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Temporal population variability in local forest communities has mixed effects on tree species richness across a latitudinal gradient

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54 72 **Statement of authorship:** T.F. and R.A.C. designed the study and performed statistical
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56 73 analyses. T.F. wrote the first draft of the paper and R.A.C. revised the paper. All other
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58 74 authors provided data and contributed to the development of the paper.
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3 75 **Data accessibility statement:** Tree census data used in this study can be requested using the
4
5 76 CTFS–ForestGEO data portal at <http://ctfs.si.edu/datarequest/>. Sources for the climate data
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8 77 are detailed in the Supporting Information.

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3 **100 Abstract**
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8 102 Among the local processes that determine species diversity in ecological communities,
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10 103 fluctuation-dependent mechanisms that are mediated by temporal variability in the
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12 104 abundances of species populations have received significant attention. Higher temporal
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14 105 variability in the abundances of species populations can increase the strength of temporal
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16 106 niche partitioning but can also increase the risk of species extinctions, such that the net effect
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18 107 on species coexistence is not clear. We quantified this temporal population variability for tree
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20 108 species in 21 large forest plots and found much greater variability for higher latitude plots
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22 109 with fewer tree species. A fitted mechanistic model showed that among the forest plots, the
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24 110 net effect of temporal population variability on tree species coexistence was usually negative,
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26 111 but sometimes positive or negligible. Therefore, our results suggest that temporal variability
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28 112 in the abundances of species populations has no clear negative or positive contribution to the
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30 113 latitudinal gradient in tree species richness.
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40 **116 Introduction**
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45 118 Variation in species diversity across the biosphere has fascinated ecologists for decades
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47 119 (Wallace 1878; Fischer 1960; Hutchinson 1961; Pianka 1966; Connell 1978; Palmer 1994;
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49 120 Chesson 2000; Hubbell 2001; Mittelbach *et al.* 2007; Levine & HilleRisLambers 2009;
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51 121 Ricklefs & He 2016). At the regional scale, community diversity is moderated by processes
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53 122 that act on large spatiotemporal scales, such as biogeographic and evolutionary processes
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55 123 (Ricklefs 1987, 2004). A proportion of species in the regional community can disperse to a
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57 124 particular location, where they are subjected to a variety of localized abiotic and biotic
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3 125 processes (Fig. 1; HilleRisLambers *et al.* 2012). These local processes filter the dispersing
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5 126 species, resulting in a locally coexisting subset of species. Laboratory experiments and
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8 127 ecological theory suggest that under the most basic conditions of a constant environment, few
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10 128 limiting resources and a lack of dispersal from a regional community, only a few species will
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12 129 coexist in a local community (Gause 1934). This observation has motivated research into
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14 130 processes that permit the coexistence of tens to hundreds of species in natural local
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17 131 communities, including lake plankton (Smith *et al.* 2005), reef corals (Roberts *et al.* 2002)
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19 132 and rainforest trees (Anderson-Teixeira *et al.* 2015).

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23 134 At a local scale, species coexistence can be facilitated by “fluctuation-dependent
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25 135 mechanisms” (Chesson 1994, 2000, 2018), which are a class of stabilizing mechanisms.
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27 136 Stabilizing mechanisms in general attenuate differences in the fitness of species in a local
28
29 137 community, thereby helping to maintain local species richness (Chesson 2000, 2018; Levine
30
31 138 *et al.* 2017; Barabás *et al.* 2018). Temporal fluctuation-dependent mechanisms in particular
32
33 139 arise when a temporally changing environment causes changes in resource use among species
34
35 140 in a local community over time, and hence variation in the abundances of the species
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38 141 populations over time. This results in “temporal niches” that may allow rare species in a local
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40 142 community to persist (Hutchinson 1961; Grubb 1977; Chesson 1994, 2000; Adler & Drake
41
42 143 2008). While the ecological theory of temporal niches suggest a positive effect of
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44 144 environmental fluctuations on species richness (Hutchinson 1961; Grubb 1977; Chesson
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46 145 1994, 2000; Adler & Drake 2008), another ecological theory suggests just the opposite – that
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48 146 greater fluctuations in local environmental conditions can erode species richness, by
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51 147 periodically reducing species population abundances and thus increasing the risk of stochastic
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54 148 extinctions (Leigh 1981; Lande 1993; Adler & Drake 2008; Danino *et al.* 2016). The net
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3 149 effect of these two opposing factors will determine how environmentally-induced temporal
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5 150 changes in species abundances contribute to local species richness.
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10 152 Recent theoretical studies (Adler & Drake 2008; Danino *et al.* 2016) suggest that temporal
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12 153 niche effects generally dominate stochastic extinction effects when temporal environmental
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14 154 variance is low, with the opposite occurring when temporal environmental variance is
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16 155 sufficiently high. To the extent that greater temporal environmental variance increases the
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18 156 average amount by which the abundance of a species population changes over time, i.e. what
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20 157 we call “temporal population variability”, the theoretical studies (Adler & Drake 2008;
21
22 158 Danino *et al.* 2016) have suggested that a small amount of temporal population variability
23
24 159 generally has a net positive effect on species coexistence and hence species richness in local
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26 160 communities, but that a large amount of temporal population variability generally has a net
27
28 161 negative effect. An unresolved question is whether this net effect tends to be positive or
29
30 162 negative in natural populations. Several studies have used empirical data to quantify the
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32 163 stabilizing strength of temporal fluctuation-dependent mechanisms in a single community
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34 164 (Cáceres 1997; Adler *et al.* 2006; Angert *et al.* 2009; Usinowicz *et al.* 2012). Although these
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36 165 studies shed light on how important these mechanisms are for coexistence of species within a
37
38 166 single community, they do not show how important they are in maintaining patterns of
39
40 167 species richness across communities. A recent empirical study (Vásquez *et al.* 2004) did
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42 168 measure temporal population variability in multiple communities, but did not relate this to
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44 169 mechanisms that help to maintain species richness.
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53 171 Here, we investigated the effect of temporal population variability on species richness in 21
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55 172 forest tree communities, using a global dataset with repeated tree censuses (Anderson-
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57 173 Teixeira *et al.* 2015). The tree communities span a large latitudinal range of 0.7°S to 45.6°N,
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3 174 with tree species richness showing a declining trend away from the tropics (Appendix S1 in
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5 175 Supporting Information). We first performed regression analyses to investigate whether there
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8 176 was a corresponding latitudinal gradient in temporal population variability of tree species in
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10 177 the forest communities. We then quantified the net effect of this variability on tree species
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12 178 coexistence in the communities by fitting a mechanistic community model (Danino *et al.*
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14 179 2016) to the observed temporal abundance dynamics of tree species populations at each plot,
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16
17 180 and used the fitted model to predict the effects of temporal population variability on
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19 181 extinction rates of tree species in the communities. The results from all these analyses
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21 182 allowed us to assess whether temporal population variability makes a clear negative or
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24 183 positive contribution to the latitudinal gradient in tree species richness.
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31 186 **Materials and methods**

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36 188 **Tree census data**

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40 190 We used data from 21 of the 67 long-term forest plots from the Center for Tropical Forest
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42 191 Science–Forest Global Earth Observatory (CTFS–ForestGEO) network (Fig. 2). We selected
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45 192 these 21 forest plots because they had at least two tree censuses and a minimum area of 16
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47 193 ha. Data from multiple censuses allowed calculations of temporal population variability.
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49 194 Using the lower limit of 16 ha on plot area helped to reduce the number of small populations
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51
52 195 and hence the effects of demographic variance (Hubbell 2001), which could complicate
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54 196 interpretation of drivers of the observed temporal population variability. Here, demographic
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56 197 variance refers to variation in the realized demographic rates of species populations due to
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58 198 the random sampling of demographic events for discrete individuals, in contrast to temporal
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3 199 environmental variance that refers to variation in the intrinsic demographic rates of species
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5 200 populations over time (Chisholm *et al.* 2014). The 21 plots covered a total of 650 ha in four
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7 201 continents and spanned a wide range of climatic and edaphic conditions (Anderson-Teixeira
8
9 202 *et al.* 2015). Approximately 3 million trees were censused in the 21 forest plots, with
10
11 203 repeated censuses over periods of 6–31 yr. Each plot was censused according to a standard
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13 204 protocol, whereby all freestanding woody plants with diameter-at-breast-height (DBH; 1.3 m
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15 205 from the ground) ≥ 1 cm were identified to the lowest taxonomic level possible, mapped and
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17 206 recorded (Condit 1998).
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24 208 Summary information for the 21 plots is provided in Appendix S1, together with further
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26 209 details on how the tree census data were processed.
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211 **Investigating latitudinal trends in temporal population variability**

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213 We performed regression analyses to quantify how temporal population variability of tree
214 species in the 21 forest plots varied with latitude, considering trees with DBH ≥ 1 cm.

215 Metrics of temporal population variability could potentially be biased by the total tree

216 abundance varying substantially across plots and, to a lesser extent, censuses, because

217 changes in total tree abundance alter the strength of density-dependent effects across plots

218 (Appendix S2). Thus, we rarefied (sampled without replacement) the data for each census in

219 each plot to a sample size of $N_{\min} = 15,299$, which was the minimum observed total tree

220 abundance at any plot in any census (this minimum abundance occurred in the third census at

221 Mudumalai plot). Although $N_{\min} = 15,299$ was usually much smaller than the number of

222 trees in a census (by a factor of around nine on average), at each plot a sample of 15,299

223 trees was large enough to give species population sizes up to hundreds or thousands of

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3 224 individuals, with dynamics that were not dominated by demographic variance (Chisholm *et*
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5 225 *al.* 2014).
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10 227 After rarefaction to the same number of individuals in each census ($N_{\min} = 15,299$), there
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12 228 remained another potential source of bias that must be accounted for: given a fixed total tree
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14 229 abundance, abundant species were over-represented in species-poor plots, while rare species
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16 230 were over-represented in species-rich plots. The resulting bias was problematic because a
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18 231 greater value of a temporal population variability metric at a plot could simply reflect species
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20 232 that were generally more abundant (abundant species tend to fluctuate more in absolute
21
22 233 abundance; Lande 2003; Chisholm *et al.* 2014) rather than greater intrinsic temporal
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24 234 variability of the community (Appendix S2), which is what we were interested in. To remove
25
26 235 this confounding factor, we corrected the rarefied changes in species abundances to account
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28 236 for the different sets of initial specie abundances in each pair of consecutive censuses, by
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30 237 only including changes in species abundances for which the corresponding initial species
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32 238 abundances are common to all plots (Appendices S2 and S3).
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40 240 To further test the robustness of our analyses to other possible sources of bias, we used
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42 241 another rarefaction procedure that standardized the sample area as well as the number of
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44 242 individuals, and that also standardized the number of individuals in a way that conserved the
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46 243 pairwise temporal correlations of species abundances in the dataset for a plot (Appendix S3).
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48 244 Standardizing the sample area removed bias due to the strength of ecological processes
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50 245 changing at different spatial scales (Levin 1992), whereas the conservation of temporal
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52 246 correlations was potentially important because these correlations are associated with the
53
54 247 strength of temporal fluctuation-dependent mechanisms (Chesson 2000, 2018; Barabás *et al.*
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56 248 2018). Standardization of the sample area resulted in fewer trees in the rarefied dataset for
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249 each plot: an average of 4,713 individuals across censuses (Appendix S3). In turn, this
 250 resulted in fewer (initial) species abundances common to all plots compared with the
 251 previous method of rarefaction – 16 compared with 222. Excluding the Mudumalai plot
 252 increased the number of species abundances common to all remaining plots from 16 to 20;
 253 excluding the Luquillo, Palanan and SERC plots as well further increased the number to 194
 254 (Appendix S3). Thus, to test robustness to the number of species abundances common to all
 255 plots, we performed three regressions using data rarefied in this way: one using data from all
 256 21 plots, one using data from the 20 plots that excluded Mudumalai, and one using data from
 257 the 17 plots that excluded Mudumalai, Luquillo, Palanan and SERC.

258

259 As our indicator of temporal population variability of tree species in each plot i , we used the
 260 mean absolute change in species abundance in a year, $\overline{\Delta N}_i$. For a dataset from plot i , we
 261 calculated this indicator by first computing the absolute change in abundance of each tree
 262 species for each pair of consecutive censuses. We then divided each absolute change by the
 263 corresponding inter-census interval length in years and calculated the mean:

264

$$265 \quad \overline{\Delta N}_i = \frac{1}{C_i - 1} \sum_{j=1}^{C_i-1} \frac{1}{S_{i,j}} \sum_{k=1}^{S_{i,j}} \frac{|N_{i,j+1,k} - N_{i,j,k}|}{T_{i,j+1,k} - T_{i,j,k}}, \quad (1)$$

266

267 where C_i is the number of censuses of plot i , $S_{i,j}$ is the total number of species in census j at
 268 plot i for the dataset, $N_{i,j,k}$ is the abundance of tree species k in census j at plot i for the
 269 dataset, and $T_{i,j,k}$ is the mean census date of individuals of species k in census j at plot i . If a
 270 species k was present in census j but absent in census $j + 1$ at plot i , then $T_{i,j+1,k}$ was set
 271 equal to the mean census date of individuals of all other species in census $j + 1$ at plot i . For
 272 each plot i , we calculated the average $\overline{\Delta N}_i$ over 1,000 rarefied datasets with a standardized

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3 273 number of individuals and correction for different sets of initial species abundances among
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5 274 plots, thus producing the metric $\overline{\Delta N_{r,c,i}}$. For each plot i , we repeated the calculation for
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8 275 rarefied datasets with a standardized area and number of individuals, conservation of the
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10 276 pairwise temporal correlations of species abundances, and correction for different sets of
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12 277 initial species abundances among plots. This produced the metric $\overline{\Delta N_{ra,c,i}}$ for plot i .
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17 279 To determine the latitudinal trend in temporal population variability for the 21 forest plots,
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19 280 we computed separate linear regressions of $\overline{\Delta N_{r,c}}$ and $\overline{\Delta N_{ra,c}}$ against absolute latitude. For
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21 281 each regression, a log-transformation was applied to both variables to reduce their skewness
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23 282 and help meet assumptions of normality and homoscedasticity (see Appendix S4 for details).
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27 284 **Relating temporal population variability to mechanisms maintaining species richness**

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33 286 For the forest plots, we related temporal population variability to mechanisms maintaining
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35 287 species richness, by fitting a dynamic, mechanistic community model to the observed values
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37 288 of temporal population variability and temporal correlations of species abundances in the
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39 289 rarefied data, and then using the fitted models to predict the rates of species extinction. Our
40
41 290 mechanistic model represented a local community of J individuals competing for resources
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43 291 under temporally changing environmental conditions. In a model community, each species
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45 292 had a fitness value that determined its recruitment rate in the prevailing environmental
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47 293 conditions. The fitness value of a species at the start of a simulation was drawn randomly
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49 294 from a lognormal distribution with mean 1 and variance A . At the beginning of each
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51 295 subsequent time-step in the simulation, the fitness values for all species were redrawn
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53 296 independently from the lognormal distribution with probability $1/\tau$, which indirectly
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55 297 represented changes in environmental conditions. Therefore, τ measured the temporal
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3 298 correlation in environmental conditions. The model we used captured the effects of
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5 299 deterministic selection (arising from fitness differences among species in a given
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7 300 environment; Vellend 2010), stochastic ecological drift (Hubbell 2001) and stochastic local-
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9 301 scale environmental fluctuations over time (Lande 2003; Chisholm *et al.* 2014; Kalyuzhny *et*
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11 302 *al.* 2014, 2015; Fung *et al.*, 2016). Fig. 3 provides a schematic diagram of the model.
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17 304 The model we used was the same as that of Danino *et al.* (2016) except that we allowed J to
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19 305 vary over time and did not allow the introduction of new species over time. Not allowing the
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21 306 introduction of new species into a model community meant that the community did not
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23 307 receive immigrants from an outside source. This was appropriate for our analysis, as we
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25 308 wanted to isolate the effects of local temporal population variability in tree species from
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27 309 regional effects introduced by immigration. For each plot, we fitted the model to the census
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29 310 data rarefied by area and the number of individuals, in a way that conserved the temporal
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31 311 correlations of species abundances within the plot. When fitting our model to the rarefied
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33 312 data, we assumed that the observed abundance fluctuations over the census periods
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35 313 approximated those that would be found in the absence of immigration. This assumption was
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37 314 justified when the number of individuals in the rarefied dataset was much larger than the
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39 315 square root of the number of individuals, because the number of immigrant propagules
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41 316 should scale roughly with the perimeter (i.e., the square root) of the area occupied by the
42
43 317 individuals whereas the number of non-immigrant propagules scales with the area. To ensure
44
45 318 that this assumption was valid, when fitting the model we excluded the Mudumalai plot,
46
47 319 which had the fewest censused individuals. This increased the mean sample size after
48
49 320 rarefaction from 4,713 to 13,000, such that the number of individuals at each plot was two
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51 321 orders of magnitude greater than the square root of the number of individuals.
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3 323 To fit the model to data from a plot, we simulated the model for different combinations of A
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5 324 and τ , representing different environmental regimes. Specifically, for each plot, we
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8 325 performed simulations for all combinations of 32 values of A in the range $[0, 10^3]$ and 14
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10 326 values of τ in the range $[1, 10^4]$, representing a large parameter space spanning several orders
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12 327 of magnitude in A and τ . During each simulation for a plot, the initial species composition
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15 328 was set equal to the species composition in the first census of a rarefied dataset. We then
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17 329 simulated model dynamics for a length of time equal to the entire census period for the plot,
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19 330 with J for the model community changing linearly in between censuses to match the number
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21 331 of individuals in the rarefied dataset at each census. At the end of each simulation, we
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23 332 calculated temporal population variability from the simulated data using eq. (1), as well as
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25 333 the mean cumulative distribution function (cdf) of pairwise temporal correlations of species
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27 334 abundances over a pair of consecutive censuses. For each plot, we performed 1,000
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29 335 simulations for each of the $32 \times 14 = 448$ combinations of A and τ , and determined the
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31 336 combination that gave the lowest typical error, where the error is defined as the average of (i)
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33 337 the percentage absolute difference between the model and observed temporal population
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35 338 variability and (ii) the percentage absolute difference between the model and observed cdf of
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37 339 temporal correlations. In addition, we determined the combinations of A and τ that produced
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39 340 similar errors to the combination giving the lowest typical error – we refer to all these as the
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41 341 “best-fit combinations” (see Appendix S5 for details, including a definition of “typical
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43 342 error”).
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52 344 For each plot and each combination of A and τ , we ran a further 100 simulations, each lasting
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54 345 the entire census period (as described in the previous paragraph) and a further 2×10^5 time-
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56 346 steps, which was sufficient time for up to tens to hundreds of species extinctions to occur. At
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58 347 the end of each simulation, we recorded the number of species that were extinct. During the
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3 348 last 2×10^5 time-steps, J was assumed to remain constant, such that it remained equal to the
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5 349 sample size in the last census. Different assumptions that involve varying J according to
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7 350 some pattern would likely have little effect on the relative number of species extinctions that
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9 351 occurred among different environmental regimes (combinations of A and τ) within a plot.
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11 352 However, because the sample size in the last census was different for each plot (only the
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13 353 mean sample size across censuses was approximately the same among plots; Appendix S3),
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15 354 simulations for different plots had different J in the last 2×10^5 time-steps (which represented
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17 355 0.655–1.31 generations). Because species extinction times change with J (e.g., Chisholm &
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19 356 O'Dwyer 2014; Danino *et al.* 2018), these simulations did not allow an unbiased comparison
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21 357 of species extinction risk across different plots. Furthermore, for different plots J might vary
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23 358 in different ways beyond the census periods. For these reasons, we restricted interpretation of
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25 359 our simulation results for a plot to patterns of species extinction risk within that plot.
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27 360 Appendix S5 provides further details of the dynamic model, how it was simulated, and how it
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29 361 was fitted to the data.
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40 363 We found that for 13 of the 20 plots, the best-fit models for the observed data gave low errors
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42 364 (see *Results*). For these 13 plots, we used our mechanistic model results to investigate
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44 365 whether greater temporal population variability was associated with a greater species
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46 366 extinction rate within each plot. To do this, we noted that temporal population variability
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48 367 almost always increased with A and τ in the model (Fig. S13 in Appendix S5), such that we
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50 368 can use these two parameters as drivers of temporal population variability. For each plot, we
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52 369 calculated the mean number of extinctions (across 100 simulations) for the different
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54 370 combinations of A and τ described above. Then, starting with the best-fit combinations of A
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56 371 and τ , we determined what the effect of further increases in either parameter – and hence in
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58 372 temporal population variability – would be on extinctions. For the model tree community
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3 373 corresponding to a particular forest plot, if increases in temporal population variability due to
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5 374 increases in a parameter led to more extinctions, then this suggested that the real tree
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8 375 community in the plot was in a regime where increases in temporal population variability due
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10 376 to that parameter have a net negative effect on species coexistence and richness. Conversely,
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12 377 if increases in temporal population variability due to increases in a parameter led to fewer
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14 378 extinctions in the model tree community, then this suggested that the real tree community
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17 379 was in a regime where increases in temporal population variability due to that parameter have
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19 380 a net positive effect on species coexistence and richness (i.e., temporal niche effects were
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21 381 strong).

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26 383 All simulations and statistical analyses described were performed using R v.3.3.3 (R
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28 384 Development Core Team 2013). As part of the Supporting Information, we have provided an
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30 385 R script with code corresponding to the dynamic model simulations used in our study
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33 386 (“R_code_for_dynamic_models.R”). The code provides two functions, one for producing
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35 387 model simulations used to assess bias in metrics of temporal population variability
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38 388 (represented schematically in Fig. S1 in Appendix S2) and the other for producing model
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40 389 simulations used to fit the dynamic model to the tree census data (represented schematically
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42 390 in Fig. 3).

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48 49 393 **Results**

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54 395 In our first regression analysis, we found that temporal population variability showed a
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56 396 substantial positive correlation with absolute latitude for the 21 forest plots examined, where
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59 397 the variability was calculated as the mean absolute change in tree species abundance per year,
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3 398 using the plot datasets rarefied by number of individuals ($\overline{\Delta N_{r,c}}$; linear regression on log-log
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5 399 axes: $R^2 = 0.350$, slope = 0.251, $P = 4.76 \times 10^{-3}$, $n = 21$; Fig. 4A; Appendix S4). In our second
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7 400 regression analysis, temporal population variability was calculated using the plot datasets
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9 401 rarefied by plot area and the number of individuals, in a way that conserved temporal
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11 402 correlations of species abundances ($\overline{\Delta N_{r,a,c}}$). In this analysis, we still found a substantial
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13 403 positive correlation of variability with absolute latitude, regardless of whether we used data
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15 404 from all 21 plots ($R^2 = 0.243$, slope = 0.326, $P = 0.0233$, $n = 21$; Fig. 4B; Appendix S4); the
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17 405 20 plots that excluded Mudumalai ($R^2 = 0.416$, slope = 0.354, $P = 2.13 \times 10^{-3}$, $n = 20$; Fig. 4C;
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19 406 Appendix S4); or the 17 plots that excluded Mudumalai, Luquillo, Palanan and SERC ($R^2 =$
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21 407 0.469, slope = 0.357, $P = 2.42 \times 10^{-3}$, $n = 17$; Fig. 4D; Appendix S4). For the first of these
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23 408 three regressions (using 21 plots), the Shapiro–Wilk test and quantile plot indicated non-
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25 409 normality (Fig. S12 in Appendix S4). Thus, we also performed a non-parametric regression,
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27 410 which again exhibited a substantial positive correlation (Spearman’s $\rho = 0.643$, $P = 2.13 \times 10^{-}$
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29 411 3 , $n = 21$).

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33 413 From the fits of our dynamic model to data from the forest plots, we found that for 11 of the
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35 414 20 plots considered (excluding Mudumalai, see *Materials and methods*), at least one
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37 415 combination of A and τ (the two parameters governing temporal population variability) gave
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39 416 values of the simulated temporal population variability and cdfs of temporal correlations of
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41 417 species abundances reasonably close to the observed data, with small typical errors of < 10%
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43 418 that we call “good model fits” (Figs. S14–S16 and Table S6 in Appendix S5). Two of the
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45 419 remaining nine plots (Lenda and Luquillo) had a combination of A and τ with a typical error
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47 420 of 10–10.5%, which we call “marginally good model fits” (Figs. S15 and S16, and Table S6).
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49 421 However, for the remaining seven plots (Gutianshan, Lambir, Pasoh, SERC, Sinharaja,
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3 422 Wabikon and Yasuni), the best-fit combination gave larger typical errors ($> 11.2\%$; Table
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5 423 S6).
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10 425 For 11 of the 13 plots with good or marginally good model fits, the best-fit models
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12 426 (corresponding to the best-fit combinations of A and τ) were within a parameter regime
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14 427 where A was sufficiently large that further increases in τ would likely increase the mean
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16 428 number of extinctions (Fig. 5 and Figs. S17 and S18 in Appendix S5). For the remaining two
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18 429 plots (Khao Chong and Lenda), the best-fit models were within a parameter regime where A
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20 430 was sufficiently small that further increases in τ would likely have negligible effect on the
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22 431 mean number of extinctions (Figs. S17 and S18). However, only six of the 13 plots (Khao
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24 432 Chong and Lenda were not among these six plots) had best-fit models that were within a
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26 433 parameter regime where τ was sufficiently large that further increases in A would likely
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28 434 increase the mean number of extinctions (Figs. 5, S17 and S18). The best-fit models for
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30 435 seven of the 13 plots were within a parameter regime where τ was sufficiently small that
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32 436 further increases in A would likely decrease (five plots) or have negligible effect (two plots)
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34 437 on the mean number of extinctions (Figs. 5, S17 and S18).
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445 **Discussion**

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450 442 For the tree communities in the 21 forest plots that we examined, we documented a strong
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452 443 trend of increasing temporal population variability of tree species with absolute latitude. The
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454 444 temporal population variability increased by three- to four-fold over 45 degrees of latitude,
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456 445 from tropical forests at the equator to temperate forests in the northern hemisphere. A
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458 446 previous study (Condit *et al.* 2006) of ten of the 21 forest plots that we used in this study
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3 447 identified a pattern of wider ranges of tree demographic rates in forests with fewer tree
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5 448 species, which is consistent with our finding of greater temporal population variability in the
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7 449 extratropical plots. However, the authors of that study (Condit *et al.* 2006) did not interpret
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9 450 their results in terms of whether greater temporal population variability increases the
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11 451 propensity for local extinctions of tree species.
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17 453 If temporal population variability increases the extinction risk of tree species in our forest
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19 454 plots, then the latitudinal increase in temporal population variability could indicate
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21 455 increasingly negative effects on tree species coexistence for higher latitude plots. This could
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23 456 partially explain the latitudinal decline in tree species richness at local scales (Ricklefs & He,
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25 457 2016; Appendix S4). In this regard, results using our mechanistic model showed that for five
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27 458 of the 13 plots with good or marginally good model fits, increases in temporal population
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29 459 variability would likely result in a greater rate of species loss. For the remaining eight plots,
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31 460 increases in temporal population variability would likely result in a greater rate of species
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33 461 loss or a rate of species loss that was lower or almost the same, depending on whether the
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35 462 increase in temporal population variability was caused by greater temporal correlation in
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37 463 environmental conditions or greater fitness variation among species. Thus, these results
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39 464 indicate that for the tree communities that we examined, greater temporal population
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41 465 variability has mixed net effects on tree species coexistence, such that extinction effects can
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43 466 outweigh temporal niche effects or vice versa. Therefore, temporal population variability
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45 467 makes no clear negative or positive contribution to the latitudinal gradient in local tree
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47 468 species richness. Our results provide a more nuanced perspective on the effects of temporal
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49 469 population variability on local tree species richness, which does not only focus on the
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51 470 positive temporal niche effects (Usinowicz *et al.* 2017).
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3 472 Overall, our results suggest that temporal population variability is one of the factors with a
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5 473 substantial impact on local tree species richness, but we emphasize that it is by no means the
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7 474 only factor. In communities such as the ones that we have examined, the effects of temporal
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9 475 population variability on species coexistence are moderated by other local processes such as
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11 476 Janzen-Connell effects (Janzen 1970; Connell 1971; Bever *et al.* 1997; Bever 2003; Mangan
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13 477 *et al.* 2010) and resource partitioning (Meinzer *et al.* 1999; Turner 2008), and regional
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15 478 processes such as dispersal from regional communities of varying composition and richness
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17 479 (Ricklefs 1987, 2004; Hubbell 2001) (Fig. 1). Therefore, an important next step is to quantify
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19 480 the relative contributions of different local and regional processes to the maintenance of local
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21 481 species richness. Most studies to date have focused on either local (e.g., temporal fluctuation-
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23 482 dependent mechanisms; Cáceres 1997; Adler *et al.* 2006; Angert *et al.* 2009; Usinowicz *et al.*
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25 483 2012, 2017; this study) or regional (e.g., dispersal; Hubbell 2001; Volkov *et al.* 2003, 2007)
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27 484 processes. A recent study (Ricklefs & He 2016) did partition variation in local tree species
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29 485 richness in 47 CTFS–ForestGEO forest plots according to local and regional processes, but
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31 486 used a statistical modeling approach that did not incorporate the actual mechanisms by which
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33 487 the processes affect richness. An alternative approach was used in other recent studies
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35 488 (Kalyuzhny *et al.* 2015; Fung *et al.* 2016), which fitted mechanistic models with dispersal,
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37 489 demographic stochasticity and local-scale temporal environmental fluctuations to the tree
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39 490 communities at the BCI and Pasoh CTFS–ForestGEO plots. However, these studies simply
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41 491 assumed that the regional community followed a log-series species abundance distribution. In
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43 492 contrast, other studies (Graham & Moritz 2006; Huntley *et al.* 2014) have considered the
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45 493 regional community more explicitly and emphasized the negative effects of temporal
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47 494 environmental fluctuations on richness at the long-term speciation–extinction balance.
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3 496 Our modeling analyses also help to shed light on the general question of how complex a
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5 497 dynamic, mechanistic model needs to be to accurately capture temporal population variability
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7 498 in an ecological community. Drift-only models with constant community sizes are inadequate
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9 499 in most cases (Chisholm & O'Dwyer 2014; Chisholm *et al.* 2014; Kalyuzhny *et al.* 2014;
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11 500 Fung *et al.* 2016). Our analyses suggest that adding temporal variation in recruitment rates
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13 501 (Chisholm *et al.* 2014; Kalyuzhny *et al.* 2015; Fung *et al.* 2016) and community sizes is
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15 502 generally sufficient to accurately capture temporal population variability. But in the six tree
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17 503 communities where our mechanistic model substantially under- or over-estimated observed
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19 504 temporal population variability, additional mechanisms are required to get a better
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21 505 approximation of the true temporal dynamics. These additional mechanisms include temporal
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23 506 variation in mortality rates of species (Chisholm *et al.* 2014) and resource partitioning
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25 507 (Meinzer *et al.* 1999; Turner 2008), which increase and decrease temporal population
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27 508 variability, respectively.
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35 510 A future research priority is to determine specific environmental variables that drive
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37 511 fluctuations of tree species abundances in specific forests. Over the time period studied, the
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39 512 forest plots we examined were buffeted by a range of environmental factors, such as drought
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41 513 (Condit *et al.* 1996), ground-fires (Baker *et al.* 2008), hurricanes/typhoons (Yap *et al.* 2016;
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43 514 Hogan *et al.* 2018) and insect herbivory (Gonzalez-Akre *et al.* 2016). Although many such
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45 515 factors can be identified, they are often idiosyncratic in nature and often act on population
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47 516 abundances via nonlinear causal pathways. Thus, the effects of different factors on temporal
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49 517 population variability are difficult to characterize in a simple way. For example, for the forest
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51 518 plots that we examined, a liner regression showed that temporal variability in mean monthly
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53 519 temperature and precipitation accounted for about a quarter to a third of the variation in the
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55 520 logarithm of temporal population variability (Appendix S4), leaving a substantial amount of
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3 521 variation unexplained. Our hope is that more analyses of long-term datasets of forest
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5 522 dynamics will permit better identification of key environmental drivers. This will ultimately
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7 523 facilitate the development of parsimonious predictive models specifying the future dynamics
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9 524 of forest tree communities.
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18
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22
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26
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50
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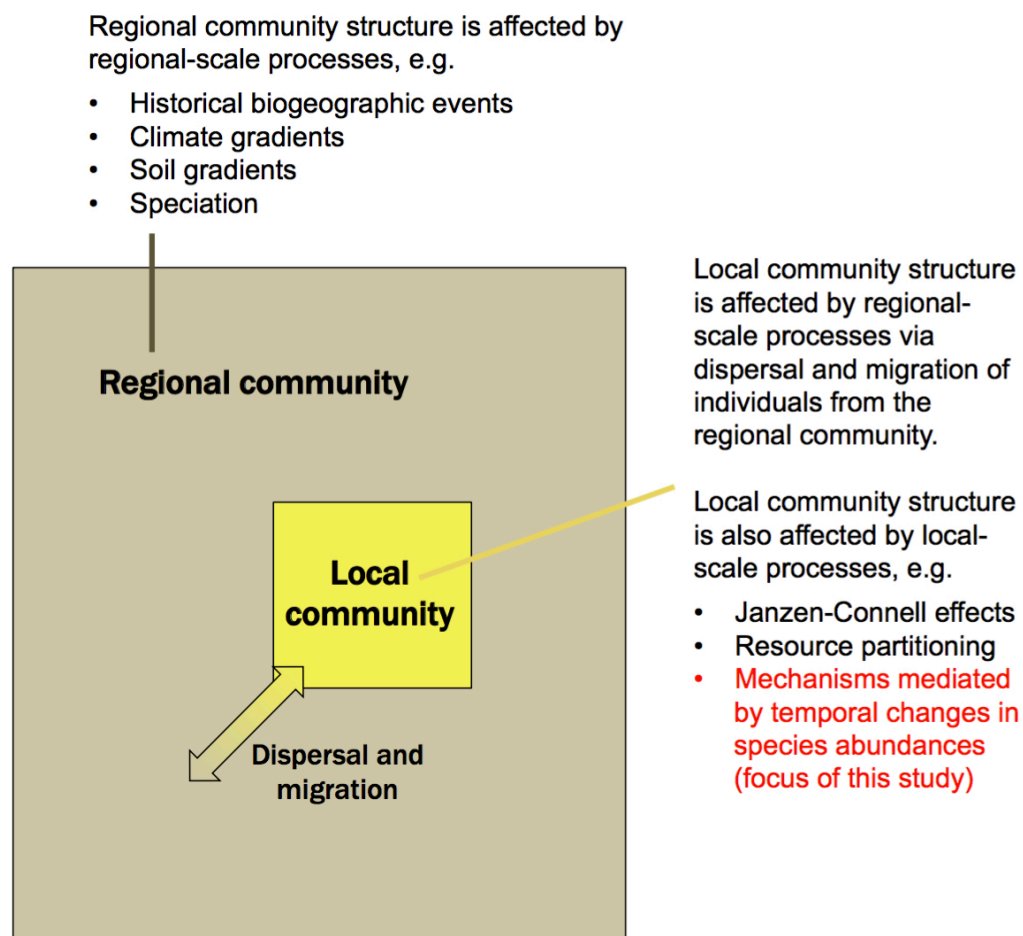
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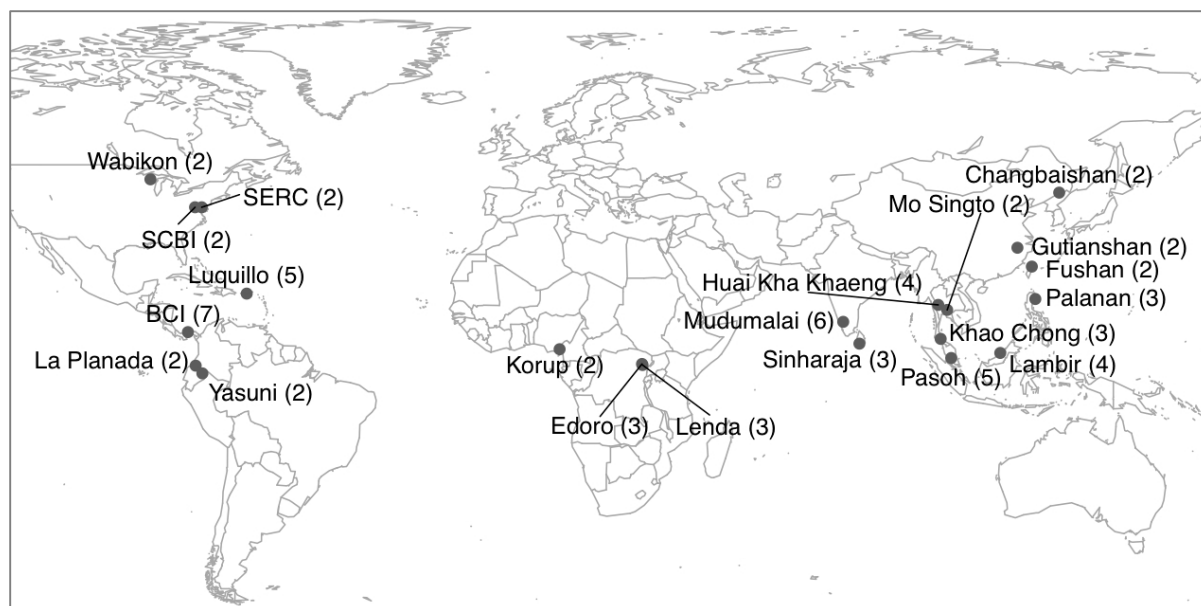
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745 **Figures**

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747 **Figure 1.** Schematic diagram showing the processes structuring a local community, including
 748 its species diversity. The local community is embedded within a regional community, which
 749 is governed primarily by regional-scale processes. Because the regional community is much
 750 larger than the local community, dispersal and migration of individuals from the local to the
 751 regional community has negligible effect on regional community structure, but dispersal and
 752 migration of individuals from the regional to the local community does have substantial
 753 effects on local community structure. Local community structure is also affected substantially
 754 by local-scale processes, including mechanisms mediated by temporal changes in abundances
 755 of species populations, which are the focus of our study.



756

757 **Figure 2.** Map of the 21 CTFS–ForestGEO forest plots considered in this study, with
 758 corresponding numbers of tree censuses in parentheses. BCI, SCBI and SERC stand for Barro
 759 Colorado Island, Smithsonian Conservation Biology Institute, and Smithsonian
 760 Environmental Research Center, respectively.

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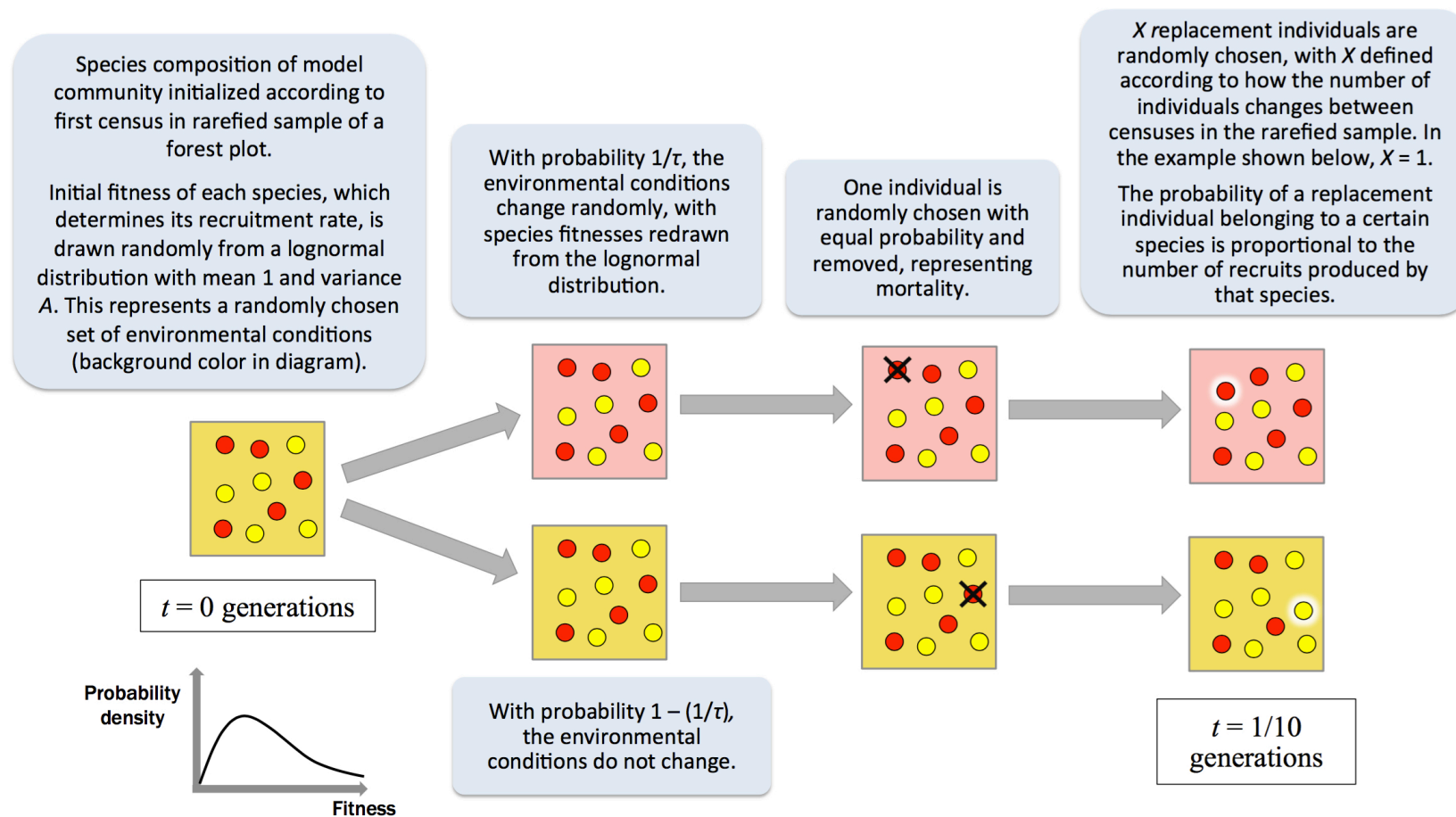
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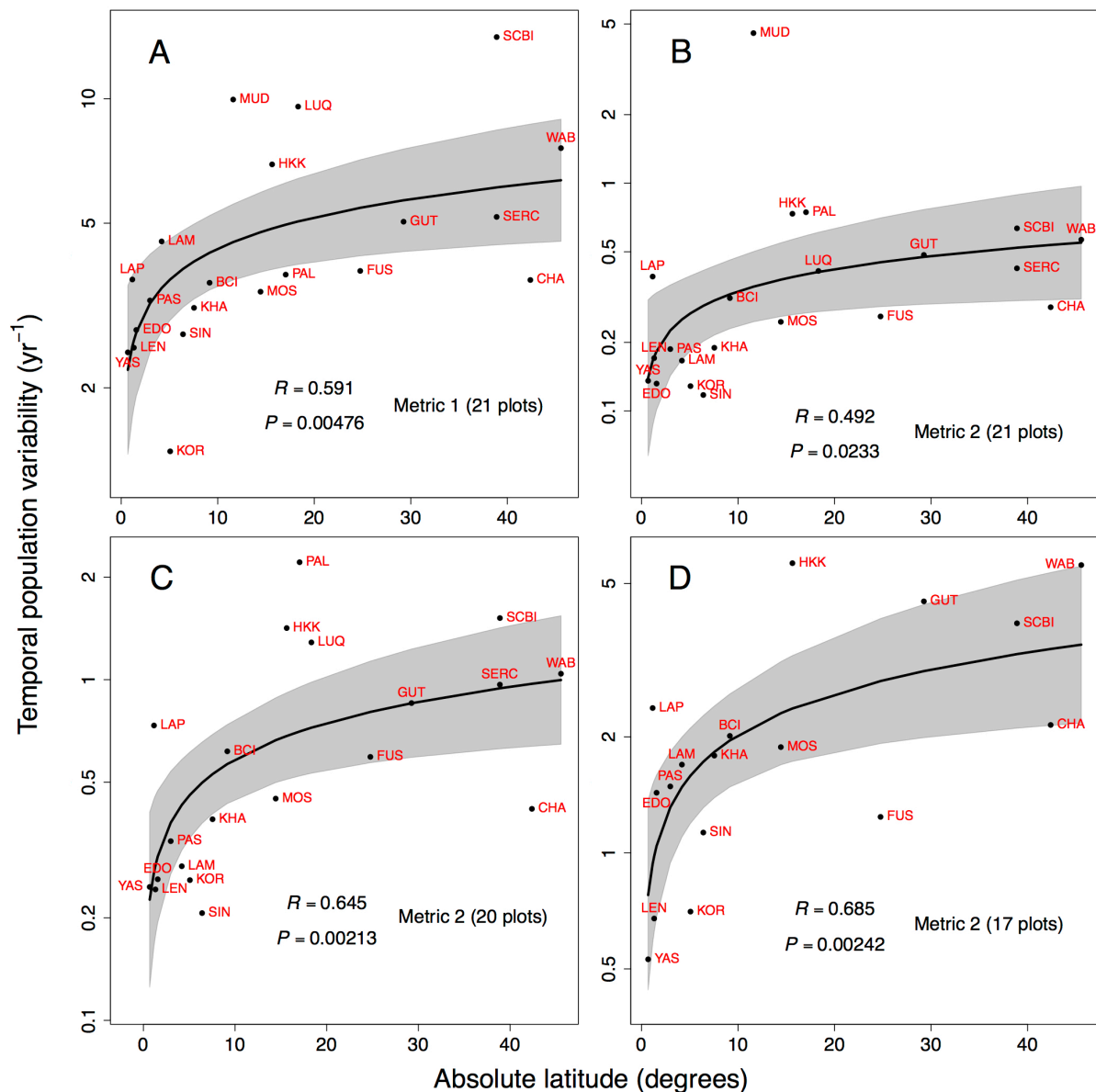
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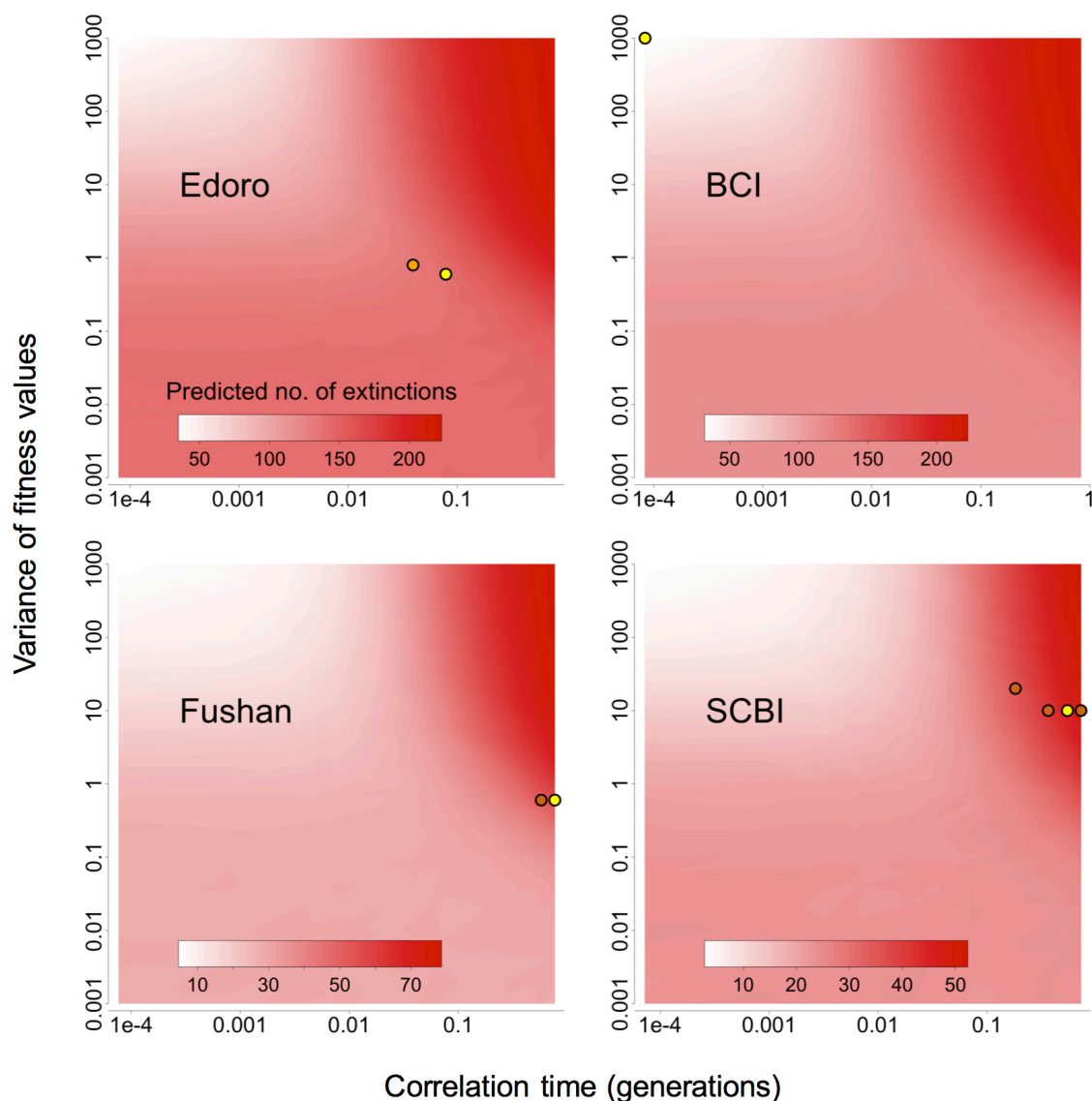
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768 **Figure 3.** Schematic diagram showing the processes operating in the dynamic, mechanistic model that we fitted to tree census data from each of
 769 20 forest plots. The diagram shows the processes operating over one model time-step. In the representations of the model communities, the
 770 yellow and red backgrounds refer to environmental conditions favoring the yellow and red species, respectively.



771
 772 **Figure 4.** (A) Relationship between temporal population variability and absolute latitude for
 773 the 21 CTFS–ForestGEO forest plots considered in this study. Temporal population
 774 variability was measured as the mean absolute change in tree species abundance per year,
 775 with rarefaction to standardize the number of individuals and correction to account for the
 776 different sets of initial species abundances in each pair of consecutive censuses (Metric 1;
 777 $\overline{\Delta N_{r,c}}$). The line represents a linear regression between the logarithms of the two variables,
 778 with the 95% confidence interval shown as the shaded region. (B) is the same as (A) except
 779 that temporal population variability was measured with rarefaction to standardize the plot
 780 area and number of individuals, in a way that conserved temporal correlations of species

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3 781 abundances (Metric 2; $\overline{\Delta N_{ra,c}}$). (C) is the same as (B) except that the plot at Mudumalai was
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5 782 excluded. (D) is the same as (B) except that the plots at Mudumalai, Luquillo, Palanan and
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7 783 SERC were excluded. Each empirical value (black dot) is labeled according to the plot it
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9 784 refers to: BCI (Barro Colorado Island), CHA (Changbaishan), EDO (Edoro), FUS (Fushan),
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11 785 GUT (Gutianshan), HKK (Huai Kha Khaeng), KHA (Khao Chong), KOR (Korup), LAP (La
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13 786 Planada), LAM (Lambir), LEN (Lenda), LUQ (Luquillo), MOS (Mo Singto), MUD
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15 787 (Mudumalai), PAL (Palanan), PAS (Pasoh), SCBI (Smithsonian Conservation Biology
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17 788 Institute), SERC (Smithsonian Environmental Research Center), SIN (Sinharaja), WAB
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19 789 (Wabikon) and YAS (Yasuni).
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806 **Figure 5.** Predicted mean number of extinctions (different colors) from simulations of a
 807 dynamic, mechanistic model for four of the CTFS–ForestGEO forest plots considered in this
 808 study. Each panel shows the predicted mean number of extinctions for different combinations
 809 of values of two key model parameters: the variance of the lognormal distribution of possible
 810 fitness values for each model species (A) and the correlation time determining how frequently
 811 the fitness values of all species were redrawn due to changes in environmental conditions (τ)
 812 (see Fig. 3). For each plot, the combination of parameter values giving the smallest median
 813 (typical) error (with respect to the temporal population variability and temporal correlations
 814 of species abundances), ξ , is marked with a yellow dot. Combinations of parameter values

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3 815 producing errors below ξ 25%–50% of the time are marked with orange dots, whereas
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5 816 combinations of parameter values producing errors below ξ 12.5%–25% of the time are
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7 817 marked with brown dots. Together, these are the “best-fit combinations” (see text in
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9 818 Appendix S5 for details). The four plots shown span a wide latitudinal gradient, with
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11 819 latitudes of 1.56°N, 9.15°N, 24.8°N and 38.9°N for Edo, BCI, Fushan and SCBI
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14 820 (Smithsonian Conservation Biology Institute), respectively.
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