

Temporal variability in population and community dynamics

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Abstract. Populations and communities fluctuate in their overall numbers through time, and the magnitude of fluctuations in individual species may scale to communities. However, the composite variability at the community scale is expected to be tempered by opposing fluctuations in individual populations, a phenomenon often called the *portfolio effect*. Understanding population variability, how it scales to community variability, and the spatial scaling in this variability are pressing needs given shifting environmental conditions and community composition. We explore evidence for portfolio effects using null community simulations and a large collection of empirical community time series from the BioTIME database. Additionally, we explore the relative roles of habitat type and geographic location on population and community temporal variability. We find strong portfolio effects in our theoretical community model, but weak effects in empirical data, suggesting a role for shared environmental responses, inter-specific competition, or a litany of other factors. Furthermore, we observe a clear latitudinal signal – and differences among habitat types – in population and community variability. Together, this highlights the need to develop realistic models of community dynamics, and hints at spatial, and underlying environmental, gradients in variability in both population and community dynamics.

Key words: ecological stability; population fluctuations; portfolio effect; temporal variability.

INTRODUCTION

Population dynamics are the result of multiple interacting processes that may influence species demographic rates (Ovaskainen and Cornell 2006, Oro 2013). For instance, environmental conditions may influence individual survival, fecundity, or mortality, and fluctuations in environmental conditions with time may drive non-equilibrium population dynamics (Kendall et al. 2000, Benton et al. 2006). Similarly, biotic interactions including competition, predation, and mutualism can link dynamics of species negatively (Brännström and Sumpster 2005) or positively (Breton and Addicott 1992). Understanding how and why populations fluctuate across time is a fundamental goal of population ecology. Apart from the intrinsic interest in understanding what causes populations to vary in size over time, population fluctuations – and the temporal autocorrelation in population fluctuations (Drake and Griffen 2010) – are related to population extinction risk (Ovaskainen and Meerson 2010).

The extent to which these fluctuations at the population level may scale to the entire community is unclear

(Gonzalez and Descamps-Julien 2004). A body of literature has developed on so-called *diversity–stability* relationships, which posits that increasing species diversity in a community stabilizes overall dynamics, either in a meaningful way (McCann 2000) or as a statistical inevitability (Doak et al. 1998, Valencia et al. 2020). Here, *stability* can be defined as the temporal variation in total community abundance, although many ecological definitions of stability exist (Mikkelsen 1997, Bodin and Wiman 2004). In the context of temporal variability in population and community dynamics, we would expect population and community variability to be equal or proportional if species responded approximately the same to fluctuating environments. Similarly, equal or proportional population and community variability would be expected when weak interactions between species lead to few constraints on overall community abundance. Conversely, fluctuating environments can change population demographic rates, while allowing for species compensatory dynamics, a phenomenon known as the temporal storage effect (Chesson and Huntly 1993, Levine and Rees 2004, Adler et al. 2006). In this case, populations would fluctuate, while density-dependent competitive effects might constrain overall community abundance, leading to lower temporal variability at the community scale. Overall community abundance could also be constrained by competition for resources or space (Gonzalez and Loreau 2009, Thibaut and

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Connolly 2013), with the extreme case being zero-sum dynamics, in which average population synchrony would be completely unrelated to community temporal variability, as populations may vary greatly over time, but the overall number of individuals in the community would remain fairly constant (Gonzalez and Loreau 2009). Understanding the interplay between population and community temporal variability is a fundamental question linking population and community ecology.

It is most likely that the composite properties of multiple interacting (or non-interacting) populations leads to a less temporally variable community relative to the dynamics of individual species. This is based on previous work on portfolio effects (Thibaut and Connolly 2013, Abbott et al. 2017), which suggested that temporal variability in community-level abundance will almost always be less than average population-level variability due to antisynchronous population fluctuations caused by differential responses to environmental pressure or through direct competitive processes between species. Examining the extent to which communities in natural systems obey this expectation relative to a simple null model could allow empirical validation of the underlying theory. More recently, Valencia et al. (2020) suggested that synchrony is far more important than species richness in influencing temporal variability (which is one measure of *stability*). This contributes to the ongoing debate surrounding the relationship between biodiversity, synchrony, and stability in ecology (Gonzalez et al. 2020). For the sake of clarity, we will not discuss ecological stability in broad terms, but simply temporal variability, which admittedly is one way of many to define ecological stability (Donohue et al. 2016). The focus on temporal variability in populations and communities, independent of discussions of stability and synchrony, allows us to address some of the other numerous confounding variables that may influence population fluctuations.

For instance, natural communities vary not only in the number of species in the community (the “diversity” part of the “diversity–stability” relationship), but also in species-specific responses to biotic and abiotic covariates, which work together to constrain population and community abundance. This suggests that independently from any scaling between mean population-scale and community-scale temporal variability, there may be corresponding effects of abiotic and biotic covariates, which may be spatially structured as a result of spatial autocorrelation in climate, community composition, and resource availability. For example, mammal populations tend to be more cyclic at higher latitudes (Kendall et al. 1998). Similar relationships in population and community dynamics have been observed along environmental and latitudinal gradients (Connell and Sousa 1983, Duarte 1989, Crowley and Johnson 1992), as latitude covaries with temperature (Hijmans et al. 2005, Pereira et al. 2017), precipitation (Hijmans et al. 2005), and species diversity (Hillebrand 2004). It might be expected that populations and communities would be more variable at more extreme

latitudes, as these habitats may correspond to species range limits (Guo et al. 2005) and have more variable climates (Janzen 1967, Sheldon et al. 2018). Finally, the nature of the community may fundamentally constrain the scaling between population and community temporal variability, or the existence of a spatial signal temporal variability. For instance, differences in environmental variation and species niche limits probably differ between terrestrial and aquatic communities (Steele et al. 2019), in addition to the fundamental differences in response to anthropogenic threats across terrestrial and aquatic habitats (Bowler et al. 2019, van Klink et al. 2020).

We explore temporal variability in populations and communities using a large database of community-level time series, BioTIME (Dornelas et al. 2018). These data have been crucial for examining global patterns of population trends (Dornelas et al. 2019), biodiversity change (Blowes et al. 2019), and the relationship between diversity and community dynamics (Gotelli et al. 2017). We used this data resource (Fig. 1) to examine temporal variability in population and community time series, exploring (1) the relationship between community-level variability and mean population-level variability, (2) a potential latitudinal signal in population and community temporal variability, and (3) the differences among freshwater, terrestrial, and marine environments in their population and community variability. Using a combination of simulated community dynamics and empirical data, we found a clear scaling between mean population and community temporal variability, with weak evidence for a portfolio effect in empirical data relative to strong evidence in simulated communities. Furthermore, temporal variability in populations and communities was greater at higher latitudes, differed across habitat types, and was related to species richness only for community temporal variability. Together, this suggests that portfolio effects may vary in their strength across communities in different environments, different latitudes, and with different numbers of species.

METHODS

BioTIME time-series data

To examine spatial gradients in temporal variability, we used the largest extant database of long-term *in situ* monitoring of all species in an assemblage, the BioTIME database (Dornelas et al. 2018). This data resource contains species abundances through time for 361 studies (Fig. 1). Each study consists of a range of plots – ranging from 1 to 147,201 – with each plot corresponding to a time series of abundance values. The median time-series length was 2,336 d (over 6 yr). We treated each study as a sampling unit, by taking the mean of plot-scale values of abundance. This was done to avoid over-weighting studies with numerous plots in the same geographic location. We explore this decision in Appendix S1.

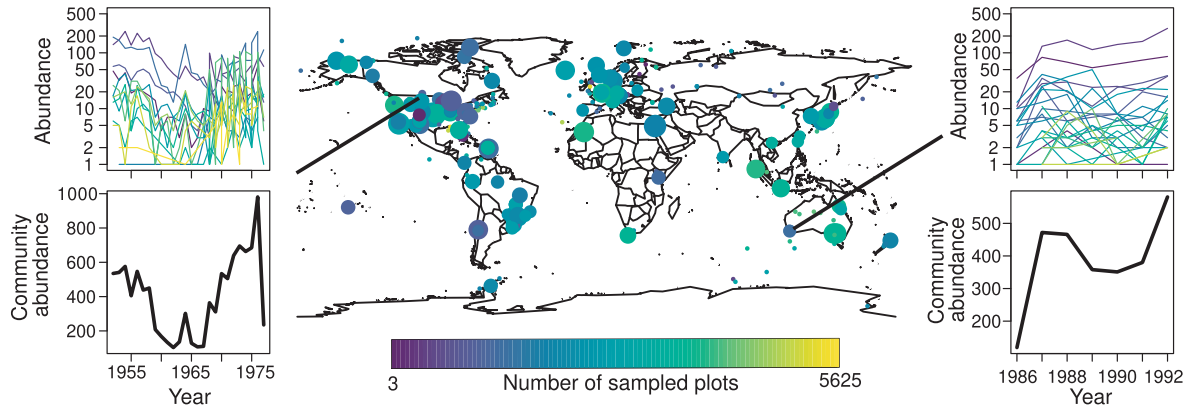


FIG. 1. The BioTIME data contain time-series data from communities sampled on the global scale. Plotted points are mean latitude and longitude values for given sampled locations, where point size is proportional to species richness and point color corresponds to the number of sampled plots per site. The two row panels highlight time series of species (top panels) and overall community abundance (bottom panels). The two selected sites also highlight differences in sampled time period, and differences in the variability of population dynamics that are inherent in this data resource.

Estimating temporal variability

To measure temporal variability, we examined two organizational scales: the population scale and the community scale. At both scales, we considered site-level mean temporal variability, which is based on a collection of plots. Therefore, a population time series represents the average abundance across plots for a single species within a study, while the community time series is the average abundance of all species across plots within a study. At the population scale, we estimated temporal variability for each species in each study site and plot for all years the species was found. At the community scale, we estimated temporal variability considering the sum of all individuals in the community for each plot, scaling to study scale by taking the mean temporal variability over all the plots in a given study.

To estimate temporal variability in time series of population and community abundance, we used the consecutive disparity index (D ; Fernández-Martínez et al. 2018). This measure has been previously used to estimate interannual climatic variability (Meseguer-Ruiz et al. 2017) and fruit production (Vergotti et al. 2019), and is measured as:

$$D = \frac{1}{n-1} \sum_{t=1}^{n-1} \left| \ln \left(\frac{p_{t+1} + k}{p_t + k} \right) \right| \quad (1)$$

where p_t corresponds to abundance at time t , where the entire length of the time series is n , and k is a constant. This value k is used to ensure that zeroes do not strongly influence the D statistic. To make estimates of D comparable across different time series, we considered k to be 1% of the time-series mean, as suggested in Fernández-Martínez et al. (2018). We also estimate temporal variability using the coefficient of variation, which does not consider the temporal order of abundance estimates, but is insensitive to the size of the abundance values (see Appendix S1: Table S1, Figs. S2–S4).

A null expectation

Due to portfolio effects, there is an expectation that temporal variability in populations and the overall community will be positively related, with communities expected to be less variable (Thibaut and Connolly 2013, Abbott et al. 2017). Developing a simulation model capable of incorporating variation in species niche limits, seasonal variability in climate, and density-dependent species interaction terms is a massive challenge when assembling realistic communities (Barbier et al. 2018). However, we can easily visualize the expected relationship while making the assumption that the communities are formed of non-interactive species i.e., interspecific competition is absent. To explore this null expectation, we modeled species dynamics based on the deterministic Ricker model:

$$N_{t+1} = N_t R e^{-\alpha N_t} \quad (2)$$

Population size (N_t) changed as a function of population growth rate R and the effect of intraspecific competition (α). To this deterministic framework, we incorporated demographic stochasticity using random variables to model (a) the number of offspring produced by each adult (R), and (b) offspring survival. Specifically, the number of offspring per adult was modeled as a Poisson random variable with mean $N_t \times R$. Furthermore, offspring survival to generation $t+1$ was modeled as a binomial random variable with probability determined by N_t and α . This corresponds to the Poisson Ricker model as described and analyzed in Melbourne and Hastings (2008, 2009), Dallas et al. (2019), and Dallas and Santini (2020). It is important to note that this is not a neutral model, as species do have different demographic rates and intraspecific competition coefficients.

We explored the scaling between population and community temporal variability by simulating population dynamics across a range of 3,610 plausible combinations

of population growth rate R ([0.9–2.5]) and intraspecific competition α ([0.0001–0.1]) values, equivalent to 10 times the number of studies in the empirical data. Values of R and α were sampled randomly for each species in a given site, with population and community dynamics simulated by starting species at their empirical mean abundance and simulating for 500 timesteps. This served to mirror the empirical species richness observed at each site, and each species population dynamics was simulated using these random values of population growth rate (R) and intraspecific competition (α). While populations limit themselves through intraspecific competition (α), there is no interspecific competition, and parameters for a species were constant over the 500 simulated generations. We calculated population and community temporal variability using these time series, removing species that did not persist in simulations. Community abundance generally tended to be stable over the course of simulations (see Appendix S1: Fig. S1).

Latitudinal signal in temporal variability

Spatial gradients in temporal variability may exist as a function of climatic variability, non-random distribution of species with certain life history parameters, or a myriad of other factors. We examined latitudinal gradients in temporal variability at population and community scales by relating the D statistic measured for each empirical population and community to the absolute latitude for the site, measured as the mean latitude of plots making up the site. The relationship was estimated using generalized linear models (Gaussian family), and we similarly explored how temporal variability scaled with species richness and habitat type. The BioTIME database classifies taxa into 13 groups at the level of the study, allowing some coarse exploration of differences among taxonomic groups. However, taxa are also non-randomly distributed and sampled, and the taxonomic resolution needed to explore evolutionary patterns of temporal variability are important but currently not present in the data. We explore the effect of taxonomic group at this coarse scale in the Appendix S1 (see section on “*Taxonomic differences in population and community-scale temporal variability*”).

Data and code used to reproduce the analyses here are provided on figshare (<https://doi.org/10.6084/m9.figshare.13911275>), and, by mandate, available in Appendix: Data S1.

RESULTS

Temporal variability in populations and communities

Average population temporal variability scaled positively with community variability in both simulated (mean population – community D correlation; $\rho = 0.53$, $P < 0.0001$) and empirical ($\rho = 0.47$, $P < 0.0001$) data (Fig. 2). In the empirical data, we

found that portfolio effects tended to be quite weak, with mean population temporal variability scaling nearly equally to community temporal variability (Fig. 2). Slopes from linear models forced through zero highlight the differences in portfolio effects, as our null model had a much smaller slope in the relationship between community and population temporal variability ($\beta = 0.096$), relative to the marine ($\beta = 1.04$), freshwater ($\beta = 0.71$), and terrestrial ($\beta = 0.82$) habitats in the empirical data (Fig. 2). This was not sensitive to the estimation of temporal variability using the coefficient of variation (see Appendix S1: “*Measuring temporal variability as coefficient of variation*”). This contrasted with observation of a strong portfolio effect in simulated communities where community-scale variability was damped as a result of being a composite measure of multiple different populations. This cause was evident from the effect of the number of species in the community in our null simulations, as increasing the number of species led to much lower community variability relative to more species-poor communities (Fig. 2), estimated here by considering the correlation between species richness and the ratio of population to community temporal variability ($\rho = 0.48$, $P < 0.0001$).

Effect of latitude, species richness, and habitat type

Mean population temporal variability (Fig. 3a, b) and community temporal variability (Fig. 3c, d) were positively associated with absolute latitude (Table 1). This suggests that both populations and communities tended to become more variable toward the poles and less variable near the equator (Fig. 3). Furthermore, sites with higher species richness had more variable temporal community dynamics (Table 1; Appendix S1: Figs. S5, S6). Differences existed among habitat types in both population and community-scale measures of temporal variability (Table 1, Fig. 3), with freshwater habitats having significantly higher population-scale temporal variability relative to marine or terrestrial sites. Interestingly, the observed differences between habitat types were not consistent when scaling from populations to communities, as marine sites did not differ from freshwater sites in community temporal variability (Table 1). We also explored the potential latitudinal signal and effect of species richness on the residuals of the relationship between population and community temporal variability, finding a clear negative effect of species richness – in which increasing species richness reduces the community variability relative to the population variability – in our null model, but there was no such effect for marine, freshwater, or terrestrial sites. A latitudinal signal in the residuals of terrestrial species was observed ($\beta = 0.00026$, $P = 0.002$), suggesting that community temporal variability was slightly elevated at higher absolute latitudes relative to expected population temporal variability (see Appendix S1: Table S2).

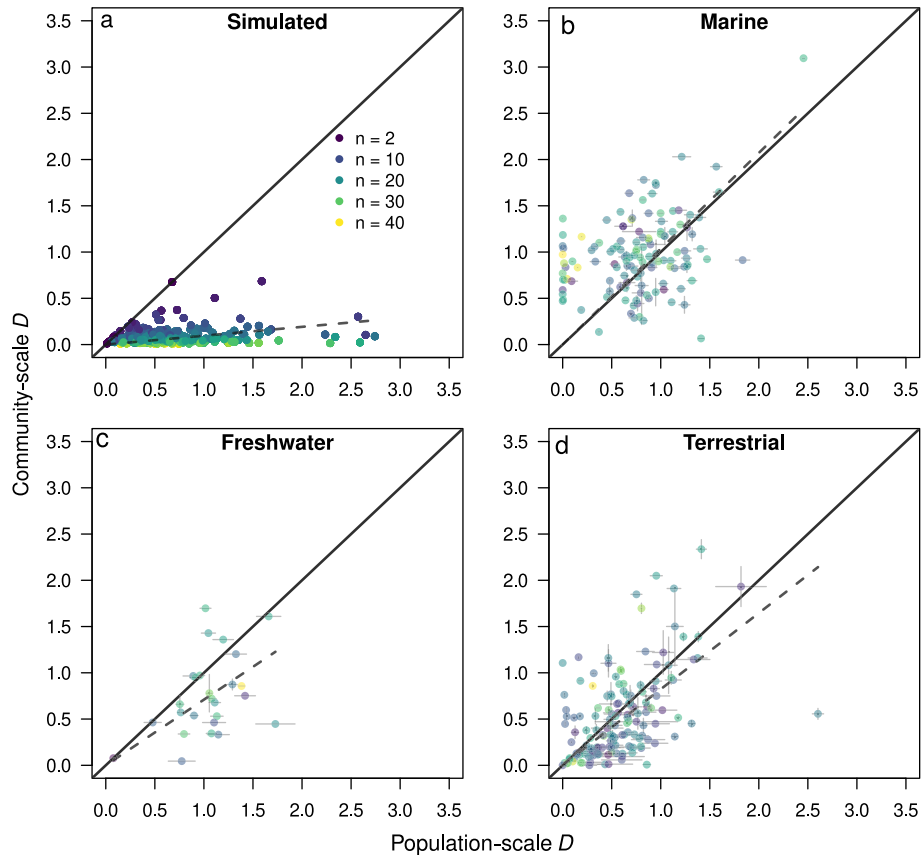


FIG. 2. The relationship between temporal variability (D) at population (x -axis) and community (y -axis) scales, using a theoretical model assuming no species interactions (a) and in empirical communities across freshwater (b), marine (c), and terrestrial (d) environments. While generally positive, suggesting that temporal variability in populations scales to communities, the relationship is quite variable. Error bars represent standard error. Lines correspond to the linear relationship between population-scale and community-scale D (dashed line) and the 1:1 line (solid line).

DISCUSSION

More temporally variable populations result in more variable communities in both null simulations and empirical data. However, we find strong portfolio effects in our simulations – in which the composite variability of the community is reduced as a function of the multiple non-interacting populations – relative to the weak effect in the empirical time-series data. Temporal variability for both populations and communities was greater at higher latitudes, and lower toward the equator. This spatial signal in population and community variability suggests the potential importance of climatic or species distributional differences on resulting temporal variability. We also found that habitats differed in their population and community variability, as freshwater habitats had high population, but low community, measures of temporal variability, compared with marine and terrestrial habitats. This suggests that portfolio effects are likely to differ depending on the environment considered, which could be expected due to the changing competitive landscape, community assembly, species

richness, and species life history (e.g., high population growth rates can result in more temporal variability through cyclic behavior). Together, our findings suggest that temporal variability in dynamics scales between populations and communities more strongly than expected under simple null assumptions, and is also distributed geographically and among habitats non-randomly. Understanding this non-random variability across geographic, climatic, and habitat gradients may provide an insight into the drivers of temporal variability and the potential disconnect in scaling variability from populations to communities.

Finding differences in the relationship between population and community variability between the null model and the empirical data should not be too surprising, as the realism of fluctuating environments, species niche dynamics, and interspecific competition were not incorporated in the null model. However, it is interesting to note that the incorporation of interspecific competition would be expected to enhance the portfolio effect, as interacting populations should promote further regulation of population abundance (Ives et al. 1999, Barabás

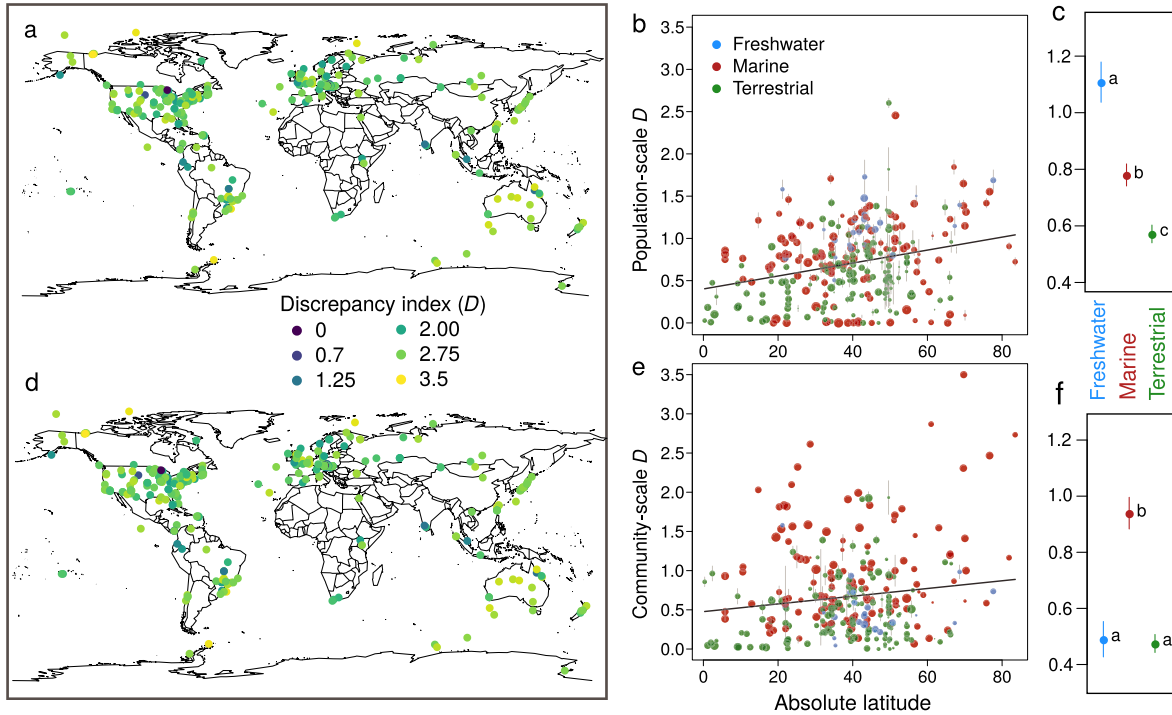


FIG. 3. The spatial distribution of population (a) and community (d) temporal variability, measured as the discrepancy index (D). A clear latitudinal signal existed for population-scale temporal variability (solid line in (b)) and community-scale variability (e), with differences observed across habitat types for both population (c) and community (f) variability. Letters next to values in (c) and (f) indicate significant differences between mean D values. Point size in (b) and (e) are proportional to the number of species present and error bars represent standard error.

TABLE 1. Generalized linear models of population and community temporal variability as a function of latitude, species richness, and realm.

Scale	Variable	Estimate	Standard error	t -value	P -value
Population	Abs latitude	0.0067	0.002	4.43	<0.0001
	Log (richness)	0.0009	0.018	0.05	0.96
	Marine	-0.2496	0.088	-2.83	0.005
	Terrestrial	-0.4350	0.084	-5.19	<0.0001
Community	Abs latitude	0.0039	0.002	2.29	0.0230
	Log (richness)	0.0426	0.020	2.13	0.0339
	Marine	0.1594	0.098	1.62	0.1059
	Terrestrial	-0.2139	0.093	-2.30	0.0220

Notes: Population and community temporal variability both contained a latitudinal signal, while only community temporal variability was influenced by species richness. Relative to freshwater systems, marine and terrestrial populations were less temporally variable at the population scale, with this effect also being true in terrestrial communities. Significant P -values at $\alpha = 0.05$ are bolded.

et al. 2016). The lack of strong portfolio effects in the empirical communities matches the expectations if species are responding similarly to shared environmental drivers and longer term environmental effects are affecting population dynamics and community dynamics in the same way. For example, a gradually warming environment could result in a similar effect on demographic rates across species, suggesting that species would track environmental change as a collective. The pattern in the empirical data also suggests that interspecific interactions

are not constraining community dynamics on the time-scales considered and that community abundance is not near a maximum limit. However, many other possible reasons exist for the discordance between our simple null and the empirical data. Reconciling the results from theoretical models and empirical data is an important research need for understanding the scaling of temporal variability across organizational scales (Ives et al. 1999).

One potentially important reason that we did not observe portfolio effects in the empirical dataset is our

estimation of temporal variability using abundance. In some communities, such as rodents, species body size can differ by an order of magnitude (White et al. 2004). If community dynamics are stable when assessed by energy or biomass, this could result in variability in population size of small-bodied species being balanced by small changes in the abundance of larger-bodied species (White et al. 2004, Ernest et al. 2008). A follow-up analysis that took into account the body size of species in the communities compiled in the BioTIME database could provide an insight into whether communities with species of similar size exhibit stronger portfolio effects and whether variability in community biomass and abundance scales differently. We note that the strong portfolio effects observed in the null model did not depend on implicit assumptions of equal body size, as no compensatory dynamics were included.

In our null expectation, a clear effect of species richness was observed, as more species-rich communities tended to have lower community variability relative to mean population variability (i.e., a clear diversity–stability relationship; Doak et al. 1998, Valencia et al. 2020). However, this pattern was not supported for the empirical communities, as we found a slight positive relationship between community temporal variability and log-transformed species richness. Instead, significant effects were found for latitude and habitat type, which were somewhat correlated with species richness in this dataset (see Appendix S1). This suggests that the relationship between temporal variability and species richness may be unable to be separated observationally from the relationship between temporal variability and variables such as latitude, temperature, habitat type, and many others, or simply that species richness is not inherently related to less variable populations or communities.

The association between temporal variability in population and communities and latitude could have multiple causes, as temperature (Hijmans et al. 2005, Pereira et al. 2017), precipitation (Hijmans et al. 2005), species diversity (Hillebrand 2004), predatory pressure (Roslin et al. 2017), and species body size (Ashton 2002) are all associated with latitudinal gradients. For instance, increased temporal variability at higher latitudes could be driven by greater variability in climate at higher latitudes as interannual variability in temperature increases toward the poles (Pau et al. 2011), and population abundances of plants and animals often respond to variation in temperature (Garsd and Howard 1981, Stenseth et al. 2002, Bouchard et al. 2018). However, precipitation can also drive variation in abundance (e.g., Milner et al. 1999, Lima et al. 2001), and interannual variability in precipitation declines at higher latitudes in the northern hemisphere (Pau et al. 2011). Therefore, if the pattern in temporal variability found here represents response to climatic drivers, this response is either differential with regards to specific climatic drivers or driven by complex interactions between these drivers.

Apart from the multitude of potential underlying causal factors for which latitude is simply a proxy, there are other potential reasons for variation in population and community variability across latitude or different habitat types. For one, the length of the time series may introduce bias as species may appear (invade) or disappear (go extinct) during the time series (Dornelas et al. 2019), meaning that compositional changes could favor certain species and make population-scale temporal variability incomparable with community-scale variability. To account for this, we weighted population-scale variability by the number of years in which the species was recorded at the site (see Appendix S1: Section “*Weighting population-scale variability*”). We also weighted population-scale variability based on the relative abundance of the species, as dominant and rare species may differ in their temporal variability, with clear implications to mean population variability (see Appendix S1: Section “*Weighting population-scale variability*”). Our findings were supported in both supplemental analyses.

There are some limitations to understanding population and community-level temporal variability that will only be addressed by the direct consideration or control of environmental variability and species life history variation. To this end, microcosm experiments examining how temporal variability is influenced by thermal variability, species number, and compositional differences among competing species represent an important research need. Compositional differences over time are a second form of community variability, as discussed in Micheli et al. (1999), but the relationship between our abundance-based measure of community variability and a compositional measure of community variability may provide an insight into how species turnover is associated with raw number of individuals present at a given time. Furthermore, the direct consideration and incorporation of multiple trophic levels could extend examinations of temporal variability to the scale of food webs (Gouhier et al. 2010). A final note relates to the use of the term “stability” to describe temporal variability. Throughout this manuscript, we have avoided referring to this as “stability,” opting instead for *temporal variability*. This avoids the confusion over the multiple potential definitions of *stability* in ecology (Grimm and Wissel 1997, Donohue et al. 2013, Yang et al. 2019), as community stability has been quantified by considering spatial or temporal changes in species diversity, abundance, or composition (MacArthur 1955, Paine 1969, Harrison 1979, Lepš et al. 1982, Doak et al. 1998, Lehman and Tilman 2000, Antão et al. 2020), let alone the more mathematically rigorous definitions of stability (May 1972, 1973, Grimm and Wissel 1997, Allesina and Tang 2012, Donohue et al. 2016).

Portfolio effects and their implications for community stability are fundamental aspects of ecological theory and applications such as maintenance of ecosystem function in response to anthropogenic change (Schindler et al. 2015). The differences observed in temporal

variability across habitat types and latitudinal gradients suggest a need for further empirical and theoretical work. A particularly pressing research need lies in the integration of concepts from spatial synchrony and network research to understand how perturbations may influence temporal variability and subsequent potential portfolio effects. Finally, exploring the disconnect between theoretical models and empirical reality will contribute to the development of realistic and predictive models of population and community dynamics, allowing advances in time-series forecasting, conservation efforts, and coexistence in complex interacting communities.

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