ECOLOGY LETTERS

Ecology Letters, (2020) **23**: 160–171 doi: 10.1111/ele.13412

LETTER

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

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Abstract

Among the local processes that determine species diversity in ecological communities, fluctuation-dependent mechanisms that are mediated by temporal variability in the abundances of species populations have received significant attention. Higher temporal variability in the abundances of species populations can increase the strength of temporal niche partitioning but can also increase the risk of species extinctions, such that the net effect on species coexistence is not clear. We quantified this temporal population variability for tree species in 21 large forest plots and found much greater variability for higher latitude plots with fewer tree species. A fitted mechanistic model showed that among the forest plots, the net effect of temporal population variability on tree species coexistence was usually negative, but sometimes positive or negligible. Therefore, our results suggest that temporal variability in the abundances of species populations has no clear negative or positive contribution to the latitudinal gradient in tree species richness.

Keywords

Biodiversity, environmental variance, extinction risk, stochastic model, storage effect, temporal niche partitioning.

Ecology Letters (2020) **23**: 160–171

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INTRODUCTION

Variation in species diversity across the biosphere has fascinated ecologists for decades (Wallace 1878; Fischer 1960; Hutchinson 1961; Pianka 1966; Connell 1978; Palmer 1994; Chesson 2000; Hubbell 2001; Mittelbach *et al.* 2007; Levine & HilleRisLambers 2009; Ricklefs & He 2016). At the regional scale, community diversity is moderated by processes that act on large spatiotemporal scales, such as biogeographic and evolutionary processes (Rickefs 1987, 2004). A proportion of species in the regional community can disperse to a particular location, where they are subjected to a variety of localised abiotic and biotic processes (Fig. 1; HilleRisLambers *et al.* 2012). These local processes filter the dispersing species, resulting in a locally coexisting subset of species. Laboratory experiments and ecological theory suggest that under the most basic conditions of a constant environment, few limiting resources and a lack of dispersal from a regional community, only a few species will coexist in a local community (Gause 1934). This observation has motivated research into processes that permit the coexistence of tens to hundreds of species in natural local communities, including lake plankton (Smith *et al.* 2005), reef corals (Roberts *et al.* 2002) and rainforest trees (Anderson-Teixeira *et al.* 2015).

At a local scale, species coexistence can be facilitated by 'fluctuation-dependent mechanisms' (Chesson 1994, 2000, 2018), which are a class of stabilising mechanisms. Stabilising mechanisms in general attenuate differences in the fitness of species in a local community, thereby helping to maintain local species richness (Chesson 2000, 2018; Levine *et al.* 2017; Barabás *et al.* 2018). Temporal fluctuation-dependent mechanisms in particular arise when a temporally changing environment causes changes in resource use among species in a local community over time, and hence variation in the abundances of the species populations over time. This results in 'temporal niches' that may allow rare species in a local community to persist (Hutchinson 1961; Grubb 1977; Chesson 1994, 2000; Adler & Drake 2008). While the ecological theory of temporal niches suggest a positive effect of environmental fluctuations on species richness (Hutchinson 1961; Grubb 1977; Chesson 1994, 2000; Adler & Drake 2008), another ecological theory suggests just the opposite – that greater fluctuations in local environmental conditions can erode species richness, by periodically reducing species population abundances and thus increasing the risk of stochastic extinctions (Leigh 1981; Lande 1993; Adler & Drake 2008; Danino *et al.* 2016). The net effect of these two opposing factors will determine how environmentally induced temporal changes in species abundances contribute to local species richness.

Recent theoretical studies (Adler & Drake 2008; Danino *et al.* 2016) suggest that temporal niche effects generally dominate stochastic extinction effects when temporal environmental variance is low, with the opposite occurring when temporal environmental variance is sufficiently high. To the

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†This article has been contributed to by US Government employees and their work is in the public domain in the USA.

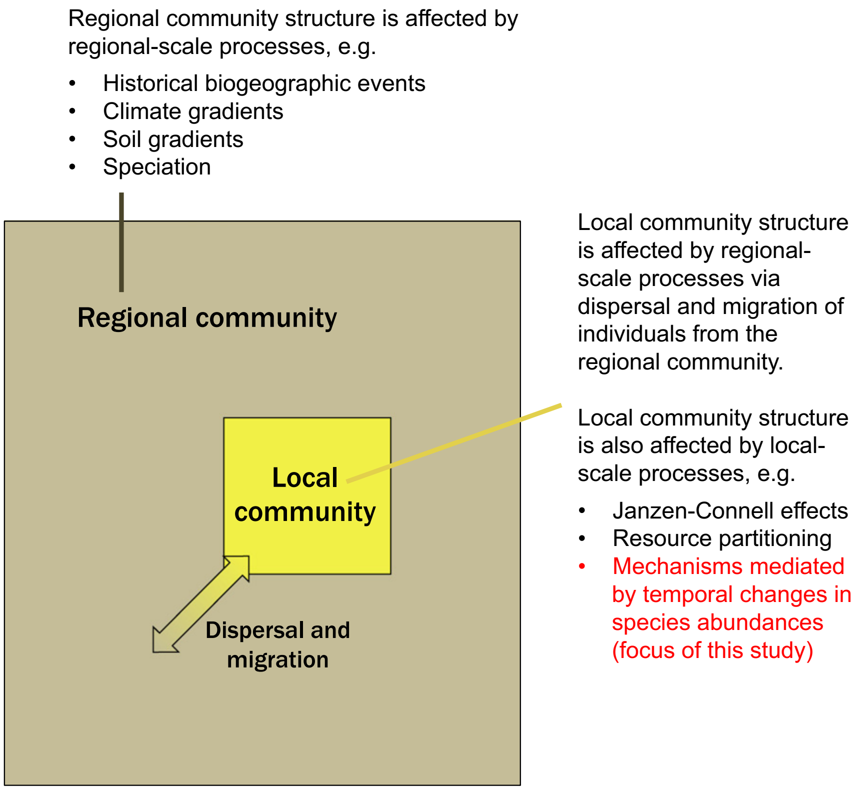

Figure 1 Schematic diagram showing the processes structuring a local community, including its species diversity. The local community is embedded within a regional community, which is governed primarily by regional-scale processes. Because the regional community is much larger than the local community,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

extent that greater temporal environmental variance increases the average amount by which the abundance of a species population changes over time, that is, what we call ‘temporal population variability’, the theoretical studies (Adler & Drake 2008; Danino *et al.* 2016) have suggested that a small amount of temporal population variability generally has a net positive effect on species coexistence and hence species richness in local communities, but that a large amount of temporal population variability generally has a net negative effect. An unresolved question is whether this net effect tends to be positive or negative in natural populations. Several studies have used empirical data to quantify the stabilising strength of temporal fluctuation-dependent mechanisms in a single community (Cáceres 1997; Adler *et al.* 2006; Angert *et al.* 2009; Usinowicz *et al.* 2012). Although these studies shed light on how important these mechanisms are for coexistence of species within a single community, they do not show how important they are in maintaining patterns of species richness across communities. A recent empirical study (Vásquez & Stevens 2004) did measure temporal population variability in multiple communities, but did not relate this to mechanisms that help to maintain species richness.

Here we investigated the effect of temporal population variability on species richness in 21 forest tree communities, using a global dataset with repeated tree censuses (Anderson-Teixeira *et al.* 2015). The tree communities span a large latitudinal range of 0.7 °S to 45.6 °N, with tree species richness showing a declining trend away from the tropics (Appendix S1 in Supporting Information). We first performed regression analyses to investigate whether there was a corresponding latitudinal gradient in temporal population variability of tree species in the forest communities. We then quantified the net effect of this variability on tree species coexistence in the communities by fitting a mechanistic community model (Danino *et al.* 2016) to the observed temporal abundance dynamics of tree species populations at each plot, and using the fitted model to predict the effects of temporal population variability on extinction rates of tree species in the communities. The results from all these analyses allowed us to assess whether temporal population variability makes a clear negative or positive contribution to the latitudinal gradient in tree species richness.

MATERIALS AND METHODS

Tree census data

We used data from 21 of the 67 long-term forest plots from the Center for Tropical Forest Science–Forest Global Earth Observatory (CTFS–ForestGEO) network (Fig. 2). We

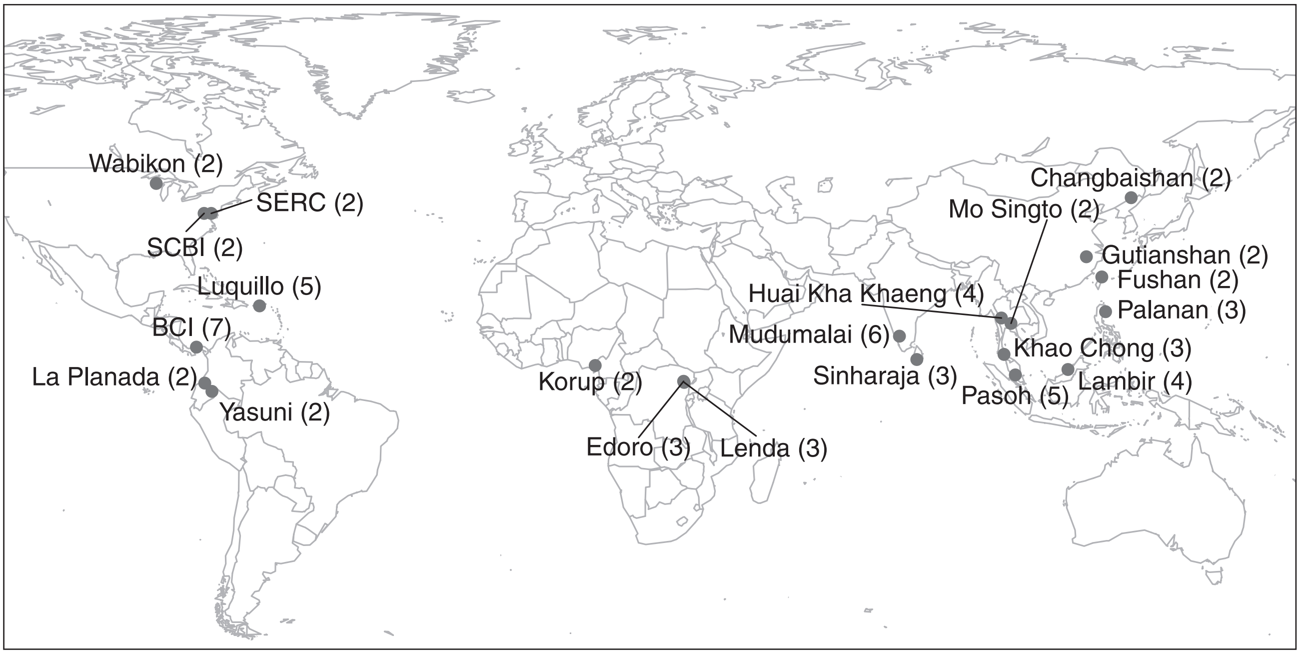

Figure 2 Map of the 21 CTFS–ForestGEO forest plots considered in this study, with corresponding numbers of tree censuses in parentheses. BCI, SCBI and SERC stand for Barro Colorado Island, Smithsonian Conservation Biology Institute and Smithsonian Environmental Research Center respectively.

selected these 21 forest plots because they had at least two tree censuses and a minimum area of 16 ha. Data from multiple censuses allowed calculations of temporal population variability. Using the lower limit of 16 ha on plot area helped to reduce the number of small populations and hence the effects of demographic variance (Hubbell 2001), which could complicate interpretation of drivers of the observed temporal population variability. Here demographic variance refers to variation in the realised demographic rates of species populations due to the random sampling of demographic events for discrete individuals, in contrast to temporal environmental variance that refers to variation in the intrinsic demographic rates of species populations over time (Chisholm *et al.* 2014). The 21 plots covered a total of 650 ha in four continents and spanned a wide range of climatic and edaphic conditions (Anderson-Teixeira *et al.* 2015). Approximately 3 million trees were censused in the 21 forest plots, with repeated censuses over periods of 6–31 years. Each plot was censused according to a standard protocol, whereby all freestanding woody plants with diameter-at-breast-height (DBH; 1.3 m from the ground) $\geq$ 1 cm were identified to the lowest taxonomic level possible, mapped and recorded (Condit 1998).

Summary information for the 21 plots is provided in Appendix S1, together with further details on how the tree census data were processed.

Investigating latitudinal trends in temporal population variability

We performed regression analyses to quantify how temporal population variability of tree species in the 21 forest plots varied with latitude, considering trees with DBH $\geq$ 1 cm. Metrics of temporal population variability could potentially be biased by the total tree abundance varying substantially across plots and, to a lesser extent, censuses, because changes in total tree abundance alter the strength of density-dependent effects across plots (Appendix S2). Thus, we rarefied (sampled without replacement) the data for each census in each plot to a sample size of $N_{\min} = 15\,299$, which was the minimum observed total tree abundance at any plot in any census (this minimum abundance occurred in the third census at Mudumalai plot). Although $N_{\min} = 15\,299$ was usually much smaller than the number of trees in a census (by a factor of around nine on average), at each plot a sample of 15 299 trees was large enough to give species population sizes up to hundreds or thousands of individuals, with dynamics that were not dominated by demographic variance (Chisholm *et al.* 2014).

After rarefaction to the same number of individuals in each census ($N_{\min} = 15\,299$), there remained another potential source of bias that must be accounted for: given a fixed total tree abundance, abundant species were overrepresented in species-poor plots, while rare species were overrepresented in species-rich plots. The resulting bias was problematic because a greater value of a temporal population variability metric at a plot could simply reflect species that were generally more abundant (abundant species tend to fluctuate more in absolute abundance; Lande 1993; Chisholm *et al.* 2014) rather than greater intrinsic temporal variability of the community (Appendix S2), which is what we were interested in. To remove this confounding factor, we corrected the rarefied changes in species abundances to account for the different sets of initial species abundances in each pair of consecutive censuses, by only including changes in species abundances for which the corresponding initial species abundances are common to all plots (Appendices S2 and S3).

To further test the robustness of our analyses to other possible sources of bias, we used another rarefaction procedure that standardised the sample area as well as the number of individuals, and that also standardised the number of individuals in a way that conserved the pairwise temporal correlations of species abundances in the dataset for a plot (Appendix S3). Standardising the sample area removed bias due to the strength of ecological processes changing at different spatial scales (Levin 1992), whereas the conservation of temporal correlations was potentially important because these correlations are associated with the strength of temporal fluctuation-dependent mechanisms (Chesson 2000, 2018; Barabás *et al.* 2018). Standardisation of the sample area resulted in fewer trees in the rarefied dataset for each plot: an average of 4713 individuals across censuses (Appendix S3). In turn, this resulted in fewer (initial) species abundances common to all plots compared with the previous method of rarefaction – 16 compared with 222. Excluding the Mudumalai plot increased the number of species abundances common to all remaining plots from 16 to 20; excluding the Luquillo, Palanan and SERC plots as well further increased the number to 194 (Appendix S3). Thus, to test robustness to the number of species abundances common to all plots, we performed three regressions using data rarefied in this way: one using data from all 21 plots, one using data from the 20 plots that excluded Mudumalai, and one using data from the 17 plots that excluded Mudumalai, Luquillo, Palanan and SERC.

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

$$\overline{\Delta N_i} = \frac{1}{C_i - 1}\sum_{j=1}^{C_i-1}\frac{1}{S_{i,j}}\sum_{k=1}^{S_{i,j}}\frac{\left|N_{i,j+1,k} - N_{i,j,k}\right|}{T_{i,j+1,k} - T_{i,j,k}}, \qquad (1)$$

where C_i is the number of censuses of plot i, $S_{i,j}$ is the total number of species in census j at plot i for the dataset, $N_{i,j,k}$ is the abundance of tree species k in census j at plot i for the dataset and $T_{i,j,k}$ is the mean census date of individuals of species k in census j at plot i. If a species k was present in census j but absent in census $j+1$ at plot i, then $T_{i,j+1,k}$ was set equal to the mean census date of individuals of all other species in census $j+1$ at plot i. For each plot i, we calculated the average $\overline{\Delta N_i}$ over 1000 rarefied datasets with a standardised number of individuals and correction for different sets of initial species abundances among plots, thus producing the metric $\overline{\Delta N_{r,c,i}}$. For each plot i, we repeated the calculation for rarefied datasets with a standardised area and number of individuals, conservation of the pairwise temporal correlations of species abundances and correction for different sets of initial species abundances among plots. This produced the metric $\overline{\Delta N_{ra,c,i}}$ for plot i.

To determine the latitudinal trend in temporal population variability for the 21 forest plots, we computed separate linear regressions of $\overline{\Delta N_{r,c}}$ and $\overline{\Delta N_{ra,c}}$ against absolute latitude. For each regression, a log-transformation was applied to both variables to reduce their skewness and help meet assumptions of normality and homoscedasticity (see Appendix S4 for details).

Relating temporal population variability to mechanisms maintaining species richness

For the forest plots, we related temporal population variability to mechanisms maintaining species richness, by fitting a dynamic, mechanistic community model to the observed values of temporal population variability and temporal correlations of species abundances in the rarefied data, and then using the fitted models to predict the rates of species extinction. Our mechanistic model represented a local community of J individuals competing for resources under temporally changing environmental conditions. In a model community, each species had a fitness value that determined its recruitment rate in the prevailing environmental conditions. The fitness value of a species at the start of a simulation was drawn randomly from a lognormal distribution with mean 1 and variance A. At the beginning of each subsequent time-step in the simulation, the fitness values for all species were redrawn independently from the lognormal distribution with probability $1/\tau$, which indirectly represented changes in environmental conditions. Therefore, τ measured the temporal correlation in environmental conditions. The model we used captured the effects of deterministic selection (arising from fitness differences among species in a given environment; Vellend 2010), stochastic ecological drift (Hubbell 2001) and stochastic local-scale environmental fluctuations over time (Lande 1993; Chisholm *et al.* 2014; Kalyuzhny *et al.* 2014, 2015; Fung *et al.,* 2016). Fig. 3 provides a schematic diagram of the model.

The model we used was the same as that of Danino *et al.* (2016) except that we allowed J to vary over time and did not allow the introduction of new species over time. Not allowing the introduction of new species into a model community meant that the community did not receive immigrants from an outside source. This was appropriate for our analysis, as we wanted to isolate the effects of local temporal population variability in tree species from regional effects introduced by immigration. For each plot, we fitted the model to the census data rarefied by area and the number of individuals, in a way that conserved the temporal correlations of species abundances within the plot. When fitting our model to the rarefied data, we assumed that the observed abundance fluctuations over the census periods approximated those that would be found in the absence of immigration. This assumption was justified when the number of individuals in the rarefied dataset was much larger than the square root of the number of individuals, because the number of immigrant propagules should scale roughly with the perimeter (i.e. the square root) of the area occupied by the individuals whereas the number of non-immigrant propagules scales with the area. To ensure that this assumption was valid, when fitting the model we excluded the Mudumalai plot, which had the fewest censused individuals. This increased the mean sample size after rarefaction from 4713 to 13 000, such that the number of individuals at each plot was two orders of magnitude greater than the square root of the number of individuals.

To fit the model to data from a plot, we simulated the model for different combinations of A and τ, representing different environmental regimes. Specifically, for each plot, we performed simulations for all combinations of 32 values of A

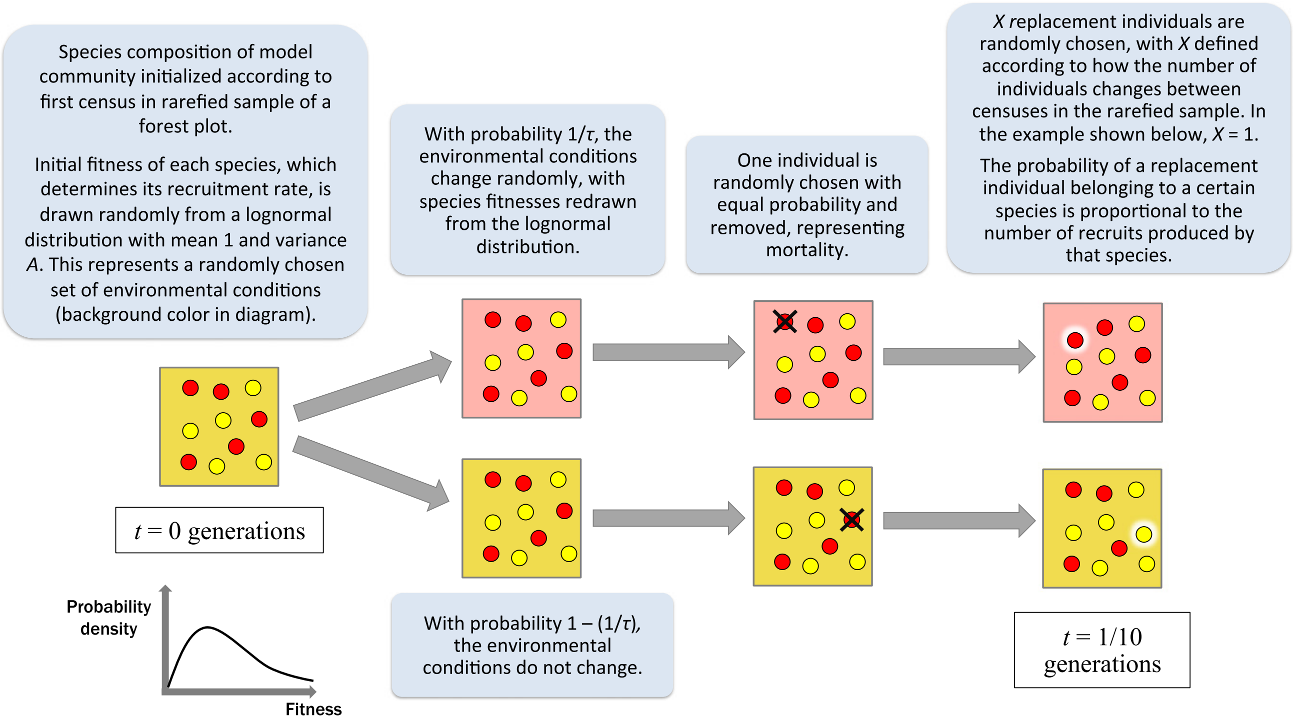

Figure 3 Schematic diagram showing the processes operating in the dynamic, mechanistic model that we fitted to tree census data from each of 20 forest plots. The diagram shows the processes operating over one model time-step. In the representations of the model communities, the yellow and red backgrounds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

in the range $[0, 10^3]$ and 14 values of τ in the range $[1, 10^4]$, representing a large parameter space spanning several orders of magnitude in A and τ. During each simulation for a plot, the initial species composition was set equal to the species composition in the first census of a rarefied dataset. We then simulated model dynamics for a length of time equal to the entire census period for the plot, with J for the model community changing linearly in between censuses to match the number of individuals in the rarefied dataset at each census. At the end of each simulation, we calculated temporal population variability from the simulated data using eq. (1), as well as the mean cumulative distribution function (cdf) of pairwise temporal correlations of species abundances over a pair of consecutive censuses. For each plot, we performed 1000 simulations for each of the $32 \times 14 = 448$ combinations of A and τ, and determined the combination that gave the lowest typical error, where the error is defined as the average of (i) the percentage absolute difference between the model and observed temporal population variability and (ii) the percentage absolute difference between the model and observed cdf of temporal correlations. In addition, we determined the combinations of A and τ that produced similar errors to the combination giving the lowest typical error – we refer to all these as the 'best-fit combinations' (see Appendix S5 for details, including a definition of 'typical error').

For each plot and each combination of A and τ, we ran a further 100 simulations, each lasting the entire census period (as described in the previous paragraph) and a further 2×10^5 time-steps, which was sufficient time for up to tens to hundreds of species extinctions to occur. At the end of each simulation, we recorded the number of species that were extinct. During the last 2×10^5 time-steps, J was assumed to remain constant, such that it remained equal to the sample size in the last census. Different assumptions that involve varying J according to some pattern would likely have little effect on the relative number of species extinctions that occurred among different environmental regimes (combinations of A and τ) within a plot. However, because the sample size in the last census was different for each plot (only the mean sample size across censuses was approximately the same among plots; Appendix S3), simulations for different plots had different J in the last 2×10^5 time-steps (which represented 0.655–1.31 generations). Because species extinction times change with J (e.g. Chisholm & O'Dwyer 2014; Danino *et al.* 2018), these simulations did not allow an unbiased comparison of species extinction risk across different plots. Furthermore, for different plots J might vary in different ways beyond the census periods. For these reasons, we restricted interpretation of our simulation results for a plot to patterns of species extinction risk within that plot. Appendix S5 provides further details of the dynamic model, how it was simulated, and how it was fitted to the data.

We found that for 13 of the 20 plots, the best-fit models for the observed data gave low errors (see *Results*). For these 13 plots, we used our mechanistic model results to investigate whether greater temporal population variability was associated with a greater species extinction rate within each plot. To do this, we noted that temporal population variability almost always increased with A and τ in the model (Fig. S13 in Appendix S5), such that we can use these two parameters as

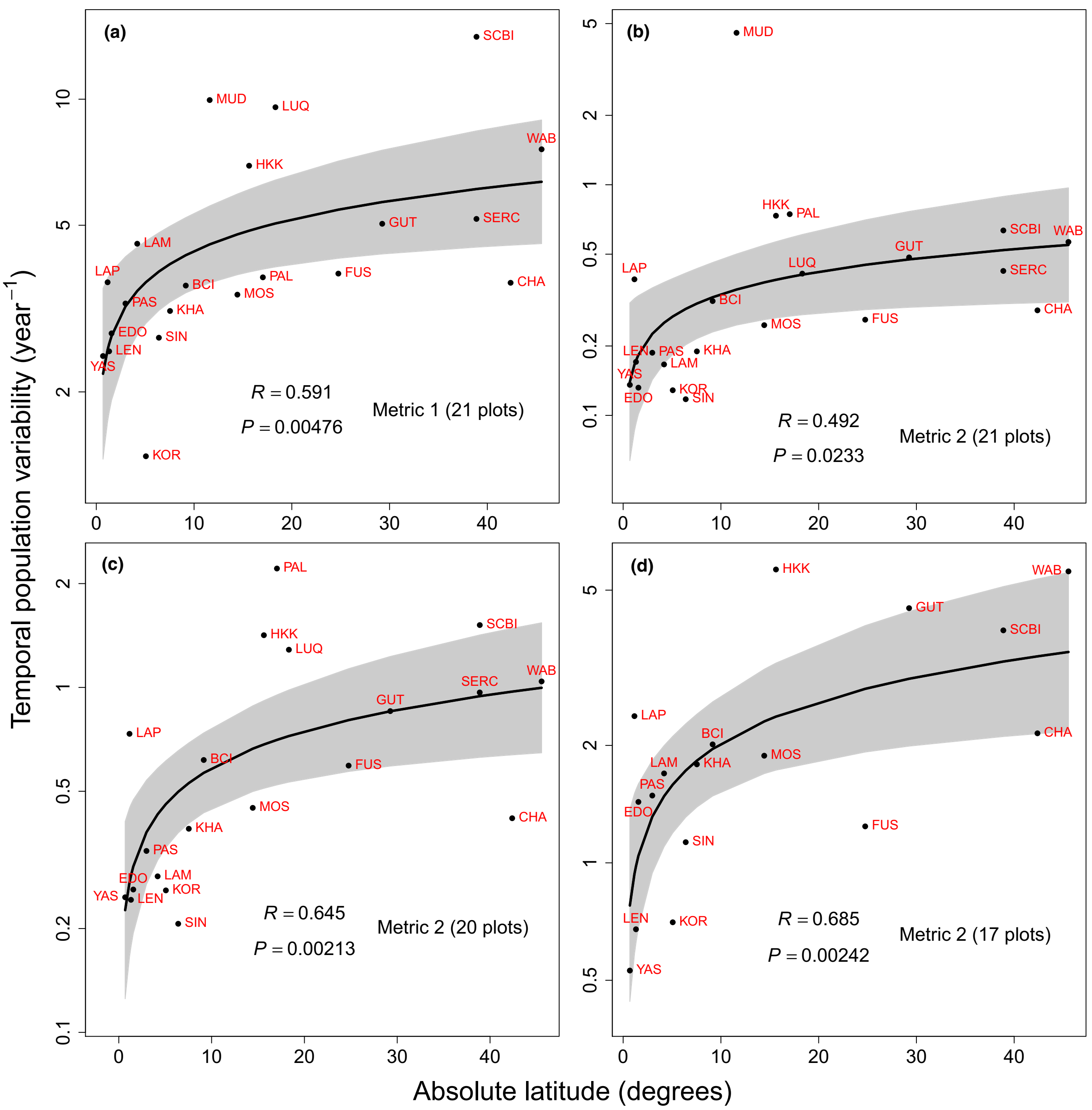

Figure 4 (a) Relationship between temporal population variability and absolute latitude for the 21 CTFS–ForestGEO forest plots considered in this study. Temporal population variability was measured as the mean absolute change in tree species abundance per year, with rarefaction to standardise the number of individuals and correction to account for the different sets of initial species abundances in each pair of consecutive censuses (Metric 1; $\overline{\Delta N_{r,c}}$). The line represents a linear regression between the logarithms of the two variables, with the 95% confidence interval shown as the shaded region. (b) is the same as (a) except that temporal population variability was measured with rarefaction to standardise the plot area and number of individuals, in a way that conserved temporal correlations of species abundances (Metric 2; $\overline{\Delta N_{ra,c}}$). (c) is the same as (b) except that the plot at Mudumalai was excluded. (d) is the same as (b) except that the plots at Mudumalai, Luquillo, Palanan and SERC were excluded. Each empirical value (black dot) is labelled according to the plot it refers to: BCI (Barro Colorado Island), CHA (Changbaishan), EDO (Edoro), FUS (Fushan), GUT (Gutianshan), HKK (Huai Kha Khaeng), KHA (Khao Chong), KOR (Korup), LAP (La Planada), LAM (Lambir), LEN (Lenda), LUQ (Luquillo), MOS (Mo Singto), MUD (Mudumalai), PAL (Palanan), PAS (Pasoh), SCBI (Smithsonian Conservation Biology Institute), SERC (Smithsonian Environmental Research Center), SIN (Sinharaja), WAB (Wabikon) and YAS (Yasuni).

drivers of temporal population variability. For each plot, we calculated the mean number of extinctions (across 100 simulations) for the different combinations of A and τ described above. Then, starting with the best-fit combinations of A and τ, we determined what the effect of further increases in either parameter – and hence in temporal population variability – would be on extinctions. For the model tree community corresponding to a particular forest plot, if increases in temporal population variability due to increases in a parameter led to more extinctions, then this suggested that the real tree community in the plot was in a regime where increases in temporal population variability due to that parameter have a net negative effect on species coexistence and richness. Conversely, if increases in temporal population variability due to increases in a parameter led to fewer extinctions in the model tree community, then this suggested that the real tree community was in a regime where increases in temporal population variability due to that parameter have a net positive effect on species coexistence and richness (i.e. temporal niche effects were strong).

All simulations and statistical analyses described were performed using R v3.3.3 (R Development Core Team 2013). As part of the Supporting Information, we have provided an R script with code corresponding to the dynamic model simulations used in our study (‘R_code_for_dynamic_models.R’). The code provides two functions, one for producing model simulations used to assess bias in metrics of temporal population variability (represented schematically in Fig. S1 in Appendix S2) and the other for producing model simulations used to fit the dynamic model to the tree census data (represented schematically in Fig. 3).

RESULTS

In our first regression analysis, we found that temporal population variability showed a substantial positive correlation with absolute latitude for the 21 forest plots examined, where the variability was calculated as the mean absolute change in tree species abundance per year, using the plot datasets rarefied by number of individuals ($\overline{\Delta N_{r,c}}$; linear regression on log-log axes: $R^2 = 0.350$, slope = 0.251, $P = 4.76 \times 10^{-3}$, $n = 21$; Fig. 4a; Appendix S4). In our second regression analysis, temporal population variability was calculated using the plot datasets rarefied by plot area and the number of individuals, in a way that conserved temporal correlations of species abundances ($\overline{\Delta N_{ra,c}}$). In this analysis, we still found a substantial positive correlation of variability with absolute latitude, regardless of whether we used data from all 21 plots

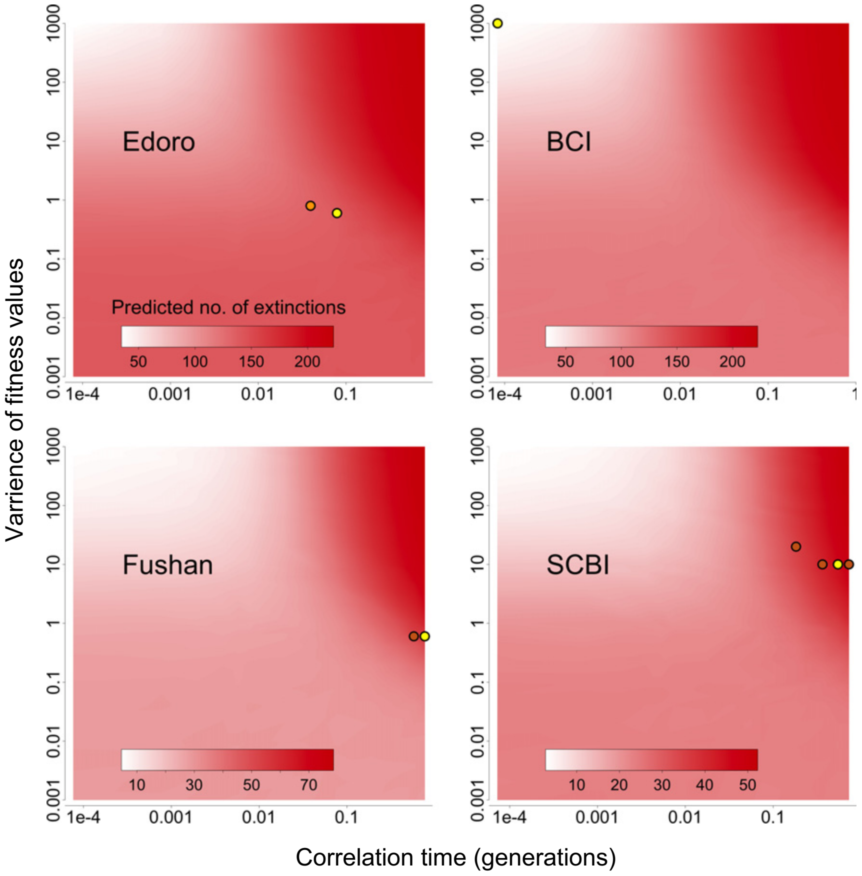

Figure 5 Predicted mean number of extinctions (different colors) from simulations of a dynamic, mechanistic model for four of the CTFS–ForestGEO forest plots considered in this study. Each panel shows the predicted mean number of extinctions for different combinations of values of two key model parameters: the variance of the lognormal distribution of possible fitness values for each model species (A) and the correlation time determining how frequently the fitness values of all species were redrawn due to changes in environmental conditions (τ) (see Fig. 3). For each plot, the combination of parameter values giving the smallest median (typical) error (with respect to the temporal population variability and temporal correlations of species abundances), ξ, is marked with a yellow dot. Combinations of parameter values producing errors below ξ 25–50% of the time are marked with orange dots, whereas combinations of parameter values producing errors below ξ 12.5–25% of the time are marked with brown dots. Together, these are the “best-fit combinations” (see text in Appendix S5 for details). The four plots shown span a wide latitudinal gradient, with latitudes of 1.56 °N, 9.15 °N, 24.8 °N and 38.9 °N for Edoro, BCI, Fushan and SCBI (Smithsonian Conservation Biology Institute) respectively.

($R^2 = 0.243$, slope = 0.326, $P = 0.0233$, $n = 21$; Fig. 4b; Appendix S4); the 20 plots that excluded Mudumalai ($R^2 = 0.416$, slope = 0.354, $P = 2.13 \times 10^{-3}$, $n = 20$; Fig. 4c; Appendix S4); or the 17 plots that excluded Mudumalai, Luquillo, Palanan and SERC ($R^2 = 0.469$, slope = 0.357, $P = 2.42 \times 10^{-3}$, $n = 17$; Fig. 4d; Appendix S4). For the first of these three regressions (using 21 plots), the Shapiro–Wilk test and quantile plot indicated non-normality (Fig. S12 in Appendix S4). Thus, we also performed a non-parametric regression, which again exhibited a substantial positive correlation (Spearman's $\rho = 0.643$, $P = 2.13 \times 10^{-3}$, $n = 21$).

From the fits of our dynamic model to data from the forest plots, we found that for 11 of the 20 plots considered (excluding Mudumalai, see *Materials and methods*), at least one combination of A and τ (the two parameters governing temporal population variability) gave values of the simulated temporal population variability and cdfs of temporal correlations of species abundances reasonably close to the observed data, with small typical errors of < 10% that we call 'good model fits' (Figs S14–S16 and Table S6 in Appendix S5). Two of the remaining nine plots (Lenda and Luquillo) had a combination of A and τ with a typical error of 10–10.5%, which we call 'marginally good model fits' (Figs S15 and S16, and Table S6). However, for the remaining seven plots (Gutianshan, Lambir, Pasoh, SERC, Sinharaja, Wabikon and Yasuni), the best-fit combination gave larger typical errors (> 11.2%; Table S6).

For 11 of the 13 plots with good or marginally good model fits, the best-fit models (corresponding to the best-fit combinations of A and τ) were within a parameter regime where A was sufficiently large that further increases in τ would likely increase the mean number of extinctions (Fig. 5 and Figs S17 and S18 in Appendix S5). For the remaining two plots (Khao Chong and Lenda), the best-fit models were within a parameter regime where A was sufficiently small that further increases in τ would likely have negligible effect on the mean number of extinctions (Figs S17 and S18). However, only six of the 13 plots (Khao Chong and Lenda were among these six plots) had best-fit models that were within a parameter regime where τ was sufficiently large that further increases in A would likely increase the mean number of extinctions (Fig. 5, Figs S17 and S18). The best-fit models for seven of the 13 plots were within a parameter regime where τ was sufficiently small that further increases in A would likely decrease (five plots) or have negligible effect (two plots) on the mean number of extinctions (Fig. 5, Figs S17 and S18).

DISCUSSION

For the tree communities in the 21 forest plots that we examined, we documented a strong trend of increasing temporal population variability of tree species with absolute latitude. The temporal population variability increased by three- to fourfold over 45 degrees of latitude, from tropical forests at the equator to temperate forests in the northern hemisphere. A previous study (Condit *et al.* 2006) of ten of the 21 forest plots that we used in this study identified a pattern of wider ranges of tree demographic rates in forests with fewer tree species, which is consistent with our finding of greater temporal population variability in the extratropical plots. However, the authors of that study (Condit *et al.* 2006) did not interpret their results in terms of whether greater temporal population variability increases the propensity for local extinctions of tree species.

If temporal population variability increases the extinction risk of tree species in our forest plots, then the latitudinal increase in temporal population variability could indicate increasingly negative effects on tree species coexistence for higher latitude plots. This could partially explain the latitudinal decline in tree species richness at local scales (Ricklefs & He, 2016; Appendix S4). In this regard, results using our mechanistic model showed that for four of the 13 plots with good or marginally good model fits, increases in temporal population variability would likely result in a greater rate of species loss. For the remaining nine plots, increases in temporal population variability would likely result in a greater rate of species loss or a rate of species loss that was lower or almost the same, depending on whether the increase in temporal population variability was caused by greater temporal correlation in environmental conditions or greater fitness variation among species. Thus, these results indicate that for the tree communities that we examined, greater temporal population variability has mixed net effects on tree species coexistence, such that extinction effects can outweigh temporal niche effects or vice versa. Therefore, temporal population variability makes no clear negative or positive contribution to the latitudinal gradient in local tree species richness. Our results provide a more nuanced perspective on the effects of temporal population variability on local tree species richness, which does not only focus on the positive temporal niche effects (Usinowicz *et al.* 2017).

Overall, our results suggest that temporal population variability is one of the factors with a substantial impact on local tree species richness, but we emphasise that it is by no means the only factor. In communities such as the ones that we have examined, the effects of temporal population variability on species coexistence are moderated by other local processes such as Janzen–Connell effects (Janzen 1970; Connell 1971; Bever *et al.* 1997; Bever 2003; Mangan *et al.* 2010) and resource partitioning (Meinzer *et al.* 1999; Turner 2008), and regional processes such as dispersal from regional communities of varying composition and richness (Ricklefs 1987, 2004; Hubbell 2001) (Fig. 1). Therefore, an important next step is to quantify the relative contributions of different local and regional processes to the maintenance of local species richness. Most studies to date have focused on either local (e.g. temporal fluctuation-dependent mechanisms; Cáceres 1997; Adler *et al.* 2006; Angert *et al.* 2009; Usinowicz *et al.* 2012, 2017; this study) or regional (e.g. dispersal; Hubbell 2001; Volkov *et al.* 2003, 2007) processes. A recent study (Ricklefs & He 2016) did partition variation in local tree species richness in 47 CTFS–ForestGEO forest plots according to local and regional processes, but used a statistical modelling approach that did not incorporate the actual mechanisms by which the processes affect richness. An alternative approach was used in other recent studies (Kalyuzhny *et al.* 2015; Fung *et al.* 2016), which fitted mechanistic models with dispersal, demographic stochasticity and local-scale temporal environmental fluctuations to the tree communities at the BCI and Pasoh CTFS–ForestGEO plots. However, these studies simply assumed that the regional community followed a log-series species abundance distribution. In contrast, other studies (Graham & Moritz 2006; Huntley *et al.* 2014) have considered the regional community more explicitly and emphasised the negative effects of temporal environmental fluctuations on richness at the long-term speciation–extinction balance.

Our modelling analyses also help to shed light on the general question of how complex a dynamic, mechanistic model needs to be to accurately capture temporal population variability in an ecological community. Drift-only models with constant community sizes are inadequate in most cases (Chisholm & O'Dwyer 2014; Chisholm *et al.* 2014; Kalyuzhny *et al.* 2014; Fung *et al.* 2016). Our analyses suggest that adding temporal variation in recruitment rates (Chisholm *et al.* 2014; Kalyuzhny *et al.* 2015; Fung *et al.* 2016) and community sizes is generally sufficient to accurately capture temporal population variability. But in the six tree communities where our mechanistic model substantially under- or over-estimated observed temporal population variability, additional mechanisms are required to get a better approximation of the true temporal dynamics. These additional mechanisms include temporal variation in mortality rates of species (Chisholm *et al.* 2014) and resource partitioning (Meinzer *et al.* 1999; Turner 2008), which increase and decrease temporal population variability respectively.

A future research priority is to determine specific environmental variables that drive fluctuations of tree species abundances in specific forests. Over the time period studied, the forest plots we examined were buffeted by a range of environmental factors, such as drought (Condit *et al.* 1996), groundfires (Baker *et al.* 2008), hurricanes/typhoons (Yap *et al.* 2016; Hogan *et al.* 2018) and insect herbivory (Gonzalez-Akre *et al.* 2016). Although many such factors can be identified, they are often idiosyncratic in nature and often act on population abundances via nonlinear causal pathways. Thus, the effects of different factors on temporal population variability are difficult to characterise in a simple way. For example, for the forest plots that we examined, a liner regression showed that temporal variability in mean monthly temperature and precipitation accounted for about a quarter to a third of the variation in the logarithm of temporal population variability (Appendix S4), leaving a substantial amount of variation unexplained. Our hope is that more analyses of long-term datasets of forest dynamics will permit better identification of key environmental drivers. This will ultimately facilitate the development of parsimonious predictive models specifying the future dynamics of forest tree communities.

ACKNOWLEDGEMENTS

We thank three anonymous reviewers for providing constructive comments that have resulted in substantial improvements in the work, particularly the reviewer who performed MATLAB simulations to assess bias in the metrics of temporal population variability that we considered. In addition, we thank the many people involved in the collection and processing of the vast quantities of data for the 21 CTFS–ForestGEO plots considered, including the hundreds of volunteers and field and laboratory staff who tirelessly contributed to the repeated censuses of each plot. The CTFS–ForestGEO network has received major support from the Smithsonian Institution – particularly the Smithsonian Tropical Research Institute, the Arnold Arboretum of Harvard University, the National Science Foundation (multiple grants), the Rockefeller Foundation, the John Merck Fund, the John D. and Catherine T. MacArthur Foundation, the Andrew W. Mellon Foundation, the Frank Levinson Family Foundation, the HSBC Climate Partnership, the Bromley Charitable Trust, John Swire & Sons Pty Ltd, Celerity, F. H. Levinson Fund, Small World Institute Fund and Jennifer and Greg Johnson. Plot-specific acknowledgements are listed in Table S2 in Appendix S1. Part of the analyses was conducted during the 2016 CTFS–ForestGEO Workshop in Hainan, China, supported by a National Science Foundation Dimensions of Biodiversity award (DEB-1545761 to S. J. Davies). We also thank Deepthi Chimalakonda, James O'Dwyer and Samuel Thompson for comments on the manuscript. This research was supported by the ISF-NRF Singapore joint research program (grant number WBS R-154-000-B09-281).

AUTHORSHIP

T.F. and R.A.C. designed the study and performed statistical analyses. T.F. wrote the first draft of the paper and R.A.C. revised the paper. All other authors provided data and contributed to the development of the paper.

DATA AVAILABILITY STATEMENT

Tree census data used in this study can be requested using the CTFS–ForestGEO data portal at http://ctfs.si.edu/datarequest/. Sources for the climate data are detailed in the Supporting Information.

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Editor,
Lauren Shoemaker
Manuscript received 28 May 2019
First decision made 4 July 2019
Manuscript accepted 29 September 2019