup>. Meta-analyses  
11 provide important insights at the aggregate population or species scale<sup>(14)</sup> but miss the volatility within  
12 and synchronicity between trees<sup>(15,16,17)</sup>. Efforts to generalize species- and site-specific results confront  
13 a diversity of methods, measurements, and scales used in each study. In this paper we integrate raw  
14 data at the individual tree-scale from all vegetated continents to allow formal inference on the joint  
15 distribution of masting components. We show that variation of masting components across the diversity  
16 of tree species depends on how seeds and pollen are dispersed, indicating that mutualists may be just as  
17 important as consumers for the evolution of masting. Results show mediation of these effects by climate,  
18 soil fertility, and nutrient demand.

19 We introduce specific definitions for volatility and periodicity that emphasize the contributions of low-  
20 frequency (long-period) variation. The masting phenomenon is remarkable (and important), because  
21 it does not simply reoccur each year; it is frequency-dependent, with low-frequency variation being  
22 especially important for its effects on animal dispersers and consumers. We define frequency-dependent  
23 variation as *volatility*, to avoid confusion with the term *variance* (and its derivatives, *variation* and  
24 *variability*), which does not depend on time. Volatility emphasizes the contribution of variance that  
25 is concentrated at low frequency (long time lags). In the context of our analysis, *periodicity* likewise  
26 emphasizes variance that is concentrated at low frequency. In both cases, variance is determined as a  
27 function of frequency, followed by transformation to frequency-weighted volatility and periodicity (see  
28 Methods).

29 The adaptive foundation for masting may involve escape from natural enemies that are satiated by  
30 large, quasi-synchronized crops and limited by intervening lean years<sup>(18,19)</sup>, but this same variation can  
31 likewise negatively impact mutualists (fig. 2a). Scatter-hoarding birds and rodents can be both seed  
32 predators and mutualists, consuming the entire seed crop in some years, while also aiding reproduc-  
33 tion through seed burial<sup>(20)</sup>. Predator satiation is most likely with high reproductive volatility, long  
34 periods between high-yield years, and synchronicity between trees; this synchronicity reduces a con-  
35 sumer’s capacity to simply average over inter-annual variation in one host tree by accessing others<sup>(13,9)</sup>  
36 (fig. 2a). For example, erratic seed production by individual trees (volatile and quasi-periodic) may  
37 not deter natural enemies if high-production years are asynchronous between trees<sup>(9)</sup>. Any negative  
38 effects of quasi-periodic variation on a tree’s consumers would be amplified by high year-to-year varia-  
39 tion, especially when concentrated at long lags<sup>(2,21)</sup>, again, defined here as *volatility*. Weighing against  
40 the benefits of unreliable fruiting for its deleterious effects on enemies are the negative effects on mu-  
41 tualist dispersers<sup>(4,2,22)</sup>; the predator satiation hypothesis might not benefit species that are reliant on  
42 specialized pollinators and seed dispersers.

43 While volatility amplifies the effects of periodicity and synchronicity on enemies and benefactors  
44 alike, this same volatility could be mediated by resource availability and climate<sup>(21,23)</sup> (fig. 2a). Limited  
45 resources might promote reproductive variation in trees<sup>(24,25,26)</sup> or not<sup>(27)</sup>. The mast interval could be  
46 prolonged where large crops deplete reserves that require years to replenish<sup>(28,29,21,30)</sup> or not<sup>(14,27)</sup>. In  
47 this global analysis, we use cation exchange capacity (CEC), a widely used index of soil fertility<sup>(31,32)</sup>,  
48 and foliar nitrogen (N) and phosphorous (P) concentrations<sup>(27)</sup> to quantify the association between  
49 masting and resource supply (CEC) and resource demand: nutrient demanding species tend to have high  
50 foliar N and P<sup>(33)</sup>.

51 In addition to site differences in resources and climate norms, weather anomalies might contribute  
52 to large seed crops (e.g. Kelly et al<sup>(34)</sup>), especially for species with limited dependence on stored re-  
53 serves<sup>(1,23)</sup> (fig. 2a). An *anomaly* is defined here as the difference between a climate variable in a given  
54 year from the average of that variable for that site (the site *norm*). At least for a few species at one or  
55 a few sites, warm and wet years may be associated with low seed production<sup>(35,36,37,38,39)</sup> and increased  
56 reproductive synchronicity<sup>(40,41)</sup> (fig. 2a).

57 Because the distribution of species across environments is uneven, species differences cannot be fully

58 assessed from observational data, which dominate the masting literature. Climate anomalies in specific  
59 seasons are clearly important for many temperate species<sup>(42,38,41,40)</sup>, but our analysis evaluates vari-  
60 ation globally, spanning seasonal and a-seasonal environments. The effect of a climate anomaly such  
61 as temperature or moisture must depend on the climate norm at each site, including seasonality. For  
62 example, the estimated effect of an spring-time temperature anomaly of 1°C is not comparable between  
63 highly seasonal taiga and a-seasonal wet tropics, where the notion of spring is not relevant. Including an  
64 interaction between anomalies and norms in data models cannot clarify their respective contributions,  
65 because species are not observed across the same combinations of norms and anomalies in the data. For  
66 this reason, environmental anomalies are limited here to annual variation in temperature and moisture  
67 deficit, and comparisons between species in fig. 2a include the caveat that we are not observing all of  
68 them in all of the same settings.

69 The three components of masting have not been analyzed together, in part, because a joint anal-  
70 ysis requires substantial data at the individual (tree-year) scale. Unless individuals are perfectly syn-  
71 chronized, periodicity at the population scale underestimates periodicity at the individual scale; in  
72 fact, asynchronicity can entirely mask periodic reproduction where observed with population-scale data.  
73 Studies that examine both individual and population variation show that fecundity is typically quasi-  
74 synchronous at best<sup>(15,43,9,17,44)</sup>. Understanding spatial scales<sup>(45)</sup>, allocation tradeoffs<sup>(46,47)</sup>, responses  
75 to climate<sup>(48,42,49,39,50)</sup>, and effects on consumers<sup>(51,9)</sup> and dispersers<sup>(4,2)</sup> all require joint analysis of  
76 reproductive variance within and between individuals.

77 Synthesis is challenged not just by the incompatible reference used in literature studies (Supplemen-  
78 tary information), but also by a need for measures of volatile, periodic, synchronous variability. All  
79 three elements vary between species and regions. The commonly used coefficient of variation (CV) omits  
80 time and frequency, one of the defining features of masting, and applications of CV to log values cannot  
81 properly incorporate zeros. This is important, because zero is the most frequent observation in many  
82 data sets (e.g., fig. 1c) (Supplementary information). Estimating periodicity requires a definition for  
83 what constitutes a mast year<sup>(30,52,53,54)</sup>, which is challenging because there is no identifiable threshold  
84 (e.g., fig. 1c) despite detectable indicators on trees (e.g., twigs hanging from seed weights) and peaked  
85 seed numbers in fig. 1a,b. The interval between mast years that would come from imposing an artificial  
86 threshold can range widely, in part due to variation within and between trees<sup>(55,56)</sup>. Using methods  
87 developed in this study, *P. monticola* (fig. 1a) and *A. grandis* (fig. 1b) share biennial variation but differ  
88 in the secondary concentration of variance at 3 to 4 yr in *P. monticola*. The period-weighted variance  
89 spectrum (to emphasize low-frequency) gives estimates of 2.4 and 3.2 yr in *P. monticola* and *A. grandis*,  
90 respectively (fig. 1e). Not only are both species strongly biennial, they are also quasi-synchronous, with  
91 mean pairwise individual correlations being especially high for *A. grandis* ( $0.72 \pm 0.12$  compared with  
92  $0.60 \pm 0.27$  in *P. monticola*) (fig. 1d). Quasi-synchronicity between trees within a species can extend  
93 over regions<sup>(40,41,45)</sup>, but it is not global. In our case, regional variation is defined at the eco-region scale,  
94 and synchronicity is evaluated at the 1-km scale (Methods).

95 Our approach that leads to the summaries in fig. 1 takes the perspective of each tree as a time  
96 series, with dependence between individuals from the same species, using a state-space representation  
97 for maturation and fecundity status<sup>(16,42)</sup>. A model that allows for dependent observations is especially  
98 important for masting, where synchronicity means that a single individual may offer almost the same  
99 information as an entire population. In our approach, dependent observations are taken up by the  
100 correlation structure contained in the posterior distribution of latent states, one for each tree-year. The  
101 approach can allow for either year effects or autoregressive [AR( $p$ ) with lag  $p$ ] terms as alternative ways  
102 to incorporate variation over time. Zeros are accommodated by a hidden Markov process for maturation  
103 status and allowance for failed crops with censoring (see Methods). Year effects that are random by  
104 ecoregion have the advantage that they do not assume a fixed AR structure over time<sup>(9)</sup>.

105 In three steps, we evaluate masting across species with contrasting reliance on mutualist dispersers at  
106 the global scale, and how the relationship between masting and mutualists varies with resources, climate,  
107 and phylogeny. We hypothesized that mutualist pollinators and dispersers select for low volatility, short  
108 periods, and low synchronicity<sup>(4,2,9)</sup> (fig. 2a). We expected that nutrient-demanding species and species  
109 that commonly occur on fertile sites tend toward low volatility, rapid replenishment times following large  
110 crops and, thus, short periods<sup>(29,23)</sup> (fig. 2a). We further hypothesized that warm climates favor low  
111 volatility and high synchronicity<sup>(2,14,40)</sup>, while dry climates (high moisture deficit) favor high volatility  
112 and synchronicity<sup>(45,41)</sup> (fig. 2a). To test those hypotheses, we begin by extracting the three compo-  
113 nents of masting (fig. 1) from inter-annual and inter-tree variation<sup>(9)</sup> using methods that derive from  
114 signal-processing for the time-series aspect of data and tree-to-tree correlation. Second, individual time  
115 series were aggregated by ecoregion-species, weighted by fecundity to emphasize large producers<sup>(57,58)</sup>

116 (Methods). Finally, we evaluated the effects of pollen and seed dispersal modes, resources, and climate  
117 on the joint response of masting components, both including and controlling for phylogeny.

## 118 Results

119 Across all species in the study, dependence on mutualist dispersers is linked to low masting volatility  
120 (fig. 3a). Volatility for species that depend on animals for seed and/or pollen dispersal is substantially  
121 lower than that for wind-pollinated flowers and wind-dispersed seeds. The link between volatility and  
122 dispersal syndrome is mediated by resources and climate (fig. 3a). In addition to wind dispersal (the  
123 positive mirror images of negative AD and AP in fig. 3a), high volatility is associated with low nutrient  
124 demand (low foliar P and N:P) and with fertile soils (cation exchange capacity, CEC in fig. 3a). Of  
125 course, there is within-species variation in response to fertility<sup>(58)</sup>, which is distinct from the mean CEC  
126 on which species are located, as used in this study. There is a weak tendency for low volatility in cold,  
127 moist climates (credible intervals include zero for Temp and Def in fig. 3a). High volatility is further  
128 associated with small seeds ( $SM < 0$ ).

129 The volatility relationships are not isolated from the two other components of masting. High peri-  
130 odicity values in fig. 3b mean that there are long periods between high-yield years. High synchronicity  
131 values in fig. 3c mean that individuals produce large crops in the same years, and vice versa. Because  
132 period and synchronicity are important only for trees with non-negligible seed production, both are  
133 weighted here by individual fecundity (see Methods). In the case of synchronicity, the distribution of  
134 pairwise correlations for trees of the same species within 1 km of one another (see Methods) has the mode  
135 near +1, but is broadly distributed over negative and positive values (fig. 4a). When aggregated to the  
136 species level (averaged over pairwise correlations for the species), the distribution shifts to predominantly  
137 positive values (fig. 4b, red). When weighted by fecundity, these averages increase further (fig. 4b,  
138 blue), due to the fact that large producers have the highest levels of synchronicity.

139 The long periods associated with animal seed dispersal (fig. 3b) may not have meaningful effects on  
140 consumers or mutualist, because these species are weakly synchronized (fig. 3c). For consumers that  
141 can move between host trees, weak synchronicity means that there will be individuals producing seed in  
142 many years. Short periods are associated with warm, wet, fertile sites (negative Temp and CEC, positive  
143 Def in fig. 3b). The quasi-synchronicity that is strongest for wind dispersal is amplified in cold, dry  
144 climates (negative AD and Temp, positive Def in fig. 3c).

145 The most volatile species are not those having the highest sensitivity to climate anomalies. It is  
146 important to first note that climate anomalies make large contributions to variation in many species,  
147 both positive and negative (large coefficients in fig. 5c, d). The absolute values of anomaly responses  
148 (fig. 5a) summarize both positive and negative sensitivity to moisture deficit and temperature anomalies  
149 (fig. 5a, b). The coefficients are less meaningful for low volatility species, because there is less total  
150 variation that could be driven by climate or intrinsic factors. Thus, the positive log volatility values in  
151 fig. 5 are most telling, and, at log volatility above zero, absolute sensitivity declines on average for both  
152 climate variables (fig. 5a, b). Because few animal-dispersed species are highly volatile, the trends in  
153 these high values are driven more by wind-dispersed species (blue symbols) with low foliar N:P (small  
154 symbols). For animal dispersed species, moisture-deficit sensitivities shift from negative to positive  
155 with increasing volatility (fig. 5c, orange, green). For both dispersal modes (wind versus animals),  
156 temperature sensitivities trend from negative to near-zero with increasing volatility (fig. 5d).

157 All elements of the three-part syndrome have phylogenetic dependence, especially strong for volatility  
158 and periodicity and less so for synchronicity (fig. 6). Volatility is highest in the temperate clades Pinales,  
159 Fagales, and Sapindaceae (prominent exceptions include the shrub maples *Acer pensylvanicum* and *A.*  
160 *spicatum*). The wind pollinated and (primarily) wind seed-dispersed genera *Abies* and *Betula* are near  
161 the highest volatility and the shortest period. Other volatile, wind-dispersed temperate groups include  
162 the Ulmaceae (*Ulmus*, *Zelkova*). Volatile animal-dispersed groups include the genera *Ficus*, *Swida*, and  
163 *Nyssa*. Synchronicity is especially high in many of the Pinales and Fagales. Low volatility is common in  
164 the tropical groups Fabales, Malpighiales, and Gentianales. For groups with mixed tropical/temperate  
165 affinities, volatility tends to be low in Magnoliids, Ericales, and Cornales. Periodicity and synchronicity  
166 of most tropical species are not included in fig. 6b, c, because their low volatility values fall below the  
167 range where period and synchrony become meaningful (Methods).

168 Taken over all ecoregion-species combinations, volatile seed production is most common for species  
169 with short periods between productive years (correlation = -0.28, 95% CI = (-0.36,-0.21), fig. S2). This  
170 negative relationship between volatility and period holds within phylogenetic groups, where there are  
171 more negative than positive correlations between volatility and period (fig. S2). High volatility aligns



172 with short periods in most temperate groups (in *Abies*, *Quercus*, *Fagus*, residual Fagaceae, Pinaceae,  
173 and Magnoliaceae), some tropical species (in Meliaceae, Melastomataceae), and some with mixed tropi-  
174 cal/temperate affinities (residual Sapindaceae). Correlations in other large temperate groups (in *Pinus*,  
175 *Acer*, Cupressaceae, Betulaceae, and Oleaceae), as well as in mixed tropical/temperate groups (in An-  
176 nonaceae, Araliaceae, Moraceae, Symplocaceae, Lauraceae), are negative but not significantly less than  
177 zero. Conversely, positive relationships are dominated by one mostly temperate group (Aquifoliaceae),  
178 others being non-significant, but predominantly tropical.

179 Across species, the relationship between volatility and synchronicity is weak (correlation = -0.039,  
180 95% CI = (-0.12, 0.043)), but strong correlations emerge within many phylogenetic groups (fig. S3).  
181 Volatile species have low synchronicity in many families of mixed temperate/tropical affinity (blue in  
182 fig. S3). High volatility combines with high synchronicity in the temperate genera *Fagus* and *Abies*, but  
183 only weakly in *Quercus* (brown in fig. S3). For the majority of species groups, high synchronicity is  
184 associated with low volatility.

## 185 Discussion

186 Seed and pollen dispersal syndromes emerge as the dominant trait associated with volatile seed pro-  
187 duction in trees; reliance on mutualist pollen and seed dispersal is among the strongest predictors of  
188 masting avoidance (fig. 3a). The selective forces that have shaped associations between masting and  
189 animal-dispersal include costs to mutualist dispersers and the benefits of reduced predation<sup>(4,2,14)</sup>. These  
190 selective forces are further complicated by the fact that at least some animal dispersers are also seed  
191 predators (e.g., in *Quercus* and other species that are dispersed by scatter-hoarding vertebrates). While  
192 animal-dispersed species are overall less volatile (fig. 3a), there are notable exceptions. For example, the  
193 volatile Fagaceae (fig. 6a) have primarily wind-dispersed pollen, but depend on scatter-hoarding seed  
194 dispersers–mutualists that suffer in low-yield years and disperse and satiate in high-yield years<sup>(59,60)</sup>.  
195 Perhaps as an exception that supports the rule, within Fagaceae the lowest volatility is estimated for  
196 *Castanea* with primarily insect-dispersed pollen<sup>(61)</sup>. The strong connection between mast volatility  
197 and wind dispersal (fig. 3a) supports the hypothesis that animal pollination may suffer from volatile  
198 masting<sup>(4,2,23,6,62)</sup>.

199 Insights from this study could not have come from a traditional treatment of variation. Traditional  
200 comparisons based on the coefficient of variation and its derivatives omit the basic attribute of frequency  
201 (fig. 1). Extracting mean intervals between events becomes highly subjective, because there is no  
202 threshold value that distinguishes an event from background (fig. 1c). All three components of mast  
203 variation require individual-scale data. Analysis of raw data, with dependence between individuals  
204 and over time, allowed quantification of the contributions of volatility, quasi-periodicity, and quasi-  
205 synchronicity.

206 Volatile species have low reliance on animal dispersal, low nutrient demands, and generally low sensi-  
207 tivity to climate anomalies (fig. 5a, b). The classic masting response–volatile, synchronized reproduction  
208 at lagged intervals–is associated with species traits and conditions that lead to low seed production. Cold,  
209 dry climates at high latitudes, where reproductive output is two orders of magnitude lower than in the  
210 wet tropics<sup>(63)</sup>, are dominated by small seeds, wind dispersed pollen and seeds, and volatile reproduc-  
211 tion (fig. 3a). Synchronized reproduction at long periods is a feature of dry climates (fig. 3b, c) where  
212 pollination efficiency is expected to be high<sup>(45)</sup>. Even the increased volatility with soil fertility fits  
213 this negative relationship between fecundity and volatility: mean fecundity declines with foliar P<sup>(58)</sup>  
214 as volatility increases (foliar nutrients and soil CEC in fig. 3a). Despite the limitations of comparing  
215 environmental responses across species that differ in their distribution of exposures to the environment,  
216 results are not consistent with the expectation that volatility at the species level increases with higher  
217 variations in climate anomalies<sup>(34)</sup>.

218 Synchronicity has the tendency to be associated with wind dispersal (fig. 3c), consistent with costs  
219 to mutualist dispersers that include not only satiated frugivores, but also competition for animal polli-  
220 nators<sup>(64)</sup>. Synchronized flowering may increase pollinator visitation rates<sup>(65,66)</sup>; however, if unreliable  
221 flowering limits specialized pollen dispersers, then benefits of synchronicity could be mixed (fig. 3c).  
222 A tendency for long intervals between mast years in mast-avoiding tree species has a muted effect on  
223 their animal seed dispersers, because it is associated with low volatility and asynchronicity (fig. 3b,  
224 c). The association of wind pollination with high volatility but not with long periods agrees with the  
225 largely untested notion that quasi-synchronous flowering effort increases pollination efficiency while long  
226 intervals between mast years have no additional benefits<sup>(1)</sup>.

227 The synchronicity that is typically emphasized for masting populations belies the overall weak tree-to-  
228 tree correlation. The distribution of inter-tree correlations weighted by fecundity (fig. 4b) could resolve  
229 the paradox of low synchronicity in species traditionally identified as iconic mast producers<sup>(15,16,17)</sup>.  
230 Low and even negative correlations characterize populations on the whole (fig. 4a), but strong producers  
231 are dominated by positive correlations (fig. 4b). The production of some non-synchronized offspring  
232 is an expected bet-hedging maternal strategy even where quasi-synchronicity is generally beneficial.  
233 The advantages of predator satiation have to balance the potential costs of concentrated intraspecific  
234 competition between sibling seedlings and of satiating mutualist pollinators and dispersers. Indeed,  
235 heterogeneous volatility-synchronicity relationships between lineages (Fig. S2) suggests the potential for  
236 region/species-scale adaptation in response to variable predation pressure<sup>(67,22)</sup>.

237 The finding that volatile species tend to have short periods (fig. 6), including within multiple phy-  
238 logenetic groups (fig. S2), is not consistent with the view that resource depletion followed by delayed  
239 replenishment is a dominant source of variation between species. This lack of association *between* species  
240 does not preclude a need for extended replenishment following high-yields *within individuals* in ways that  
241 differ between species. Although less studied, it is also important to understand how local adaptation  
242 (i.e., genetic differences among populations<sup>(68)</sup>) and gene  $\times$  environment interactions that affect seed  
243 enemies and dispersers<sup>(69,5)</sup> may contribute to the evolution of volatility, periodicity and synchronicity.

244 If consistently high nutrient concentrations obviate the need for prolonged nutrient recovery, then we  
245 expect the observed negative association between foliar nutrients and volatility (fig. 3a). By allowing  
246 for the effects of both foliar nutrient concentrations and site fertility, our results diverge from previous  
247 studies suggesting low volatility on fertile sites. However, comparisons have to consider that previous  
248 studies include few species<sup>(24,25,26)</sup>. The effects of nutrient demand versus supply can be confounded by  
249 the fact that nutrient-demanding species are most abundant on fertile sites. By including differences in  
250 foliar nutrients as a species-level trait with the CEC where trees occur, this global analysis finds that  
251 low volatility is associated with nutrient-demanding species, not low-fertility sites. The association of  
252 high volatility and short periods with nutrient-rich habitats (CEC in fig. 3) could result from accelerated  
253 nutrient replenishment on fertile soils. However, as noted above, volatile species are not those with short  
254 periods in general. Not only do nutrient-demanding species (as reflected in foliar nutrient content) have  
255 lower species seed production (SSP, defined as seed number  $\times$  seed size)<sup>(58)</sup>; they also are less volatile  
256 (fig. 3a). Limited effects of resources on synchronicity can be related to the weak effects of soil CEC on  
257 seed production<sup>(58)</sup> and intense competition on nutrient-rich sites<sup>(42)</sup>.

258 The expectation that large seeds might demand long recovery intervals was not supported by compar-  
259 isons between species. Using data from Schopmeyer et al<sup>(70)</sup>, Sork et al<sup>(30)</sup> found a positive relationship  
260 between acorn size and mast period for 18 temperate *Quercus* species. We find a negative relationship  
261 at the global scale: species with large seeds are less volatile and have short periods in fig. 3a, b. In  
262 the limited dataset<sup>(70)</sup>, the negative correlation is driven by a longer interval for *Quercus alba* than *Q.*  
263 *falcata*. In general, we find that red oaks (*Q. falcata*, *Q. rubra*, *Q. velutina*, *Q. coccinea*) have longer  
264 periods than white oaks (*Q. alba*, *Q. montana*, *Q. pubescens*, *Q. robur*, *Q. stellata*, *Q. serrata*), Cerris  
265 oaks (*Q. cerris*, *Q. ilex*, *Q. suber*) and *Fagus* (fig. 6b), perhaps related to the two-yr development time  
266 for red oak seeds.

267 The wide variation in seed production<sup>(57,58)</sup> emphasizes the importance of large data sets to estimate  
268 effects, represented here by 12 million tree-years at a global scale. As is common in observational studies,  
269 the geographic coverage of raw observations is not uniform across different regions (Fig. S1). Expanding  
270 the MASTIF network with additional sites in South America and Africa would contribute to a more  
271 balanced global coverage.

272 The negative association between masting intensity and fecundity suggests the view of masting as  
273 desperation: an evolutionary option most common in species and settings where seed production is  
274 limited primarily by climate and habitat and where animal dispersal is less common. There is no  
275 question that predator satiation occurs, and seedling escape can result<sup>(71,72,73)</sup>. Despite the fact that  
276 it is not uncommon for a given tree species to have multiple pollinators and seed dispersers<sup>(74)</sup>, the  
277 diet breadth of seed consumers (e.g., specialist and generalist) clearly affects masting<sup>(9)</sup>. Quantifying  
278 different degrees of specialization between seed predators, pollinators and dispersers is an important  
279 future research avenue. Still, at the global scale, species differences in masting depend on their reliance  
280 on animal dispersers.

281 The emergence of dispersal syndrome as a dominant link to species differences in masting intensity  
282 (fig. 3) supports the view that mutualist relationships could be just as important as predator satiation–  
283 the cold, dry settings where masting is intense coincides with the low reliance on mutualist dispersers.  
284 The conundrum faced by species that depend on animal dispersal while also suffering from seed predation

285 makes for conflicting selection pressures that are evident when viewed across the diversity of tree species.

## 286 Methods

### 287 MASTIF summary

288 The MASTIF model allows us to jointly model individual trees, with their dependence on one another  
 289 and over time. This hierarchical, state-space model and the Gibbs sampling used for posterior simulation  
 290 are detailed in Clark et al. (9), with only key elements that relate to mast syndromes summarized here.  
 291 Model fitting includes approximately 12 million tree-years from 898 species (fig. S1). MASTIF model is  
 292 open-access with R package MASTIF on CRAN.

293 The core quantity of interest is the tree-year fecundity  $f_{ijr,t}$  for tree  $i$  on stand  $j$ , in ecoregion-  
 294 species  $r$ , and year  $t$ . Fecundity varies individually with tree size and crowding, locally with interannual  
 295 climate anomalies, geographically with climate norms, soil and drainage, and regionally through shared  
 296 year effects. The shared variation between trees in year effects are random between ecoregion-species  
 297 combinations, allowing for covariation that is broader than local climate but still regionally variable.  
 298 Because the model includes interannual anomalies at the local scale, year effects quantify shared variation  
 299 beyond that explained by climate anomalies and at a coarse (ecoregion) scale.

300 The MASTIF model incorporates two data types including crop counts and seed traps. Crop counts  
 301  $c_{ijr,t}$  are conditionally beta-binomial, which allows for the uncertainty in fraction of the crop that is  
 302 observed,

$$betaBinom(c_{ijr,t}|f_{ijr,t}, a_{ijr,t}, b_{ijr,t}) = \int_0^1 binom(c_{ijr,t}|f_{ijr,t}, q_{ijr,t}) beta(q_{ijr,t}|a_{ijr,t}, b_{ijr,t}) dq_{ijr,t} \quad (1)$$

303 where  $q_{ijr,t}$  is an estimate of the fraction of the crop observed, and  $(a_{ijr,t}, b_{ijr,t})$  are parameters selected  
 304 have mean fraction  $q_{ijr,t}$  (i.e., the fraction reported), but error that increases with small  $q_{ijr,t}$ . This  
 305 approach allows for the fact that the lower the reported crop fraction, the less certain it is.

306 Seed trap counts are conditionally Poisson,

$$Poi(\mathbf{y}_{jr,t}|A_{j,t}\mathbf{S}\mathbf{f}_{jr,t}) \quad (2)$$

307 where trap area  $A_{j,t}$  can vary by study and year  $t$ ,  $\mathbf{y}_{jr,t}$  is a vector of seed counts for  $S_j$  traps,  $\mathbf{S}$  is the  
 308  $S_j \times n_j$  kernel matrix that determines dispersal from each of  $i = 1, \dots, n_j$  trees to  $S_j$  traps, depending  
 309 tree-to-trap distances, and  $\mathbf{f}_{jr,t}$  is the length- $n_j$  vector of tree fecundities. The dispersal kernel follows (75).

310 Fecundity is the product of latent states for maturation status and conditional fecundity,  $f_{ijr,t} =$   
 311  $\psi_{ij,t}\rho_{ijr,t}$  having the joint distribution  $[\psi_{ijr,t}, \rho_{ijr,t}] = [\psi_{ijr,t}|\rho_{ijr,t}][\rho_{ijr,t}]$ . (We use bracket notation  $[x]$   
 312 to indicate a distribution or density of  $x$ ). Maturation is a one-way process, modelled as a probit hidden-  
 313 Markov model. The maturation status  $\rho_{ijr,t} \in \{0, 1\}$  is known to be 1 (i.e., mature) for trees that have  
 314 been observed to produce seed in the past, i.e.,  $[\rho_{ijr,t} = 1|\rho_{ij,t-1} = 1] = 1$ , and 0 if known to be immature  
 315 subsequently  $[\rho_{ijr,t} = 1|\rho_{ij,t+1} = 0] = 0$ . For tree-years of unobserved maturation status, the probability  
 316 of being mature in year  $t$ , given past and future status is the probit,

$$\begin{aligned} \rho_{ijr,t}|\rho_{ijr,t-1}, \rho_{ijr,t+1} &\sim Bernoulli(p_{ijr,t}) \\ p_{ijr,t} &= \rho_{ijr,t-1} + (1 - \rho_{ijr,t-1})\rho_{ijr,t+1}\Phi(\mathbf{v}'_{ijr,t}\boldsymbol{\beta}^v) \end{aligned} \quad (3)$$

317 where  $\Phi(\cdot)$  is the standard cumulative normal distribution,  $\mathbf{v}_{ijr,t}$  are predictors, and  $\boldsymbol{\beta}^v$  are fitted coeffi-  
 318 cients. All unknown statuses must be imputed, so that  $\rho$  coefficients in eq. (3) are the currently imputed  
 319 values in Gibbs sampling.

320 The process model for fecundity is log-normal and dynamic,

$$\log \psi_{ijr,t}|\rho_{ijr,t} \sim N(\mathbf{x}'_{ij,t-1}\boldsymbol{\beta} + \alpha_{ij} + \gamma_{r,t}, \sigma^2)I(\psi_{ijr,t} \leq 1)^{1-\rho_{ijr,t}}I(\psi_{ijr,t} > 1)^{\rho_{ijr,t}} \quad (4)$$

321 where  $\mathbf{x}_{ij,t}$  are predictors in the model with coefficients  $\boldsymbol{\beta}$ ,  $\alpha_{ij}$  is the random effect for tree  $ij$ ,  $\gamma_{r,t}$  is the  
 322 year effect for ecoregion-species  $r$ , and  $\sigma^2$  is the residual variance. The factors containing the indicator  
 323 function specify that mature individuals have latent conditional fecundity sufficient to generate at least  
 324 one seed. Importantly, the approach allows for observed zero fecundity for both seed traps and crop  
 325 counts while latent fecundity remains finite. This approach follows the approach used in Tobit models  
 326 for discrete zeros in otherwise continuous data (76,77). Predictors in the design vector  $\mathbf{x}_{ijr,t}$  include known  
 327 climate and habitat variables combined with variable selection by DIC.

## 328 Masting syndromes

329 The analysis of masting components at individual level is based on the estimate of the fecundity,  $f_{ijr,t}$ ,  
 330 on the log (proportionate) scale. The mast syndrome consists of three elements  $M = (M_v, M_p, M_c)$ , the  
 331 volatility  $M_v$  having units of variance in  $\log f$ , period  $M_p$  in years, and the dimensionless synchronicity  
 332  $M_c$ . The first two elements emerge from the spectral density  $S_f(\omega)$ , evaluated in the frequency  $\omega$  domain.  
 333 Technically,  $S_f(\omega)$  is obtained by transforming the auto-covariance function  $C(t)$  from the time domain  
 334 to the frequency domain or, alternatively, by taking the Fourier transform of the autocorrelation function  
 335  $C(t)/C(0)$ . There is an associated spectral *variance*, obtained by integrating the spectral density over  
 336 frequency

$$Var_\omega(f) = \frac{1}{\pi} \sum_{k=0}^{\omega^*} S_f(\omega_k) \quad (5)$$

337 where  $\omega^*$  is the last frequency term. Period (years) is the reciprocal of frequency,  $\omega^{-1}$ . To capture the  
 338 defining feature of masting, that of variance concentrated at low frequency, we define *volatility* as the  
 339 period-weighted spectral variance,

$$E_\omega(M_v) = \frac{1}{\pi T} \sum_{k=0}^{T-1} \omega_k^{-1} S_f(\omega_k) \quad (6)$$

340 where  $T$  is the number of terms included in the summation. The subscripts of tree  $i$ , stand  $j$ , and  
 341 ecoregion-species  $r$  are omitted to reduce clutter. Because short time series could be dominated by  
 342 noise, we focused on mature individuals that include at least 10-year of observations (139,785 trees and  
 343 2,841,238 tree-years from 468 species). Detailed data distribution can be found in the supplementary  
 344 csv file. We set  $T$  to be half of the threshold, i.e,  $T = 5$  yr. Likewise, *periodicity* emphasizes variance at  
 345 low frequency,

$$E_\omega(M_p) = \frac{1}{\pi Var_\omega[f]} \sum_{k=0}^{T-1} \omega_k^{-1} S_f(\omega_k) \quad (7)$$

346 with variance

$$Var_\omega(M_p) = \frac{1}{\pi Var_\omega(f)} \sum_{k=0}^{T-1} \omega_k^{-2} S_f(\omega_k) - E_\omega^2(M_p) \quad (8)$$

347 The span of variance captures the quasi-periodic nature of masting, being broad where period is un-  
 348 predictable (fig. 1d). We obtained the spectral density  $S_f(\omega_k)$  for each tree ( $\log f_{ijr}$ ) using the R  
 349 package `spectrum`. Volatility and periodicity complement currently-used metrics for masting. Volatil-  
 350 ity measures variance in the frequency domain, capturing the out-sized importance of variation at the  
 351 multi-year scale, moving beyond lag-0 (CV) or lag-1 approaches. Periodicity side-steps the need to de-  
 352 fine a threshold productivity for mast years or the fact that a simple mean interval may not represent  
 353 quasi-periodic variation.

The ecoregion-species masting syndromes,  $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$ , are the expectations of individual  
 level estimates  $M_{ijr}$ . Because individual volatility  $M_{v,ijr}$  and quasi-periodicity  $M_{p,ijr}$  could be dominated  
 by large numbers of small and thus low fecundity trees, we evaluated the  $M_{v,r}$  and  $M_{p,r}$  in a weighted  
 way to increase signal-to-noise ratio and to emphasize the large seed producers:

$$M_{v,r} = \frac{\sum_{ij} ISP_{ij} M_{v,ijr}}{\sum_{ij} ISP_{ij}} \quad (9)$$

$$M_{p,r} = \frac{\sum_{ij} ISP_{ij} M_{p,ijr}}{\sum_{ij} ISP_{ij}} \quad (10)$$

354 where ISP is individual standardized productivity<sup>(58,63)</sup>. It is defined as seeds per tree times mass per  
 355 seed and divided by tree basal area and averaged across multiple years.

356 We evaluated the weighted synchronicity at ecoregion-species level following a similar procedure as  
 357 that of volatility and periodicity. Tree-to-tree correlation coefficients were calculated between all con-  
 358 specific individuals within 1 km of one another. We included correlations  $M_{c,k}$  over years for which both  
 359 trees of a pair  $k$  that are estimated to be in the mature state (3,539,315 tree-years and 274,024 trees  
 360 from 468 species). For the tree-to-tree correlations, both the correlation and the product of fecundity

361 were calculated for each pair, the latter having large values for trees with high production. A weighted  
362 synchronicity over all trees of a species within 1 km was evaluated as

$$M_{c,r} = \frac{\sum_k M_{c,kr} C_k}{\sum_k C_k} \quad (11)$$

363 for all pairwise correlations  $M_{c,kr}$  at ecoregion-species  $r$ , with weight  $C_k$  being the absolute value of the  
364 pairwise covariance, i.e., the product of fecundities for each pair of trees  $k$ .

## 365 Analyses at ecoregion-species level

366 We evaluated variations in the  $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$  jointly at ecoregion-species level ( $n = 583$ )  
367 through incorporating phylogeny, species traits, soil, and climate covariates in a generalized joint at-  
368 tribute model (GJAM). Our analyses were implemented at ecoregion-species level because 15% of the  
369 total species ( $n = 468$ ) have within-species variations across ecoregions (supplementary csv file). The  
370 remaining (85%) species that are sampled at one ecoregion are primarily tropical species. As of now,  
371 MASTIF coverage could be improved with the addition of more sites in South America, Africa, and  
372 Asia. One of the masting families, Dipterocarpaceae, is not included in the network. But the MASTIF  
373 network is continuously expanding to achieve a more balanced global coverage. Ecoregions in this study  
374 follow the same definition as World Wildlife Fund (WWF) terrestrial ecoregions<sup>(78)</sup>.

## 375 Phylogeny

376 We quantified the phylogenetic signal in volatility and quasi-periodicity using *Pagel's*  $\lambda$ . Species dif-  
377 ferences in masting syndromes were averaged across ecoregion-species combinations. Phylogeny was  
378 obtained for 394 species (84% of the total 468 species) from<sup>(79)</sup>. We used the continuous character  
379 mapping method from the R package `phytools`<sup>(80)</sup> to visualize the phylogenetic coherence in volatility,  
380 periodicity, and synchronicity.

381 To account for phylogeny in the joint model of three masting syndromes, we depart from traditional  
382 assumptions concerning residual covariance, turning instead to direct inference on the effects of phylo-  
383 genetic groups. The aim to control for phylogenetic association in comparative studies<sup>(81,82)</sup> suggests a  
384 capacity to take up variation that might be linked to relatedness in a general sense. Instead, current  
385 methods impose a highly specific assumption that residual variance between species traits results from  
386 a random walk that proceeds at a fixed rate across species pairs. However, natural selection would not  
387 operate in this way, not for a given species pair and certainly not across a large number of species.  
388 Residual variance constitutes all sources of variation that are not taken up by the mean structure of  
389 the model. Just as there could be massive phylogenetically constrained traits between specific species  
390 pairs that have diverged under differing intensities of selection, there could be minimally constrained  
391 pairs within the same comparative study where others are strong. The important modeling concern for  
392 valid inference on coefficients is a covariance matrix that can take up relationships that remain after  
393 accounting for the mean, regardless of their source, and without imposing specific assumptions about  
394 rates of divergence.

395 Our joint analyses of masting syndromes explored phylogenetic contributions with species groups  
396 treated as random effects and covariance that is unconstrained by assumptions on divergence rates.  
397 Rather than assume a fixed relationship between residual covariances, our approach provides a transpar-  
398 ent estimate for differences between species groups, allowing that they need not be anchored to pairwise  
399 divergence times. For genera having at least 10 species in the MASTIF data, species were grouped at  
400 the genus level. All remaining species in families having at least 5 species were grouped at the family  
401 level. Remaining species were aggregated into an 'other' group for purposes of model fitting, but they are  
402 displayed separately in the correlation plots (e.g., Fig. S3). Relationships between masting syndromes  
403 within each phylogenetic group were evaluated using Pearson's correlation coefficient.

## 404 Joint modeling of masting syndromes

405 To evaluate masting as a syndrome and the variables associated with it, we conducted joint analyses  
406 of mast attributes against predictors that include species traits, environment, and phylogeny. Species  
407 traits included dispersal mode (anemochory vs zoochory), pollination mode (animal vs wind pollinated  
408 syndromes), mean foliar N and P (percentage of dry mass), and seed size (gm per seed). Traits infor-  
409 mation are obtained from collections in our labs and supplemented with the TRY database<sup>(83)</sup>. Genus-

410 or family-level means were used where seed size and foliar nutrients were missing at the species level.  
 411 Similarly, genus- or family- modes were used for dispersal and pollination syndromes. Foliar N:P were  
 412 calculated as the ratio between the two nutrients. Foliar N:P measures the nutrient limitations<sup>(33)</sup> and  
 413 could affect the masting syndrome<sup>(29)</sup>. Environmental covariates include soil fertility (Cation Exchange  
 414 Capacity, CEC), mean annual temperature, and accumulated annual moisture deficit (differences between  
 415 potential evapotranspiration and precipitation) averaged at ecoregion-species level. We used generalized  
 416 joint attribute modeling (GJAM)<sup>(77)</sup> to allow for the dependence between mast components and the fact  
 417 that masting components are non-negative (they are non-Gaussian),

$$\mathbf{w}_r \sim MVN(\mathbf{x}'_r \boldsymbol{\beta}, \Sigma) \times \prod_{l=1}^S I(w_{r,l} \leq 0)^{I(M_{r,l}=0)} I(w_{r,l} > 0)^{I(M_{r,l}=w_{r,l})} \quad (12)$$

418 where  $\mathbf{w}_r$  is the length- $S$  vector holding the latent (and uncensored) mast response for ecoregion-species  
 419  $r$  and  $\mathbf{M}_r$  is the length- $S$  observation vector ( $S = 3$  for the three components). Covariates occupy the  
 420 length- $Q$  vector  $\mathbf{x}'_r$ , including species traits and environmental conditions. Responses to covariates are  
 421 included in the  $Q \times S$  matrix of coefficients  $\boldsymbol{\beta}$ . The latent variable has the mean vector  $\mathbf{x}'_r \boldsymbol{\beta}$  and  $S \times S$   
 422 covariance matrix  $\Sigma$ . The product including indicator functions  $I(\cdot)$  allows for negative values on the  
 423 latent scale, essentially a multivariate Tobit<sup>(77)</sup>.

424 Model fitting with GJAM included phylogeny as random groups (previous section). Variable selection  
 425 was done using Deviance Information Criterion (DIC) as the criterion for additional predictors in the  
 426 model. Volatility (response) and seed mass (covariates) were modeled on the log (proportionate) scale.  
 427 Dispersal and pollination modes were included as factors. Standardized coefficients  $\boldsymbol{\beta}$  was summarized  
 428 using the posterior median, 90%, and 95% credible intervals from the MCMC chains. GJAM fitting is  
 429 open-access with R package GJAM on CRAN.

## 430 Data availability

431 Seed production data are available at the Duke Data Repository <https://doi.org/10.7924/r4348ph5t>.  
 432 Species traits are downloaded from TRY Plant Trait database at [https://www.try-db.org/TryWeb/](https://www.try-db.org/TryWeb/Home.php)  
 433 [Home.php](https://www.try-db.org/TryWeb/Home.php). Cation exchange capacity data are obtained at <https://soilgrids.org/>. Climate data  
 434 are extracted from Terraclimate at <http://www.climatologylab.org/> and CHELSA at [https://](https://chelsa-climate.org/)  
 435 [chelsa-climate.org/](https://chelsa-climate.org/).

## 436 Code availability

437 R statistical software v4.0.2 was used in this work. All analyses used published R packages, with details  
 438 stated in the section Methods. MASTIF includes code in R and C++, which is published on CRAN at  
 439 <https://cran.r-project.org/web/packages/mastif/index.html>.

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## 456 Author contributions statement

457 J.S.C and T.Q. designed the study, performed analyses, and wrote the paper. J.S.C. compiled the  
458 MASTIF data and wrote the MASTIF model and software. M.B, B.C., V.J, and G.K. co-wrote the  
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## 466 Competing interests statement

467 The authors declare no competing interests.

## 468 Figure caption

469 **Fig. 1: Illustration of three masting components** for *Pinus monticola* and *Abies grandis* from the  
470 central Cascades, U.S.A. Crop counts for these species (a, b) vary between individual trees, and they  
471 drift over time. The frequency of counts (c) in both species shows that zeros dominate, and there is no  
472 threshold that could be used to define masting events. *A. grandis* shows higher synchronicity between  
473 individuals (mean pairwise correlations between trees and their standard deviations are shown in d)  
474 and higher volatility, especially concentrated at the 2-yr period (e). *P. monticola* also shows variance  
475 concentrated at 2-yr, with a secondary peak at 3.4 yr. The (volatility, period) for this example are shown  
476 beneath species names in (e).

477 **Fig. 2: Hypothesized effects (a) and summary of results (b)** of mutualists (green), resources  
478 (blue), and climate (red) on the three masting components. Arrows with + and - represent positive  
479 and negative effects, respectively. We expect tree species with low volatility, short periodicity, and low  
480 synchronicity benefit most from their mutualist pollinators and dispersers (a). Resources reduce volatil-  
481 ity and periodicity (a). High temperature decreases volatility while promoting synchronicity (a). Dry  
482 sites (deficit) have higher volatility and synchronicity than wet sites (a). The summary of results in (b)  
483 comes from the joint model in fig. 3. Dashed lines indicate that 90% credible intervals contain zero.

484 **Fig. 3: Variables that contribute to the joint response of masting components** including  
485 volatility (a), periodicity (b), and synchronicity (c) at ecoregion-species scales. Predictors include verte-  
486 brate dispersers (animal seed dispersal (AD), animal pollination (AP)), resources (soil cation exchange  
487 capacity (CEC), foliar P (FP), and foliar N:P ratio (FNP)), seed mass (SM), and climate (accumulated  
488 moisture deficit (Def, ranging from wet to dry) and mean annual temperature (Temp, ranging from cold  
489 to warm)). Dispersal and pollination syndromes are included as two-level factors, so the negative coeffi-  
490 cients for animal seed dispersal (AD) and pollination (AP) have as mirror images the (positive) effects  
491 of wind dispersal and pollination. The analysis accounts for phylogeny as a random effect (Methods).  
492 Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded  
493 by 68% credible intervals (CI), with 95% CI whiskers. Colors highlight different variable types, with  
494 opacity increasing from 90% to 95% of the distribution outside of zero. Variables included in the model  
495 were based on the lowest Deviance Information Criterion (DIC). Coefficients are on the standard deviation  
496 scale for predictors and the correlation scale for responses (Methods). Results are summarized in  
497 fig. 2b to compare with hypotheses.

498 **Fig. 4: Quasi-synchronicity at individual and species level** a) Correlations between every pair  
499 of trees of the same species within 1 km show a mode near one, but a broad range. b) Species average  
500 correlations are concentrated near zero (red), but fecundity-weighted correlations are substantially higher  
501 (blue) (Methods).

502 **Fig. 5: Volatility, dispersal mode, climate anomalies, and foliar N:P.** Each point locates species  
503 volatility (variability between years on log scales) with its coefficients to climatic anomalies in moisture  
504 deficit (panel a and c) and temperature (panel b and d). Coefficients were obtained from the fitted  
505 model (see methods). Overall sensitivity with no grouping by dispersal/pollination syndromes is shown  
506 as absolute values in the above panel (a, b); and with their signs in the below panel (c, d). The mean  
507 temperature from the previous year and accumulated moisture deficit from both the previous and current

508 year were used to calculate anomalies. Symbol size scales with foliar N:P ratio. “Both animal” species  
509 (orange) have both pollen and seeds dispersed by animals. “Animal/wind” species (green) have either  
510 pollen or seeds dispersed by animals. High volatility is associated with positive responses to moisture  
511 deficit (c) and temperature (d) in animal-dispersed species, but generally declining absolute sensitivity  
512 to both variables (a and b). Loess regressions on parameter estimates (dots), weighted by the standard  
513 errors of the estimate (error bars), summarize trends with their confidence intervals (the colored shades)  
514 in absolute sensitivity (a, b) and for the three dispersal groups (c, d).

515 **Fig. 6: Phylogenetic coherence in the three masting components.** (a) Volatility (on log scale)  
516 has a phylogeny component (*Pagel’s*  $\lambda = 0.83$ ,  $p < 10^{-9}$ ,  $n = 394$ ). (b) Quasi-periodicity (left) exhibits  
517 a weaker phylogenetic coherence compared to volatility (*Pagel’s*  $\lambda = 0.52$ ,  $p = 0.0023$ ,  $n = 142$ ). Quasi-  
518 synchronicity (right) shows the weakest signal (*Pagel’s*  $\lambda = 0.21$ ,  $p = 0.0064$ ,  $n = 142$ ). Species with  
519 volatility of at least 0.94 (62.5% quantile) are shown in (b) because periodicity becomes noisy and less  
520 meaningful at low level of volatility.

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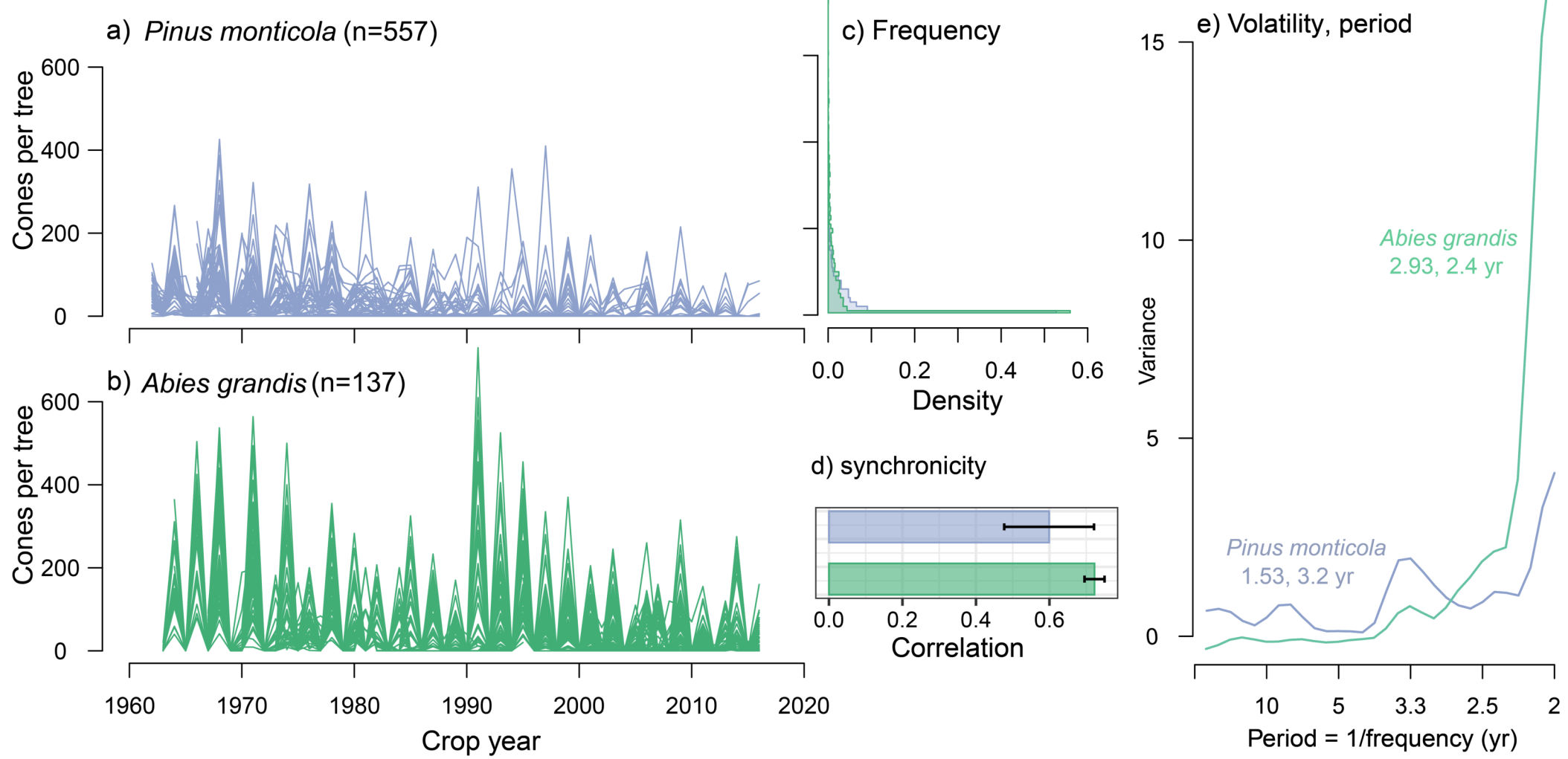
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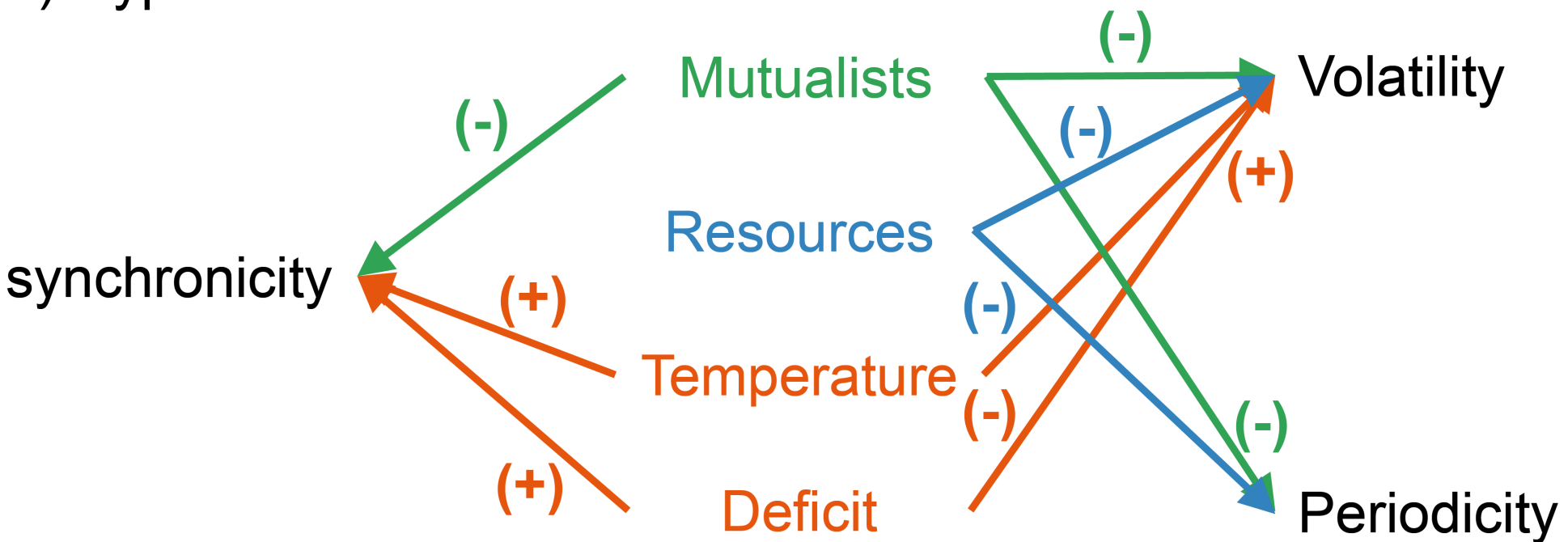
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842 M. Reichstein, D. E. B. Reid, M. Rejou-Mechain, V. Resco de Dios, S. Ribeiro, S. Richardson,  
843 K. Riibak, M. C. Rillig, F. Riviera, E. M. R. Robert, S. Roberts, B. Robroek, A. Roddy, A. V. Rodrigues,  
844 A. Rogers, E. Rollinson, V. Rolo, C. Roemermann, D. Ronzhina, C. Roscher, J. A. Rosell,  
845 M. F. Rosenfield, C. Rossi, D. B. Roy, S. Royer-Tardif, N. Rueger, R. Ruiz-Peinado, S. B. Rumpf,  
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847 A. Carolina Santacruz-Garcia, J. Santos, J. Sardans, B. Schamp, M. Scherer-Lorenzen, M. Schleuning,  
848 B. Schmid, M. Schmidt, S. Schmitt, J. V. Schneider, S. D. Schowanek, J. Schrader, F. Schrodtt,  
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851 V. Silva, M. Silva, T. Sitzia, H. Sjoman, M. Slot, N. G. Smith, D. Sodhi, P. Soltis, D. Soltis,  
852 B. Somers, G. Sonnier, M. V. Sorensen, E. E. Sosinski, Jr., N. A. Soudzilovskaia, A. F. Souza,  
853 M. Spasojevic, M. G. Sperandii, A. B. Stan, J. Stegen, K. Steinbauer, J. G. Stephan, F. Sterck,  
854 D. B. Stojanovic, T. Strydom, M. Laura Suarez, J.-C. Svenning, I. Svitkova, M. Svitok, M. Svoboda,  
855 E. Swaine, N. Swenson, M. Tabarelli, K. Takagi, U. Tappeiner, R. Tarifa, S. Tauougourdeau,  
856 C. Tavsanoğlu, M. te Beest, L. Tedersoo, N. Thiffault, D. Thom, E. Thomas, K. Thompson, P. E.  
857 Thornton, W. Thuiller, L. Tichy, D. Tissue, M. G. Tjoelker, D. Y. P. Tng, J. Tobias, P. Torok,  
858 T. Tarin, J. M. Torres-Ruiz, B. Tothmeresz, M. Treurnicht, V. Trivellone, F. Trolliet, V. Trotsiuk,  
859 J. L. Tsakalos, I. Tsiripidis, N. Tyskland, T. Umehara, V. Usoltsev, M. Vadeboncoeur, J. Vaezi,

860 F. Valladares, J. Vamosi, P. M. van Bodegom, M. van Breugel, E. Van Cleemput, M. van de Weg,  
861 S. van der Merwe, F. van der Plas, M. T. van der Sande, M. van Kleunen, K. Van Meerbeek,  
862 M. Vanderwel, K. A. Vanselow, A. Varhammar, L. Varone, M. Y. Vasquez Valderrama, K. Vassilev,  
863 M. Vellend, E. J. Veneklaas, H. Verbeeck, K. Verheyen, A. Vibrans, I. Vieira, J. Villacis, C. Violle,  
864 P. Vivek, K. Wagner, M. Waldram, A. Waldron, A. P. Walker, M. Waller, G. Walther, H. Wang,  
865 F. Wang, W. Wang, H. Watkins, J. Watkins, U. Weber, J. T. Weedon, L. Wei, P. Weigelt, E. Wei-  
866 her, A. W. Wells, C. Wellstein, E. Wenk, M. Westoby, A. Westwood, P. J. White, M. Whitten,  
867 M. Williams, D. E. Winkler, K. Winter, C. Womack, I. J. Wright, S. J. Wright, J. Wright, B. X.  
868 Pinho, F. Ximenes, T. Yamada, K. Yamaji, R. Yanai, N. Yankov, B. Yguel, K. J. Zanini, A. E.  
869 Zanne, D. Zeleny, Y.-P. Zhao, J. Zheng, J. Zheng, K. Zieminska, C. R. Zirbel, G. Zizka, I. C. Zo-  
870 Bi, G. Zotz, C. Wirth, and N. Network, “Try plant trait database – enhanced coverage and open  
871 access,” *Global Change Biology*, vol. 26, no. 1, pp. 119–188, 2020.

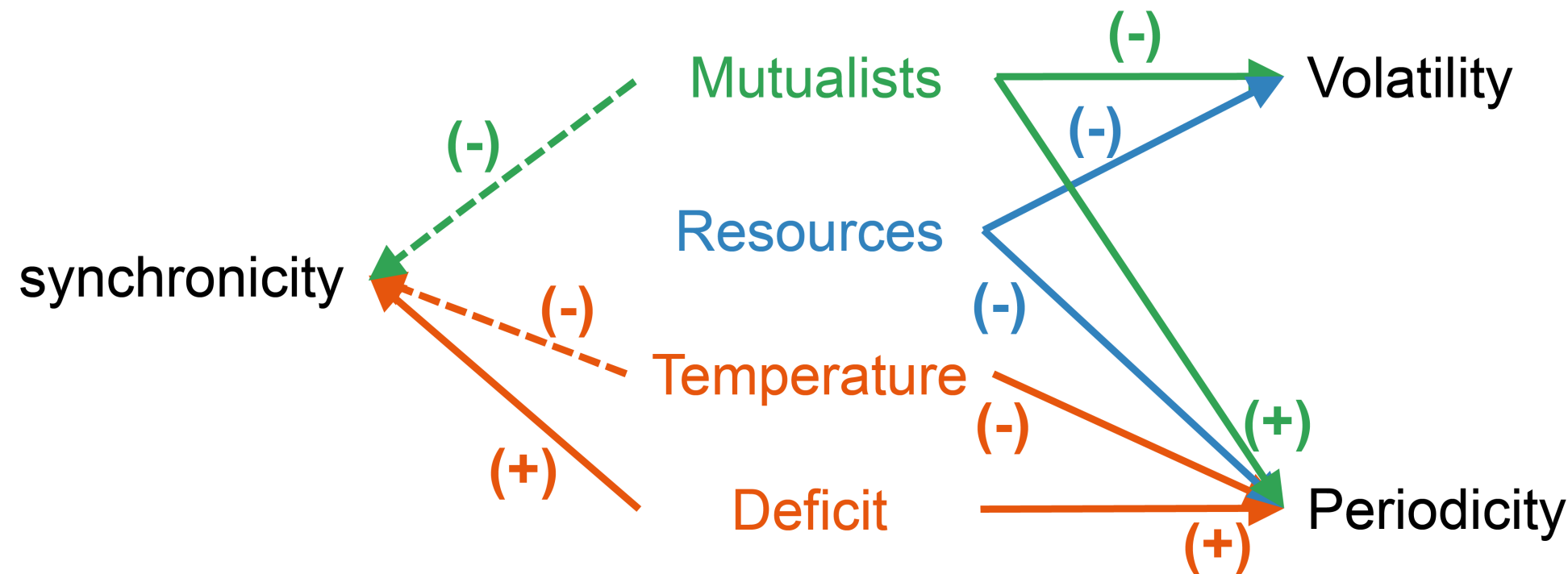




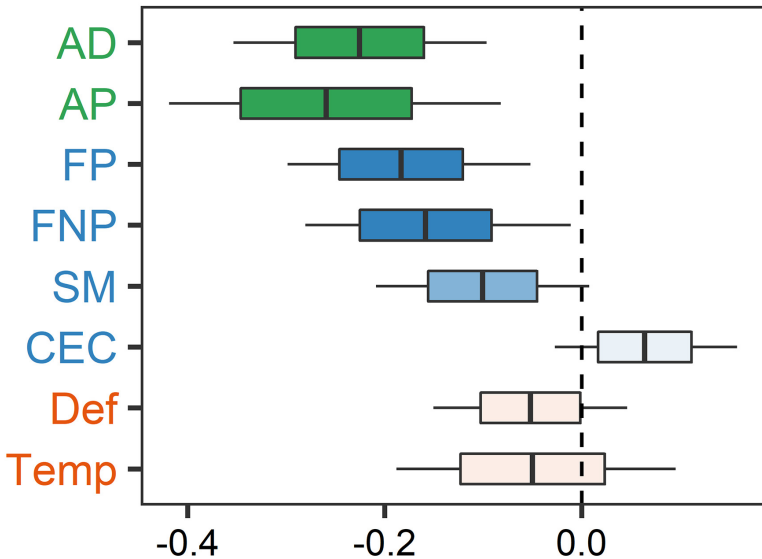
## a) Hypotheses



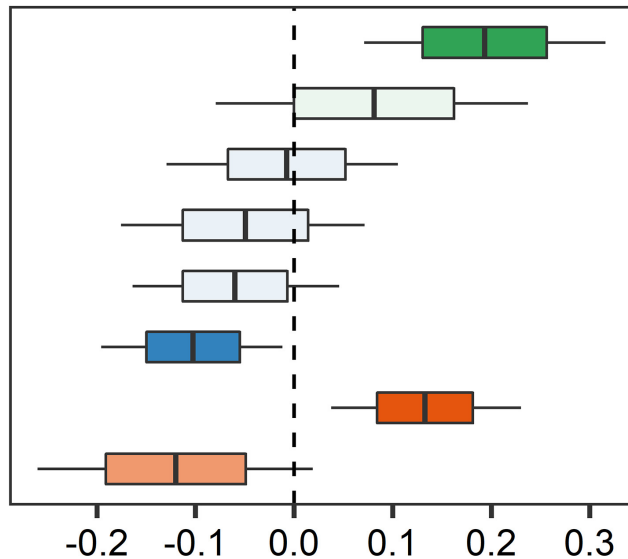
## b) Results



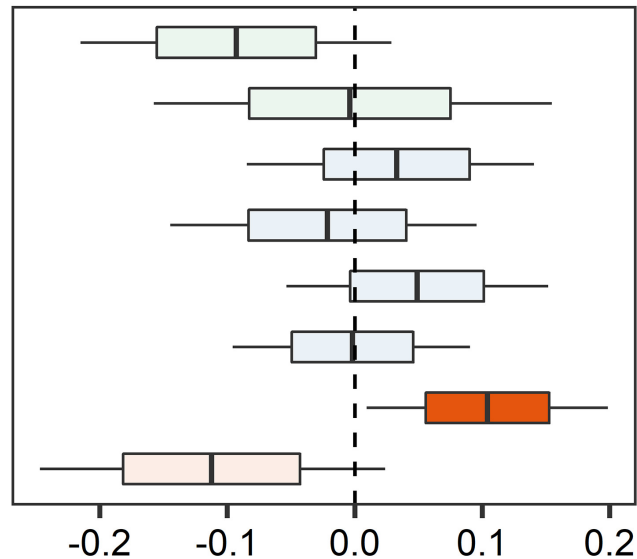
a) Volatility (log variance)



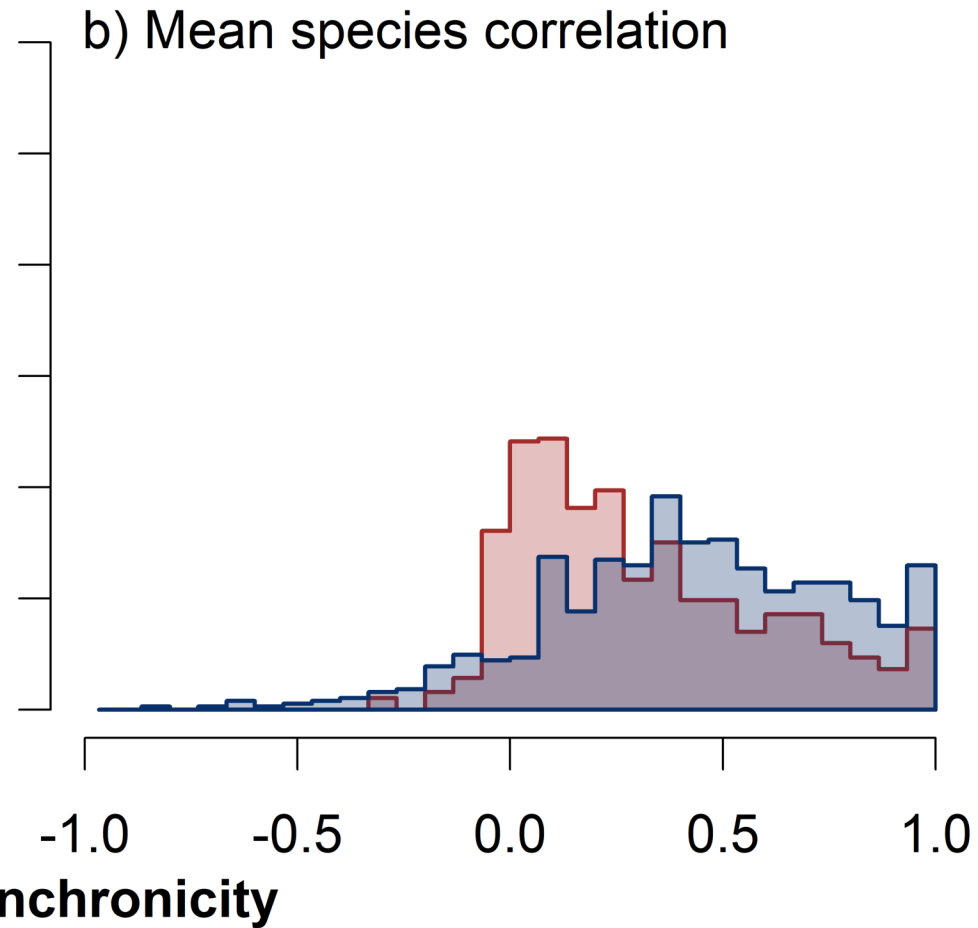
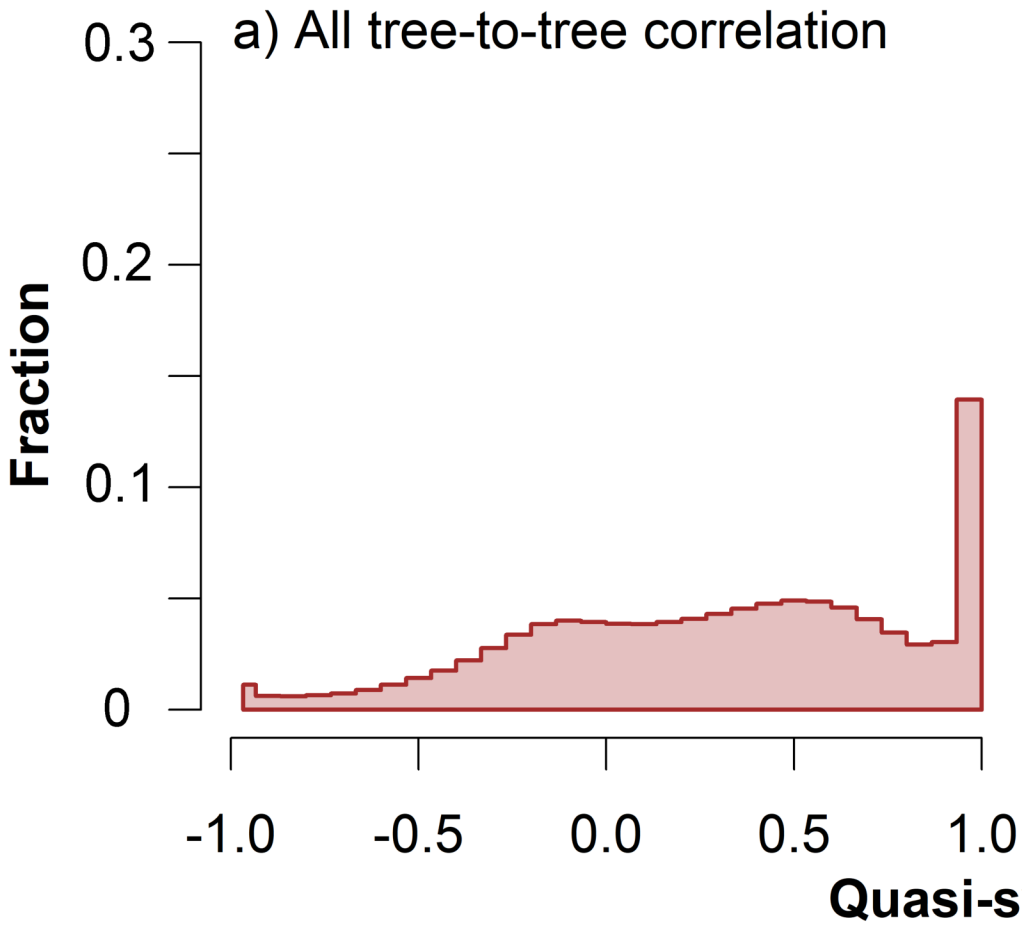
b) Periodicity (years)

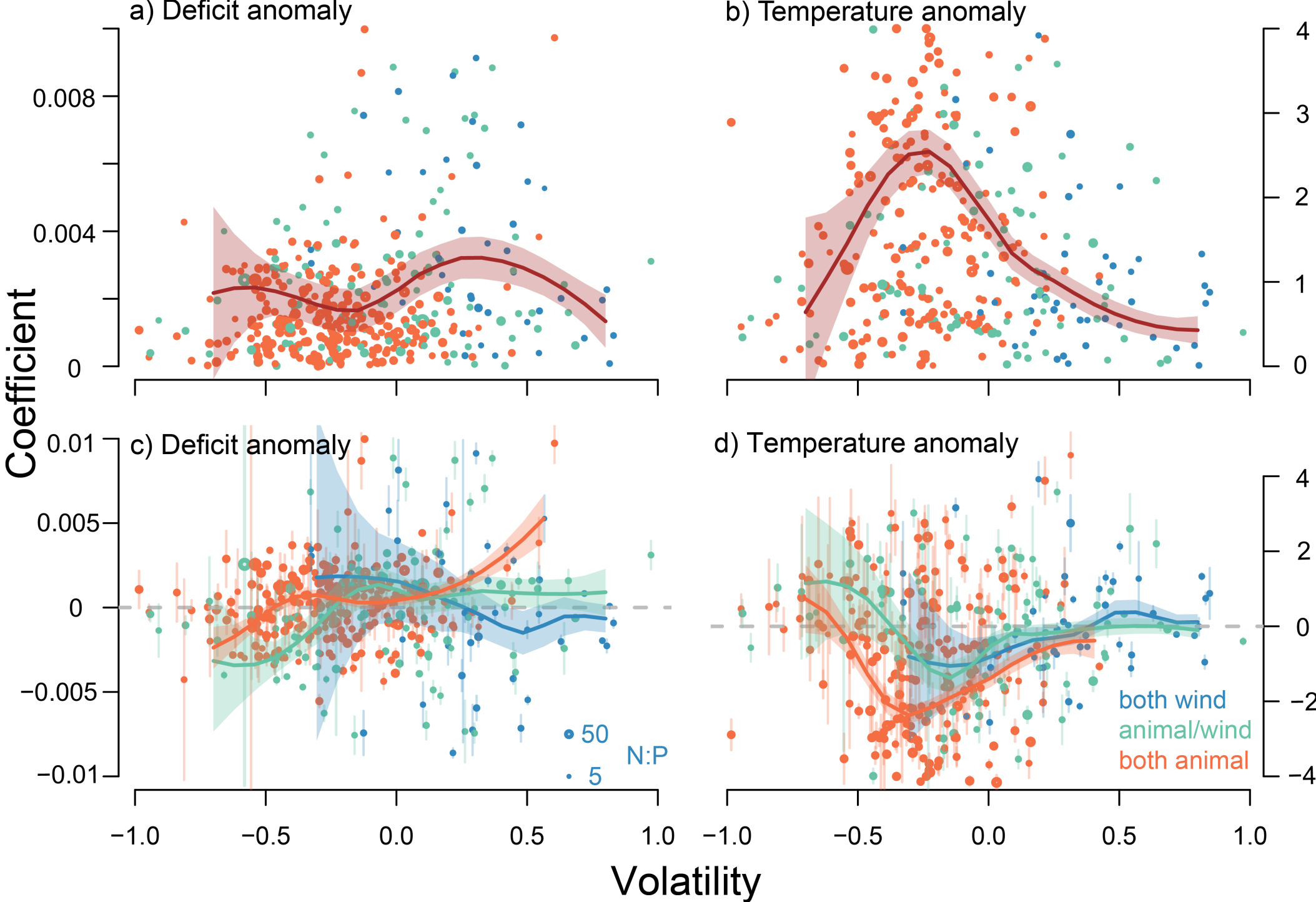


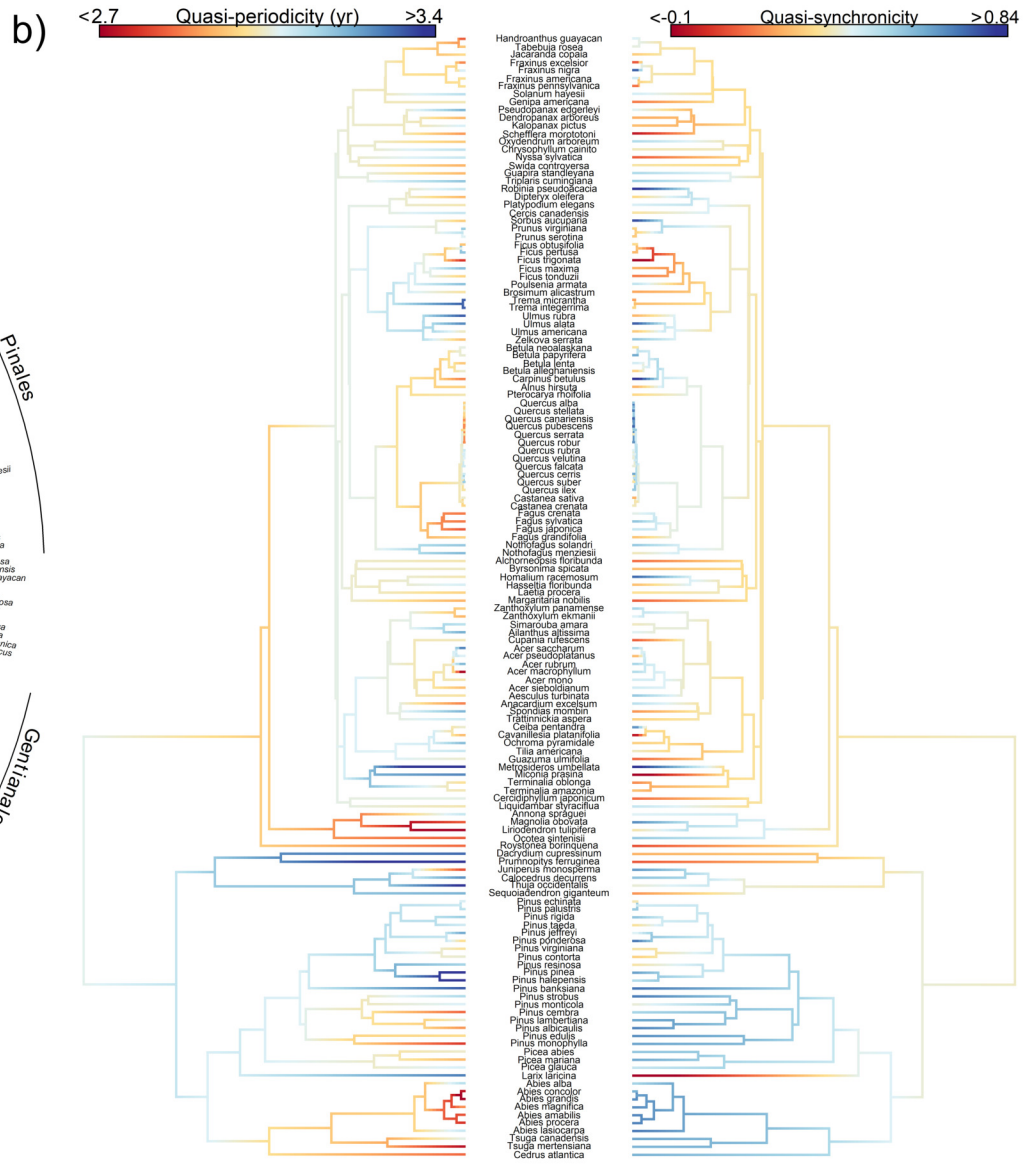
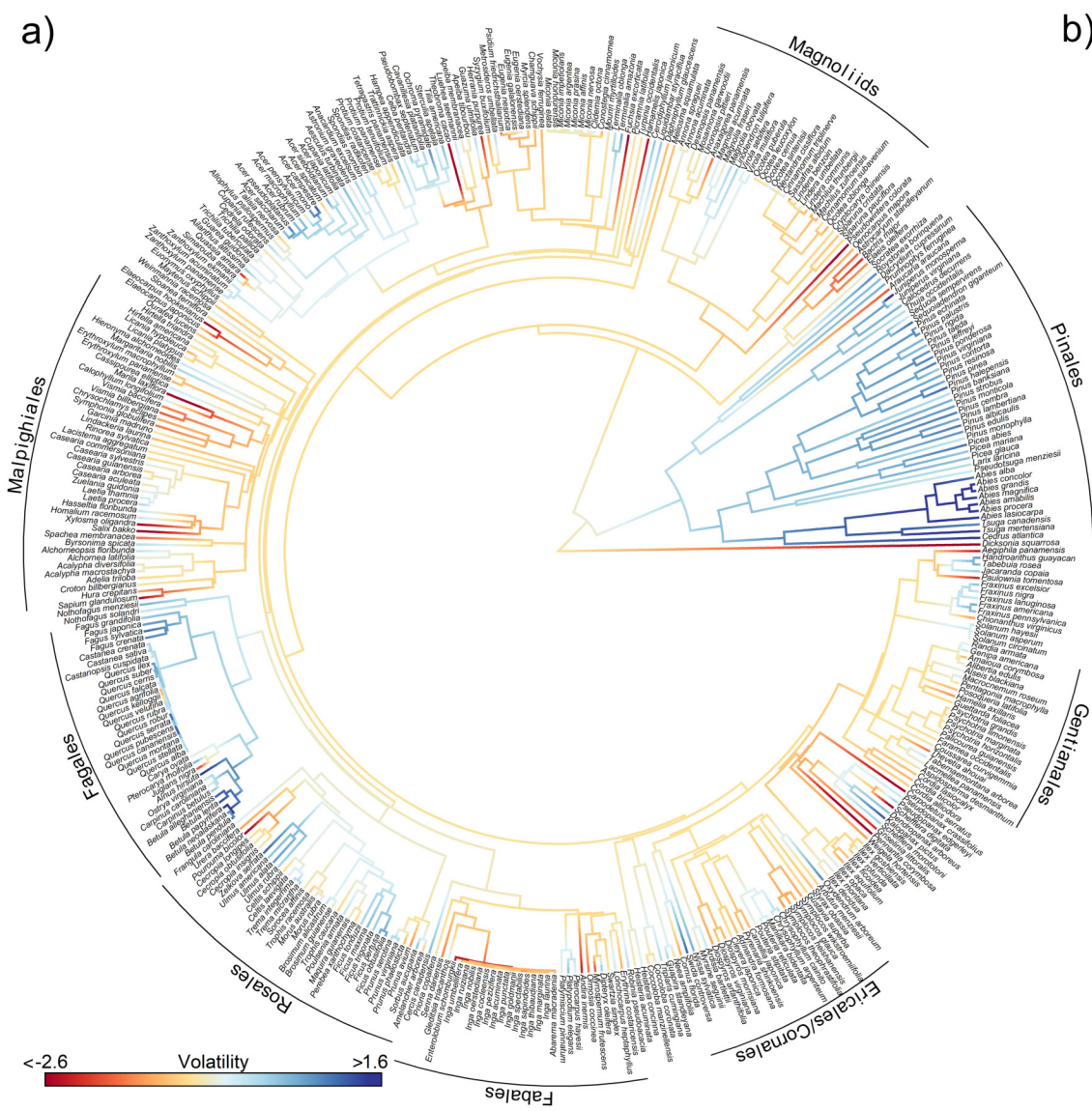
c) Synchronicity (correlation)

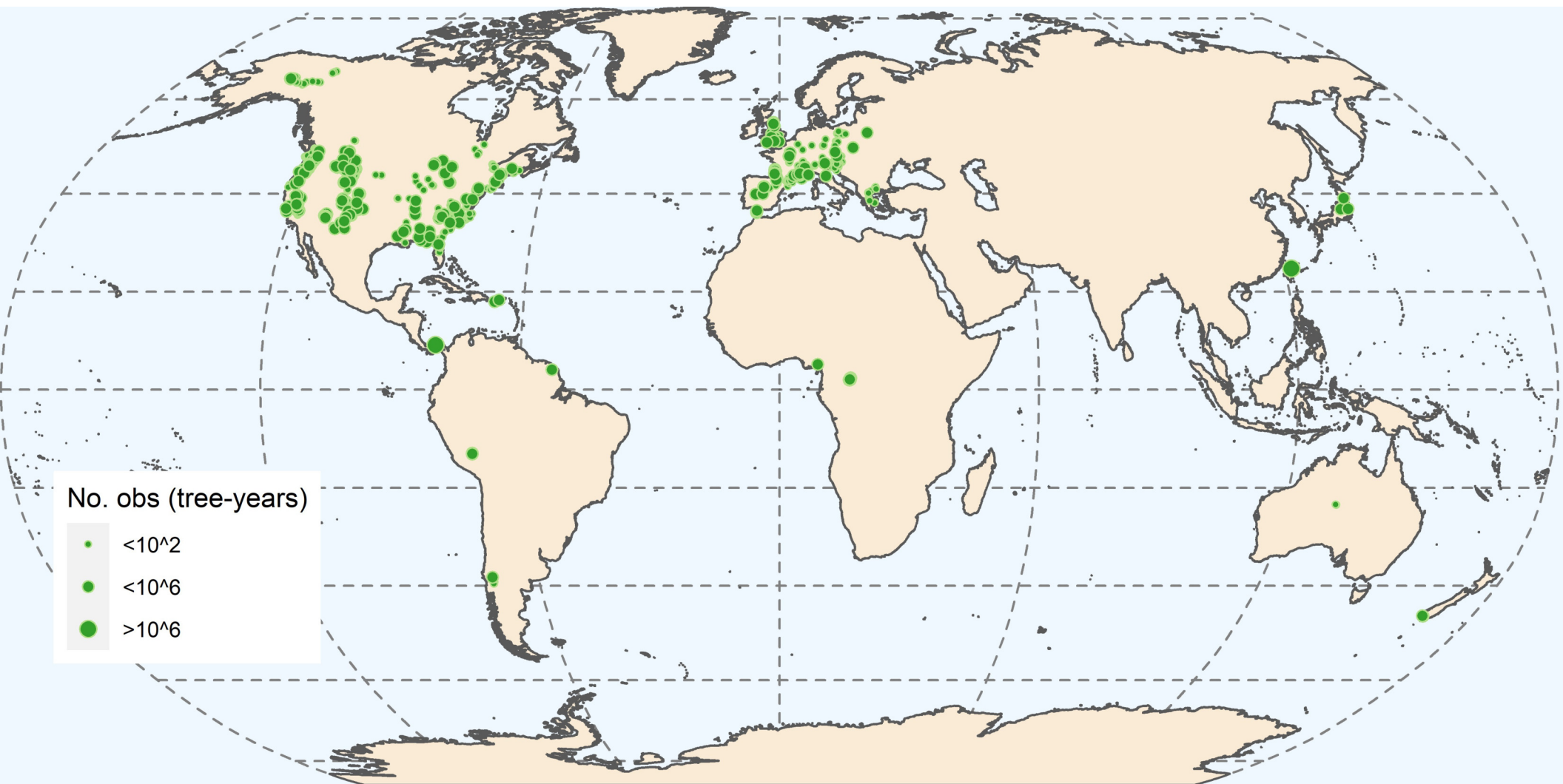


**Standardized coefficients**



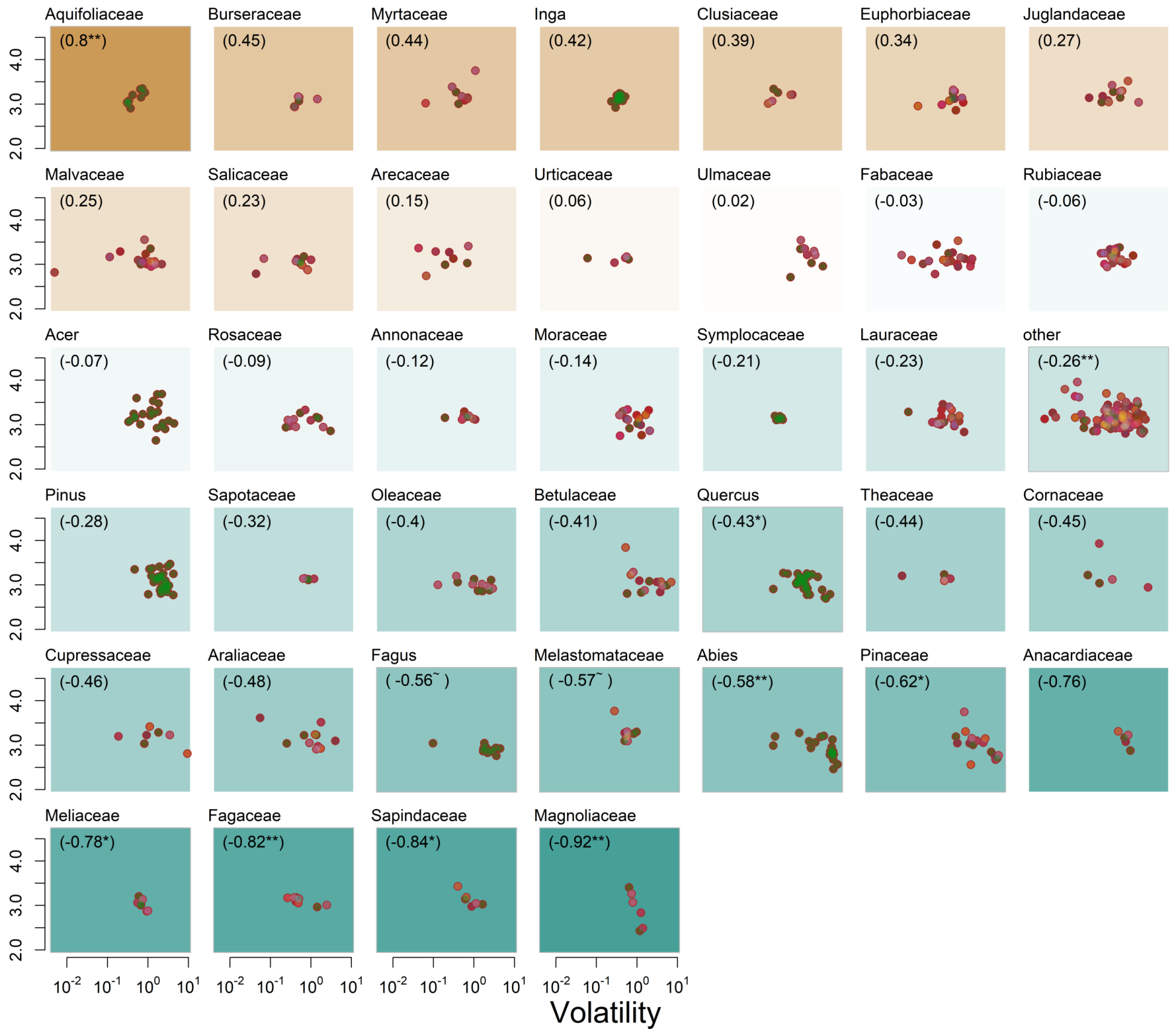








Quasi-periodicity



Quasi-synchronicity

