Title: Global assemblage stability is driven by asynchrony shaped by environmental heterogeneity

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Abstract:

Evidence suggests the diversity-stability relationship relies on asynchrony among populations. Yet our limited understanding of how the mechanisms underlying stability and asynchrony manifest across ecological scales prevents reliable forecasts of ecological stability amid ongoing biodiversity change. Here, linking stability, asynchrony and species richness across plant, bird, mammal, amphibian, and fish assemblages worldwide, we unveil a U-shaped diversity-stability relationship, with population- and assemblage-level stability greatest at both low and high diversity. Across taxa, we illustrate how this relationship is predominantly realised through patterns in population asynchrony, which itself is enhanced in communities exposed to greater environmental heterogeneity but erased by human impacts. Together, these findings stress how anthropogenic pressure and losses of environmental heterogeneity jeopardise the asynchrony required for sustaining the stability of natural ecosystems worldwide.

Main Text:

Introduction

Understanding how biodiversity affects the stability of ecosystems has long been a major focus of ecological research (*1–7*). The reliance of humans on the stable supply of abundant life, coupled with the profound changes humans are imposing on the planet, makes understanding this relationship both crucial and urgent. Yet, over 50 years since it was first challenged, the diversity-stability relationship remains unresolved. On one hand, the insurance hypothesis, or portfolio effect, posits that aggregate ecosystem properties (*e.g.*, abundance) vary less overtime in more diverse communities as declines in the abundances in some species are compensated for by increases in the abundances of others (*5*, *8*). However, conflicting evidence has sustained long running debate regarding how diversity affects stability across natural ecosystems worldwide (*2*, *3*). Continued assessments of the diversity-stability relationship suggest the relationship is not always positive across taxa (*9–12*), nor is the pattern consistent across scale, with diversity often having opposing effects on the stability of populations and communities (*13–15*).

Logically, diversity *per se* does not necessarily promote the stability of natural systems (*2*). Instead, asynchrony among coexisting species or populations enhances the stabilising effect of diversity (*16*, *17*). Varying phenological cycles, differing disturbance responses, functional specialisation, and niche partitioning are mechanisms that promote population asynchrony (*16*, *18–20*), thereby benefitting the stability of natural systems. However, the expression of these mechanisms is extrinsically mediated by environmental heterogeneity in space and time (*21–23*). Hence, we can expect that ongoing global change will reshape the environmental heterogeneity underlying population asynchrony and its effects on species interactions (*24*). Moreover, while asynchrony among individuals can buffer populations against environmental stress (*25*, *26*), our understanding of the stabilising effect of asynchrony is largely focused at the community and ecosystem level (*22*, *27*). As a result, we currently cannot reconcile how the mechanisms driving population asynchrony and its stabilising effects within natural systems operate across ecological scales (*13*, *28*), limiting our ability to reliably forecast global ecosystem stability (*29*).

Here, we present a global, multi-taxon empirical synthesis assessing how spatio-temporal drivers of asynchrony and species richness cascade through natural ecosystems to shape population and assemblage stability. We compile 526,519 records of population asynchrony and paired population- and assemblage-level stability from across plant (n = 1,238), bird (10,470), mammal

(2,619), fish (17,310), and amphibian (2,407) assemblage time series worldwide (*30*). Combining these data with spatio-temporally linked estimates of species richness and abiotic environmental heterogeneity we use structural equation modelling (SEM) to evaluate the extent to which different drivers of abiotic heterogeneity influence species diversity and population asynchrony to shape the stability of global biodiversity (Fig 1).

For abiotic heterogeneity we specifically focused on variables concerning landscape complexity and climate variability. More complex landscapes promote niche partitioning and habitat diversity, and mediate how and whether organisms access available resources (*31*). Subsequently, by elevating habitat diversity, more complex landscapes can both increase species richness (*32*) and sustain greater asynchrony between co-occurring populations (*33*, *34*). However, the greater niche partitioning associated with more complex landscapes is expected to reduce interspecific competition (*32*), thereby simultaneously reducing the need for asynchronous dynamics between populations that would otherwise temporally partition available resources. Meanwhile, the changing resource availability and physiological stress associated with differing climate variability regimes can either elevate or limit population asynchrony and species diversity depending on species niche distributions (*35–37*). Alongside forecasted changes in climatic regimes and landscape topography, these contradictory effects of abiotic heterogeneity on patterns of asynchrony require disentangling to determine how heterogeneity mediates stability across natural systems worldwide. Overall, our approach here distils a mechanistic understanding of the nuanced patterns underpinning stability to highlight pathways through which we can promote the stability of natural systems amid ongoing global change.

Stable populations require stable assemblages

While intuitively, assemblage stability arises from the combined effects of population stability and asynchrony, this relationship is underpinned by several auxiliary patterns shaping how stability cascades through ecological systems (Fig. 2). We derived population- and assemblage-level stability from coefficient of variation (*CV*) estimates calculated from a comprehensive compilation of temporal nested population and assemblage abundance records across plants, birds, mammals, amphibians, and fish (*30*). We estimated population asynchrony using a measure correlating the standard deviations among the abundances of co-occurring populations to the standard deviation in total abundance across their assemblages, referred to as community-wide synchrony (φ_S) (*38*).

Asynchrony then equals 1 - φ_S and lies on a bounded scale from 0 (perfect synchrony) to 1 (perfect asynchrony). We then constructed a hierarchical SEM quantifying the causal pathways through which environmental heterogeneity affects species diversity and population asynchrony to influence population- and assemblage-level stability, positioning assemblage stability as the terminal dependent outcome and population stability and asynchrony as intermediate mediating variables (Fig. 1). As such, we explicitly model the pairwise interactions across both population- and assemblage-level stability and population asynchrony, within a wider network of (a)biotic covariates.

Firstly, unstable assemblages do not have stable populations (Fig. 2A). We found a weakly positive relationship between population- and assemblage-level stability, underpinned by a (triangular relationship. While unstable populations do exist within stable assemblages, assemblages largely consisting of stable populations are more likely to be more stable themselves (see Appendix S1). However, the arrangement of our stability data relative to its 1:1 reference (*i.e.*, consistent stability across populations and assemblages) indicates that stable populations do not persist within unstable assemblages. This finding carries major conservation significance in showing how conservation interventions aimed at ensuring the stability of natural systems should prioritize their efforts at the assemblage-scale. Strong interspecific density-dependent feedbacks promote community stability by maintaining stable abundances across the more abundant species within a community (*39*). Presumably, however, within unstable assemblages, constant fluxes in abundance across core populations and/or the prevalence of transient species prevent the establishment and maintenance of these interspecific interactions needed for the abundance of any one population to remain constant through time (*40–42*). Conservation biology was founded to mediate and mitigate the effects of global change on the dynamics of threatened species and populations (*43*). Despite efforts to expand the cross-disciplinary nature of conservation research, there remains a disconnect between assessments of species extinction risk and assemblage-level monitoring (*44*). Indeed, the International Union for Conservation of Nature (IUCN) Red List of Threatened Species has long quantified extinction risk based on trends in population size (*45*, *46*). Yet, echoing calls for the targeted conservation of taxonomically related or functionally similar species (*i.e.*, assemblage-level conservation) (*47*), our finding that unstable assemblages cannot support stable populations argues for greater cross-scale integration of conservation efforts.

Secondly, although population asynchrony strongly affects assemblage stability (Fig. 2B), we found little evidence that it influences population stability (Fig. 2C). Asynchrony is an important driver underlying community stability (*22*). Greater asynchrony between populations reduces resource competition and sustains differentiated responses to recurrent disturbances, allowing for more diverse, stable assemblages (*16*, *17*). Accordingly, we observed that more asynchronous assemblages typically exhibit greater stability (Fig. 2B). Yet, the reverse is not as definitive; not all stable assemblages display greater asynchrony. Asynchrony among co-occurring populations can destabilise key phenologically timed interactions (*48*). For instance, assemblages with well-defined trophic structures require synchrony between populations at different trophic levels to ensure that peaks in the abundances of consumer populations coincide with peaks in their food sources (*49*). Meanwhile, we observed population asynchrony to have little effect on population-level stability (Fig. 2C). Logically, one might assume that the spatiotemporal partitioning of resources associated with greater asynchrony, hypothesised to benefit assemblage stability through reduced competition, likely also benefits the stability of their constituent populations. However, with delayed responses to extrinsic stressors often a strong predictor of population performance (*50*), the asynchrony observed within assemblages over time t may be more impactful on the stability of populations over time $t+1$. The community-wide synchrony (φ_S) measure we used to estimate population asynchrony links coincident measures of variance in population and assemblage abundance. Thus, while the measure directly links population asynchrony to variance in assemblage abundance, it does not consider any delayed effects of population asynchrony on population stability.

Finally, it is difficult to ignore the effect human activities have on our observed stability-asynchrony patterns. Although our data do not allow us to attribute causality to this visual pattern, environments exposed to greater human impact typically appear to support unstable assemblages comprising unstable, more synchronous populations (Fig. 2). Whilst we cannot determine whether anthropogenic impacts at the assemblage or population level are responsible for initiating the patterns we show here, across global ecosystems human activities have routinely been illustrated to have significant impacts across mechanisms associated with population- and assemblage-level stability and population asynchrony (*28*, *51–53*). Particularly concerning is the number of assemblages underlain by low population asynchrony (*i.e.*, high synchrony) exposed to high levels of human impact (Fig 2B). Increases in synchrony across ecological time series can signal

imminent system collapse (*54*, *55*). We do not discern here whether the low asynchrony estimates we present reflect the normal state of the associated assemblages or whether asynchrony across these assemblages is declining over time. However, evidently, further effort to understand patterns of change in asynchrony is warranted to facilitate adaptive and timely conservation responses across these imperiled assemblages.

A diversity-dependent effect of diversity?

We uncover a nonlinear relationship between diversity and stability that persists at the population and assemblage levels, and across taxa; although the shape of the relationship is not consistent across taxa (Fig. 3). We extracted spatially linked estimates of species diversity from species richness data for each assemblage's corresponding taxonomic group: vascular plants (*56*); land birds and mammals (*57*); amphibians (*58*, *59*); algae, seabirds, marine mammals, and fish (*60*). We then modelled species diversity as an intermediary mediator variable within our SEM, influenced by underlying abiotic heterogeneity, whilst affecting the realisation of population- and assemblage-level stability and population asynchrony (Fig. 1). Globally, we demonstrate a U-shaped relationship between diversity and population- and assemblage-level stability (Fig. 3A & B). As such, both population and assemblage stability peak at very low and very high diversities. While consensus suggests a positive association between diversity and stability across natural systems (*61–67*), consistently conflicting evidence has sustained longstanding debate regarding the diversity-stability relationship (*9*, *13–15*, *68–71*). Our unveiling of a nonlinear diversity-stability relationship reinforces the idea that this debate has persisted not because our understanding is inconclusive, but because the pattern is non monotonic (*2*).

A U-shaped diversity-stability relationship is grounded in both ecological theory and empirical evidence from natural systems worldwide (*67*). Specifically, closer examination of our stability-diversity plots reveals the right-hand portions of the relationships between population- and assemblage-level stability with diversity (*i.e.* the stabilising effect of increasing diversity) correspond with the latitudinal diversity gradient (Fig. 3A & B). Consistent with low latitude tropical assemblages possessing the necessary diversity levels for sustaining greater population and assemblage stability, both population- and assemblage-level stability increase from high to low latitude. Indeed, this pattern is consistent with latitudinal gradients observed in the stability of moth and forest communities (*71–73*). This section of the diversity-stability relationship also

validates the expectation that hyper-diverse tropical ecosystems destabilise rapidly following declines in their biodiversity (*74*). However, extremely low-diversity mid-latitude systems appear to also possess greater stability (*i.e.*, the left-hand curves, Fig. 3A & B). Low phylogenetic diversity can enhance the stability of natural systems, although the realisation of this effect depends on the functional identities of the species present, with greater stabilisation in assemblages comprising species that prioritise survival over growth and reproduction (*70*, *75*). However, the concentration of these stable, low diversity systems at the mid-latitudes also raises a fundamental question: are these systems truly naturally stable? Globally, mid-latitude regions are associated with a high density of farming and crop production (*76*). Accordingly, these regions comprise highly human-modified environments characterised by lower diversity, but whose stability is artificially maintained to secure agricultural yields (*77*, *78*).

Consistent with established evidence, our findings show the impacts of diversity on assemblage stability to be primarily affected through the mediating effects of population asynchrony (Fig. 3C). Our hierarchical SEM framework allowed us to partition the relative pathways through which each of our underlying variables of species richness, population asynchrony, and population stability influence assemblage stability (Fig. 1). Specifically, therefore, we were able to quantify the proportional extent (::) to which the effect of species richness on assemblage stability is realised indirectly through its effects on population stability and asynchrony. Across taxa, ≥60% of the effect of species richness on assemblage stability manifests through the effect of diversity on population asynchrony, with diversity having a negligible direct impact on assemblage stability (Fig. 3C). The exception to this pattern are mammals, in which neither the direct effect of species richness nor its effects via asynchrony are major determinants of assemblage diversity. Instead, species richness largely affects mammal assemblage stability via its effects on population stability (:: = 0.604 [95% CI: 0.0600, 0.608]). Our findings agree with an overwhelming recent body of work, focused largely on plant assemblages, evidencing the central role population asynchrony plays in modulating the stabilising effect of increased diversity (*22*, *49*, *63*, *79–87*). However, our findings highlight that the interactions among diversity, asynchrony, and stability across natural systems are complex and multifaceted. Thus, it is not solely asynchrony that determines stability (*88*), nor can we assume the effects of asynchrony on the diversity-stability relationship manifest consistently across ecosystems and taxa.

Heterogeneity affects stability through asynchrony, not diversity

Consistent with evidence that climatic variation has a strong effect on the relative asynchrony among co-occurring species (*89*), we report environmental heterogeneity to almost ubiquitously mediate assemblage stability through its effects on population asynchrony (Fig. 4). We quantified drivers of abiotic environmental heterogeneity using measures of landscape structural complexity and climate variability. Specifically, we isolated geometric measures of fractal dimension and rugosity associated with each assemblage's local environment from maps that describe geometric complexity patterns across global land and seascapes (*90*). Fractal dimension describes the convolution of a surface, whilst rugosity is a measure of true surface area (*91*, *92*). Using Copernicus ERA5 climate records (*93*), we quantified climate variability using four measures of the temporal variability in temperature and precipitation experienced by each assemblage over their survey timeline: temperature periodicity, temperature autocorrelation, rainfall periodicity, and rainfall autocorrelation. Briefly, temporal autocorrelation describes the predictability of a time series, with negative and positive autocorrelation reflecting transitions between more disparate and more similar conditions, respectively. Meanwhile, periodicity refers to the frequency of variation in a time series, described along a gradient from more frequent, abrupt variability to slower, less frequent oscillations (*94*). Within our hierarchical SEM, we then modelled our temperature and rainfall periodicity and autocorrelation variables as confounding independent variables (Fig. 1), allowing us to simultaneously model the direct and indirect pathways through which the effects of each environmental covariate propagate through natural systems to shape patterns in population- and assemblage-level stability.

While abiotic heterogeneity largely affects assemblage stability via its effects on population asynchrony, important inconsistencies are evident across taxa. Firstly, rugosity, temperature periodicity, and rainfall appear to have a marginally greater effect on the stability of bird assemblages via their impacts on species richness rather than population asynchrony (Fig. 4B, C, D & F). Climate and coarse-scale topography have been demonstrated as key drivers of bird species richness across the Americas, with variability in temperature and precipitation, particularly recurrent heatwaves and droughts, major determinants of stability across North American bird assemblages (*95*, *96*); which we note are a major contributor to the dataset used here. The high dispersal capacity of many bird species likely diminishes the effect of fine-scale heterogeneity on their population dynamics and viability. Instead, patterns in evapotranspiration associated with the

elevational gradients of more complex landscapes impact how bird species move across regional landscapes (*97*). Likewise, regional climate shifts can change the biogeographical movements of long-distance migratory bird species (*98*). With migratory species being an important component of many bird assemblages, changing how these species move among different communities will have knock-on effects on species compositions and community abundances. Lastly, it is difficult to disentangle the pathways through which temperature variability affects the stability of natural systems (Fig. 4A & C). Across the globe, populations of the same or similar species vary considerably in their sensitivity to climate variability following their acclimation to local climate regimes (*99*). Hence, large error distributions are to be expected when assessing the effects of climate variability on global biodiversity. However, temperature in particular, is a pervasive determinant of individual physiology and performance, population dynamics and viability across taxa (*100*, *101*). Subsequently, it is likely that temperature variability has more pronounced effects across all pathways and variables underlying population- and assemblage level stability.

Discussion

Revealing a non-linear empirical relationship between diversity and stability across global ecosystems, our findings present a resolution for the long-running diversity-stability debate, explaining the lack of consistent effects of diversity on stability. Moreover, consistent with previous evidence (*22*, *79*, *80*, *83*, *84*, *86*), we show that this nuanced relationship is largely determined by the intermediary effects of population asynchrony. Despite efforts to evaluate the role of asynchrony across natural ecosystems, we still lack insight into the environmental drivers of stability and asynchrony, especially how these effects cascade through natural systems (*34*, *36*, *72*). Here, our findings support the importance of climatic variability and landscape complexity in mediating how population asynchrony affects stability across populations and assemblages worldwide. Environmental heterogeneity, enhanced by landscape complexity and climate variability, promotes spatial-temporal partitioning of environmental resources. Whilst temporal partitioning allows more populations to utilise the same resources (*37*), spatial partitioning promotes beta diversity, and selects for differing demographic profiles among populations, thus generating asynchronous dynamics across communities (*102*, *103*). Indeed, such is the effect of heterogeneity on population asynchrony, that increases in asynchrony under extreme climate

variability are thought to buffer assemblage and community stability despite expected declines in species richness (*36*).

However, the maintenance of population asynchrony by abiotic heterogeneity also underpins a key vulnerability of population- and assemblage-level stability. Climate forecasts indicate that highly variable climate regimes are to become increasingly commonplace across natural environments, comprising an increase in the recurrence of extreme disturbance events (*104*). Frequent extreme disturbances that result in highly correlated mortalities across co-occurring populations and species will enforce greater synchrony among the affected populations (*37*). Likewise, a consistent theme across our findings here is the adverse effect of anthropogenic activity on the stability of natural systems. Through the removal of habitat diversity and microclimates, the anthropogenic homogenisation of natural landscapes decreases population asynchrony inhibiting the capacities for species to respond to climate shifts (*105*). Notably, we evidence how population asynchrony and both population- and assemblage-level stability are all lowest across more human impacted environments. Concurrently, global change threatens population asynchrony across global assemblages, pushing global ecosystems towards imminent collapse. More alarmingly, our demonstration of the complex network of causal drivers through which abiotic heterogeneity, diversity and asynchrony affect stability highlights how quickly this collapse could cascade through affected systems. Indeed, a loss of heterogeneity undermines population asynchrony, a loss of asynchrony undermines assemblage stability, a loss of assemblage stability undermines population stability, and a loss of population stability will further exacerbate assemblage destabilisation. Evidently, preserving the stability of global biodiversity requires that we conserve the abiotic heterogeneity underpinning population asynchrony (*72*).

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Supplementary Materials:

Materials and Methods [1535 words]

Supplementary Text

Figs. S1 - S3

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Figures & Tables

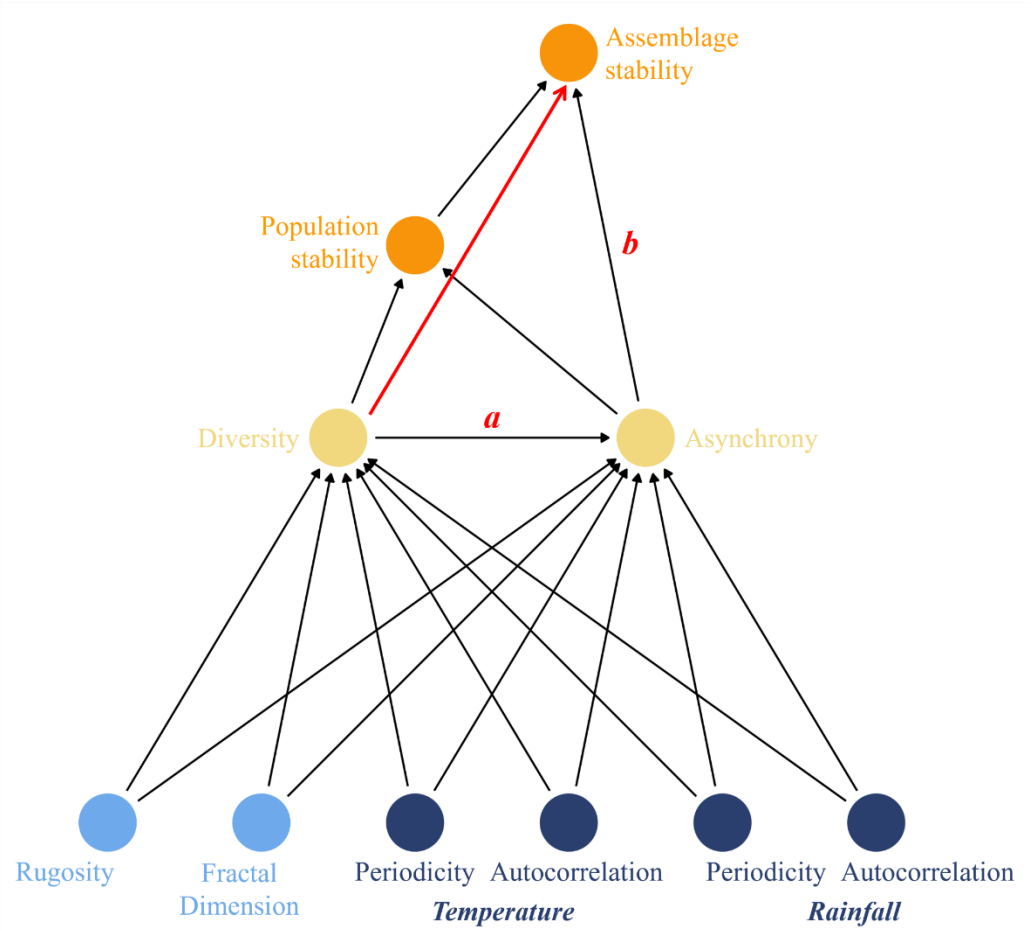


Figure 1. We used a network of causal pathways to model how environmental heterogeneity influences population- and assemblage-level stability via the mediating effects of diversity and asynchrony. We used a structural equation modelling framework to quantify the underlying effects of spatio-temporal environmental heterogeneity (specifically, fractal dimension [D], rugosity [R], temperature periodicity [β_T], temperature autocorrelation [a_T], rainfall periodicity [β_R], and rainfall autocorrelation [a_R]) on each of the biotic attributes of diversity, population asynchrony, and population- and assemblage-level stability. The hierarchical framework we used ensured we could partition the direct and indirect pathways through which the causal effects of underlying variables cascade through to affect population- and assemblage-level stability. For instance, diversity can influence assemblage stability both directly (red arrow) and indirectly via population asynchrony (pathways a and b).

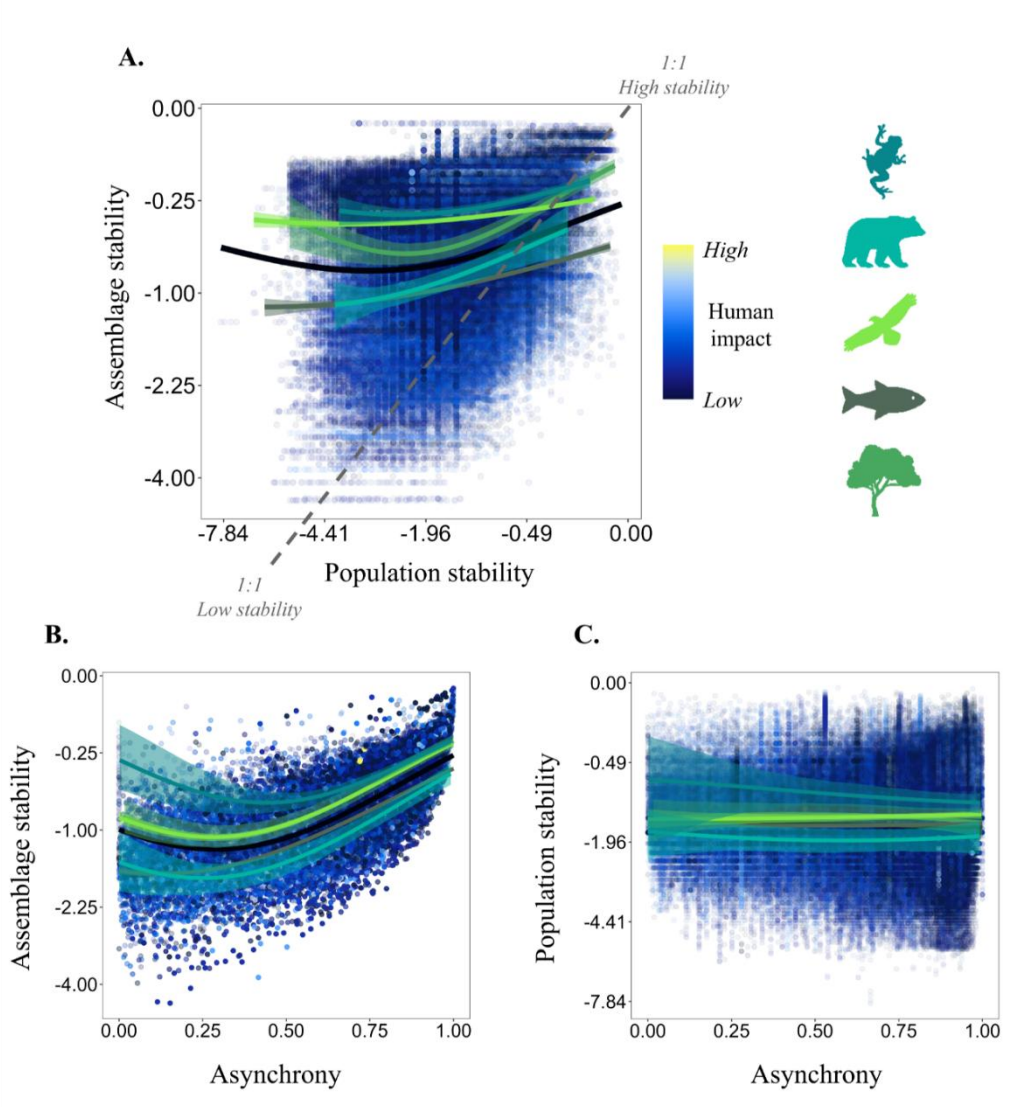


Figure 2. Population-level patterns of stability and asynchrony combine to promote assemblage stability across taxa. The pairwise relationships between: **(A)** temporal variation in total assemblage abundance and the abundance of their constituent populations, with the dashed line reflecting the 1-to-1 relationship; **(B)** population asynchrony and assemblage stability; and **(C)** population asynchrony and population stability. We quantified stability as the coefficient of variation (CV) in population or assemblage abundance and display all CV estimates on an inverted scale such that higher values reflect reduced temporal variability (*i.e.*, greater stability). Across all panels, the solid black line represents the grand-mean pattern estimated across 30 rarefaction iterations, with the coloured lines corresponding to the separate patterns observed in plants, fish, birds, mammals, and amphibians. Error is shown as 95% CI. Point colour reflects the level of human impact associated with each population's local habitat.

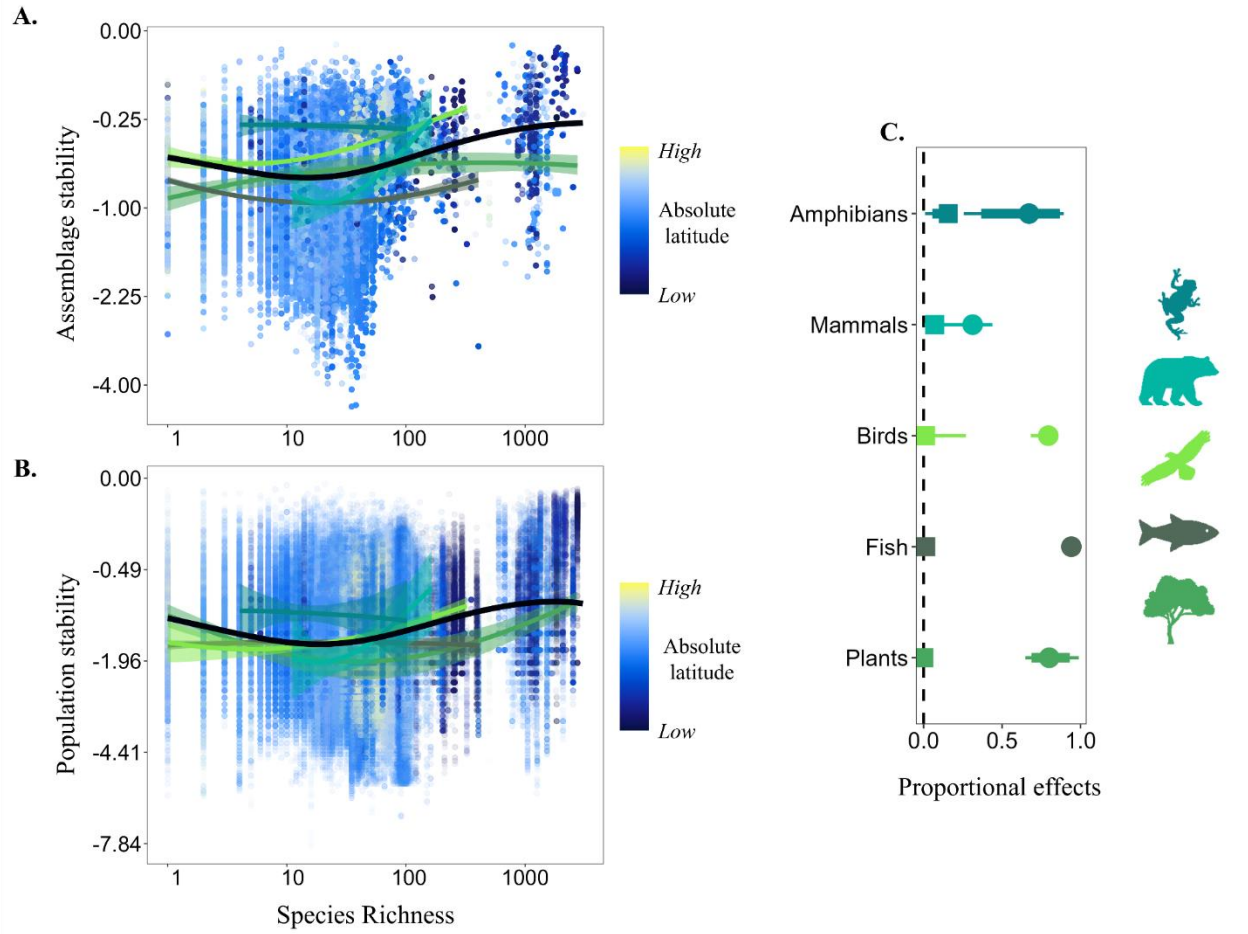
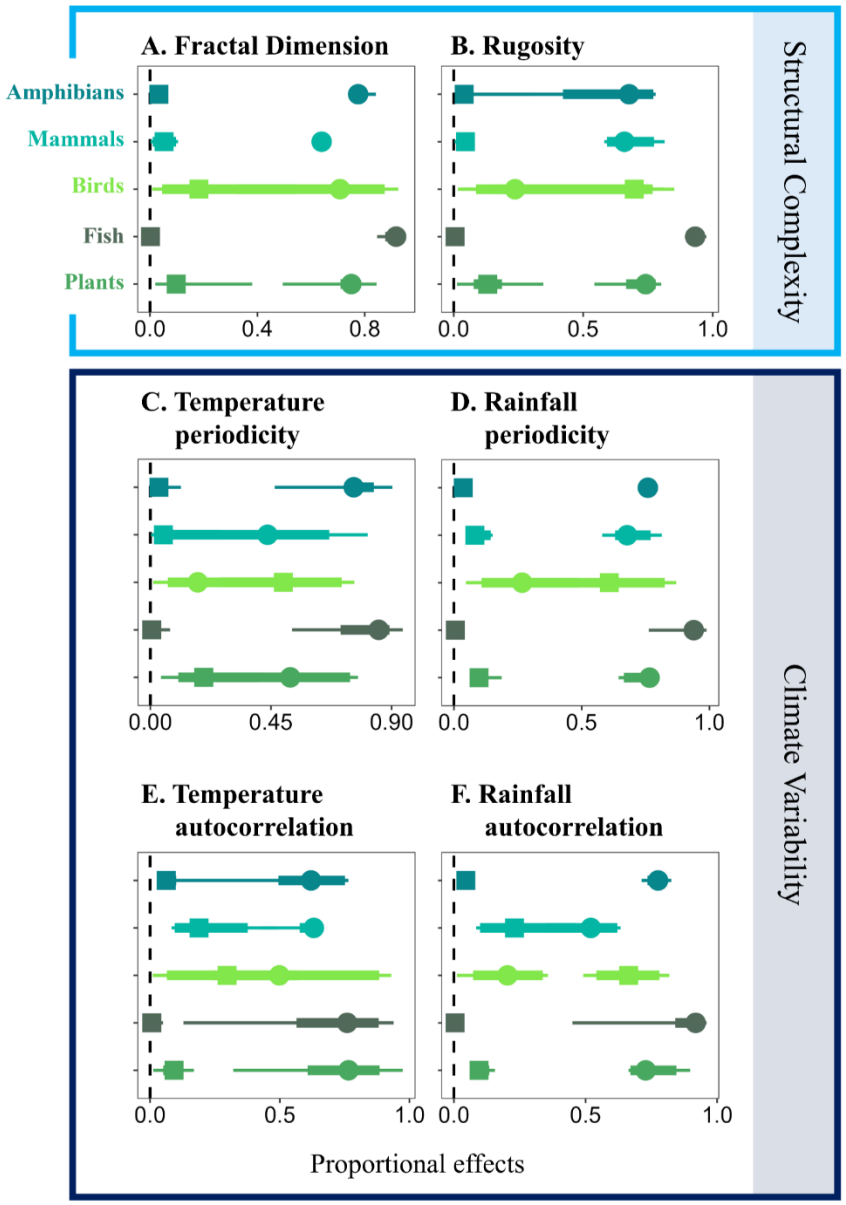


Figure 3. Diversity maintains a nonlinear relationship with both population- and assemblage-level stability, a pattern that is primarily mediated by between-population asynchrony. The relationship between species richness and stability in **(A)** population abundance and **(B)** total assemblage abundance. Note, for clarity species richness is displayed on a $\log_{10}$-transformed scale. Across both panels, the solid black line represents the grand-mean pattern in species richness and system stability across 30 rarefaction iterations, with the coloured lines corresponding to the separate patterns observed in plants, fish, birds, mammals and amphibians. Point colour reflects each assemblage's absolute latitude. **(C)** Comparison of the causal effects of diversity on assemblage stability, manifesting directly (squares) versus through the effect of population asynchrony (circles). Across all panels, error is displayed as 95% CI.



821

822 **Figure 4. Abiotic heterogeneity mediates the diversity-stability relationship through its**
823 **effects on population asynchrony.** Proportional posterior draws comparing whether the causal
824 effects of **(A)** fractal dimension, **(B)** rugosity, **(C)** temperature periodicity, **(D)** precipitation
825 periodicity, **(E)** temperature autocorrelation, and **(F)** precipitation autocorrelation, on assemblage
826 stability manifest via the mediating effects of species diversity (squares) or population asynchrony
827 (circles) across plants, fish, birds, mammals and amphibians. Across all panels, error is displayed
828 as 95% CI. Across all panels, the vertical dashed lines indicate the no-effect position, with the
829 interval bars showing the 95% CI bounds estimated from 30 rarefaction iterations.

Supplementary Materials for

Global assemblage stability is driven by asynchrony shaped by environmental heterogeneity

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The PDF file includes:

Materials and Methods [1535 words]

Supplementary Text

Figs. S1 - S3

References (106 - 115)

Materials and Methods

Our methodology comprised the following sequence of steps: [1] quantifying assemblage- and population-level stability, and population asynchrony, [2] isolating local species richness estimates, [3] establishing patterns in drivers of heterogeneity, [4] modelling the causal relationships through which these drivers of heterogeneity modulate the effects of asynchrony and diversity on population- and assemblage-level stability. All analyses were carried out in R (*106*), with all code to be archived open access on Zenodo following journal submission.

Quantifying stability and asynchrony indices

Patterns in assemblage- and population-level stability and population asynchrony were evaluated using abundance time-series data from the BioTIME database (v2.0) (*30*). We extracted all BioTIME abundance records with associated data detailing taxonomic classifications, survey location, and survey dates. Using the corresponding functions from *BioTIMEr* (*107*), we gridded these records into equal-area regions (~96 km^2) and applied rarefaction resampling (30 resampling iterations) to ensure a standardised spatial extent and sampling effort. Focusing only on assemblages surveyed on three or more separate occasions, we then sequentially generated matrices for each assemblage, detailing recorded changes in the abundance of their constituent populations over time. From each assemblage matrix, we extracted the temporal sequence of total abundance (populations pooled) and the temporal sequences of the individual population abundances. Next, we computed the coefficient of variation (*CV*) for each abundance time series. At the assemblage level, these *CV* estimates provided a measure of each assemblage's relative temporal instability, calculated as the standard deviation of total abundance divided by the mean total abundance. At the population level, we omitted any leading zeros from each time series before computing the relative temporal instability in population abundances. We then square-root-transformed our population- and assemblage-level *CV* estimates to remove any signal arising from Taylor's power law (see Appendix S2). During the analyses described below, we maintained our population- and assemblage-level *CV* estimates on a positive scale, such that higher estimates corresponded with greater instability. However, before visualising our analysis outputs, we inverted all *CV* estimates to a negative scale with higher values indicating greater stability.

Following the computation of population- and assemblage-level stability, we quantified the extent of asynchrony across population abundance records within each assemblage. For each

assemblage, we computed asynchrony using the community-level synchrony (φ_S) formula described in Loreau *et al*. (*38*) (Equation 1), which relates the standard deviations across *n* population-level abundances (σ_i) to the standard deviation of their overlying total assemblage abundance (σ_A).

$$\varphi_S = \frac{\sigma_A^2}{\left(\sum_i^n \sigma_i\right)^2} \quad (1)$$

With asynchrony then equal to 1 - φ_S. To compute σ_i, we used the full abundance time series available for each population, retaining any leading zero abundance counts. Finally, we filtered our data sample to remove any entries for which corresponding estimates of population- and/or assemblage-level instability could not be obtained, as well as any entries collected before 1940 (due to a lack of climate data pre-1940s; see *Quantifying drivers of heterogeneity*).

Quantifying species diversity

We estimated the local diversity associated with our estimates of population- and assemblage-level stability and asynchrony from global maps detailing high-resolution patterns in species richness across various taxonomic groups. Using the species identities and GPS locations assigned to each population in BioTIME, we linked each population in our sample to species richness estimates for their corresponding taxa. For terrestrial plant species, we extracted species richness estimates from maps predicting global vascular plant richness trends using machine-learning algorithms linking species distributions and abiotic predictors (*56*). Terrestrial bird and mammal species richness patterns were sourced from global area-of-habitat maps that combine IUCN range estimates with the availability of suitable habitats (*57*). Amphibian species richness patterns were sourced from global maps generated during assessments of global conservation efforts (*58*, *59*). Finally, global maps used to establish marine conservation priorities (*60*) were used to determine species richness patterns across algae, seabirds, marine mammals, and fish. We subsequently excluded population and assemblage records for which species richness data could not be sourced.

Quantifying drivers of environmental heterogeneity

First, we quantified drivers of spatial environmental heterogeneity using measures of structural habitat complexity. Specifically, we used the geometric measures of fractal dimension (*D*),

rugosity (R), and height range (ΔH), which describe how landscape topography across the Earth's surface influences the distribution of natural habitats and supports niche differentiation (*90*). Briefly, D describes the convolution of a surface; R is a measure of true surface area; and ΔH is the difference between maximum and minimum elevation (*91*, *92*). We used the GPS coordinates associated with each population in BioTIME to extract estimates of D, R, and ΔH from maps depicting patterns in the three geometric measures across global land and seascapes (*90*). Note, following extraction, we omitted entries for which $R = 0$, $\Delta H = 0$ and $D = 2$, as these locations defy geometric constraints, before $\log_{10}$-transforming our R and ΔH estimates.

Next, we quantified drivers of temporal environmental heterogeneity using four measures capturing temporal variability in local temperature and precipitation regimes: temperature periodicity (β_T), temperature autocorrelation (a_T), rainfall periodicity (β_R), and rainfall autocorrelation (a_R). We derived global mean monthly precipitation and temperature estimates from hourly climate records (1940-2026) sourced from the Copernicus ERA5 climate program (*93*). We isolated the specific monthly temperature and precipitation records for each population in our sample by using each population's GPS coordinates and survey dates to match records in both space and time. We then computed autocorrelation estimates from these monthly temperature and precipitation sequences using the *colourednoise* package (*108*), before applying a power transformation (y^5) to our temperature autocorrelation estimates to reduce negative skew. Next, we estimated the periodicities of the monthly temperature and precipitation sequences as the negative slope coefficients of the log-log relationships between the spectral density and frequency properties of each temperature and precipitation time series (*109*).

Finally, to account for any anthropogenic influence on our derived estimates of species richness, stability and asynchrony, we established a *Human Impact* (*HI*) variable reflecting the level of exposure of our assemblages to anthropogenic pressures across their local environments. For each assemblage and its corresponding populations, we extracted *HI* from a comprehensive synthesis of land-use satellite imagery, forest-loss modelling, livestock-density data, and commercial-fisheries monitoring data (*110*). Specifically, we used the location details associated with each assemblage/population in BioTIME to determine the level of human impact documented for their local environment.

<u>Quantifying causal inference</u>

To evaluate how spatio-temporal environmental heterogeneity influences the roles of diversity and asynchrony in shaping the stability of natural systems, we used a structural equation modelling framework (SEM) implemented in *brms* (*111*). Specifically, we used SEM to quantify the hierarchical causal relationships between our measures of heterogeneity, species diversity, population asynchrony, and population- and assemblage-level stability (Fig. 1). Before parameterising our SEMs, we conducted tests of collinearity across our measures of environmental heterogeneity: D, R, ΔH, β_T, a_T, β_R, and a_R, using variance inflation factors (VIFs). Assessing initial VIF scores obtained from these tests resulted in our exclusion of ΔH from further analyses due to very high collinearity (VIF = 304.30), with a subsequent retest of VIF across our remaining variables confirming little evidence of any further collinearity (VIF: $R = 1.23$, $D = 1.06$, $\beta_T = 1.21$, $a_T = 1.32$, $\beta_R = 1.80$, $a_R = 1.92$). We then implemented our SEM (Equation 2) using default weakly informative priors to reflect the cascading network of pathways through which the confounding effects of environmental heterogeneity ($X\beta_i$) propagate through the mediating effects of diversity (*richness*) and asynchrony (*async*) to influence population- and assemblage-level stability ($stability_P$ and $stability_A$, respectively) (Fig. 1):

$$
\begin{aligned}
stability_A &\sim gamma\left(\alpha_1 + poly\left(stability_P\right) + poly(async) + poly(\log10(richness)) + \boldsymbol{X\beta_1} + u_1 + \varepsilon_1\right) \\
stability_P &\sim gamma\left(\alpha_2 + poly(Async) + poly(\log10(richness)) + \boldsymbol{X\beta_2} + u_2 + \varepsilon_2\right) \\
async &\sim xbeta\left(\alpha_3 + poly(\log10(richness)) + \boldsymbol{X\beta_3} + u_3 + \varepsilon_3\right) \\
richness &\sim negbinomial\left(\alpha_4 + \boldsymbol{X\beta_4} + u_4 + \varepsilon_4\right)
\end{aligned}
\tag{2}
$$

Where $X\beta_i$ comprises our environmental heterogeneity variables: D, R, ΔH, β_T, a_T, β_R, and a_R, as well as the fixed error terms of *HI* and absolute latitude. The term u_i then represents a random grouping term to account for nested population-level attributes within assemblages. Including the confounding effects of D, R, ΔH, β_T, a_T, β_R, and a_R across each SEM component allowed us to not only explicitly quantify the separate effects of these environmental covariates on each of our variables of species richness, population asynchrony, and population- and assemblage-level stability, but also to partition the direct and indirect pathways through which they influence assemblage stability (Fig. 1). Likewise, the structure of our SEM ensured that we could partition the extent to which species richness affects assemblage stability, both directly and indirectly through the pathway of population asynchrony. We used expected log predictive density (ELPD) estimates from preliminary leave-one-out (LOO) comparisons to determine whether to model the individual causal pathways within our SEM framework (*e.g.*, $R \rightarrow$ *richness*) as linear or nonlinear.

In all cases, a polynomial approach was deemed most appropriate, except for the direct pathways linking β_R to asynchrony, diversity and assemblage stability, and R to population stability, for which linear approaches were used, since there was no statistical value to adding the additional complexity. Collating our data into the coarse taxonomic categories of plants (terrestrial plants and algae), birds (both land and seabirds), mammals (marine and terrestrial), amphibians, and fish, we ran our SEM using a Monte Carlo resampling approach, with models implemented separately on 5% data subsamples extracted for each taxonomic category across each of our 30 rarefied data samples. Each model comprised a single chain of 2000 iterations. Model outputs were then pooled both within and across taxonomic groups to generate taxonomic and grand mean estimates.

Supplementary Text

Appendix S1: The impact of dominant species on observed stability-diversity patterns

Focusing only on temporal stability patterns in the abundance of the most dominant species within each assemblage does not change the relationships we observed between population- and assemblage-level stability (Fig. S1A), and species richness and population stability (Fig. S1B). We evaluated how isolating only the abundance records of the most dominant species within each assemblage could be expected to change our observed patterns, thus providing a reference for how sensitive our observed stability patterns are to changes in the stability of the most dominant species across each assemblage. We identified the most dominant species as those with the highest mean abundance across an assemblage time-series. On occasions when multiple species displayed equally high mean abundances within the same assemblage, each species was retained for this sensitivity analysis. This sensitivity test entailed repeating our analyses exploring the relationship between population- and assemblage-level stability and between population stability and species diversity using only population stability estimates derived for the most dominant species in each assemblage. Both models were implemented in brms, initialised with uninformed priors, and included absolute latitude and assemblage identity as random effects variables. As in our original models, ELPDs estimated using LOO comparison confirmed polynomial distributions to be the most appropriate fit for both models. Both sensitivity models were run using a Monte Carlo resampling approach, with each model repeated across 5% data subsamples extracted for each of our 30 rarefied data samples, with each repetition comprising a single chain of 2000 iterations.

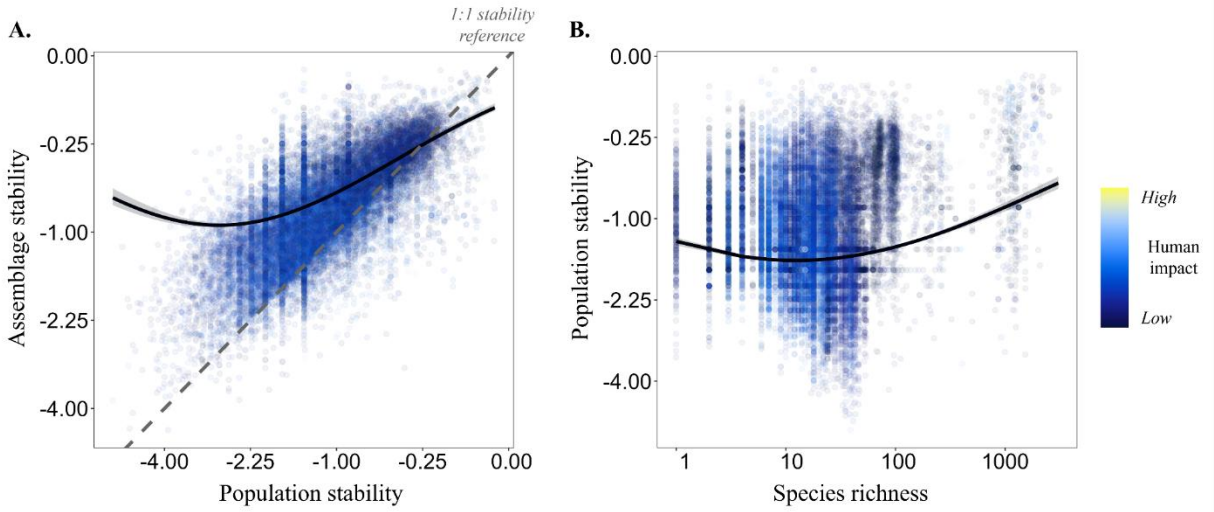

Figure S1. Considering only temporal stability patterns in the abundance of the most dominant species within assemblages does not change our observed patterns in population *vs* assemblage stability or diversity *vs* population stability. (A) The relationship between temporal variation in the abundance of the most dominant species within each assemblage (*i.e.,* highest mean abundance) and total assemblage abundance, with the dashed line indicating the position of equal population and assemblage stability. **(B)** The relationship between species richness and the stability of the most dominant species within each assemblage. Across both panels, the solid black line represents the mean pattern for each relationship, estimated from 30 rarefaction iterations, with error displayed as 95% CIs. Point colour reflects the level of human impact associated with each population's local habitat.

Appendix S2: Assessing the effect of Taylors Power Law on measures of stability

Previous work has suggested that Taylor's Power Law (TPL) can bias crop yield stability records reliant on coefficient of variation (*CV*) estimates derived from abundance or biomass time-series data (*112*). Briefly, TPL posits that, due to a linear association in the log-log relationship between sample variances and means, *CV* estimates will decrease as sample means increase (*113*). Indeed, TPL is evident in the relationship between our population-level *CV* estimates and their associated sample mean abundances (Fig. S2). A linear log-log relationship between the variances and mean estimates obtained from our population abundance time-series ensures that more abundant populations are more likely to achieve greater stability (Fig. S2A & B). One method suggested for removing any mathematical artefacts associated with TPL is the Power Law Residuals framework (POLAR) (*114*). Here, we applied the POLAR framework to our estimates of population-level *CV*s to compute adjusted *CV* estimates (CV_A). Curiously, however, these CV_A estimates maintained evidence of an inverted TPL, with stability now negatively correlated with mean abundance (Fig. S2C). Thus, rather than apply the POLAR framework to remove the effect of TPL from our reported stability patterns, we instead square-root-transformed our population- and assemblage-level *CV*s, which allowed us to more effectively dissociate stability and mean abundance (Fig. S2D).

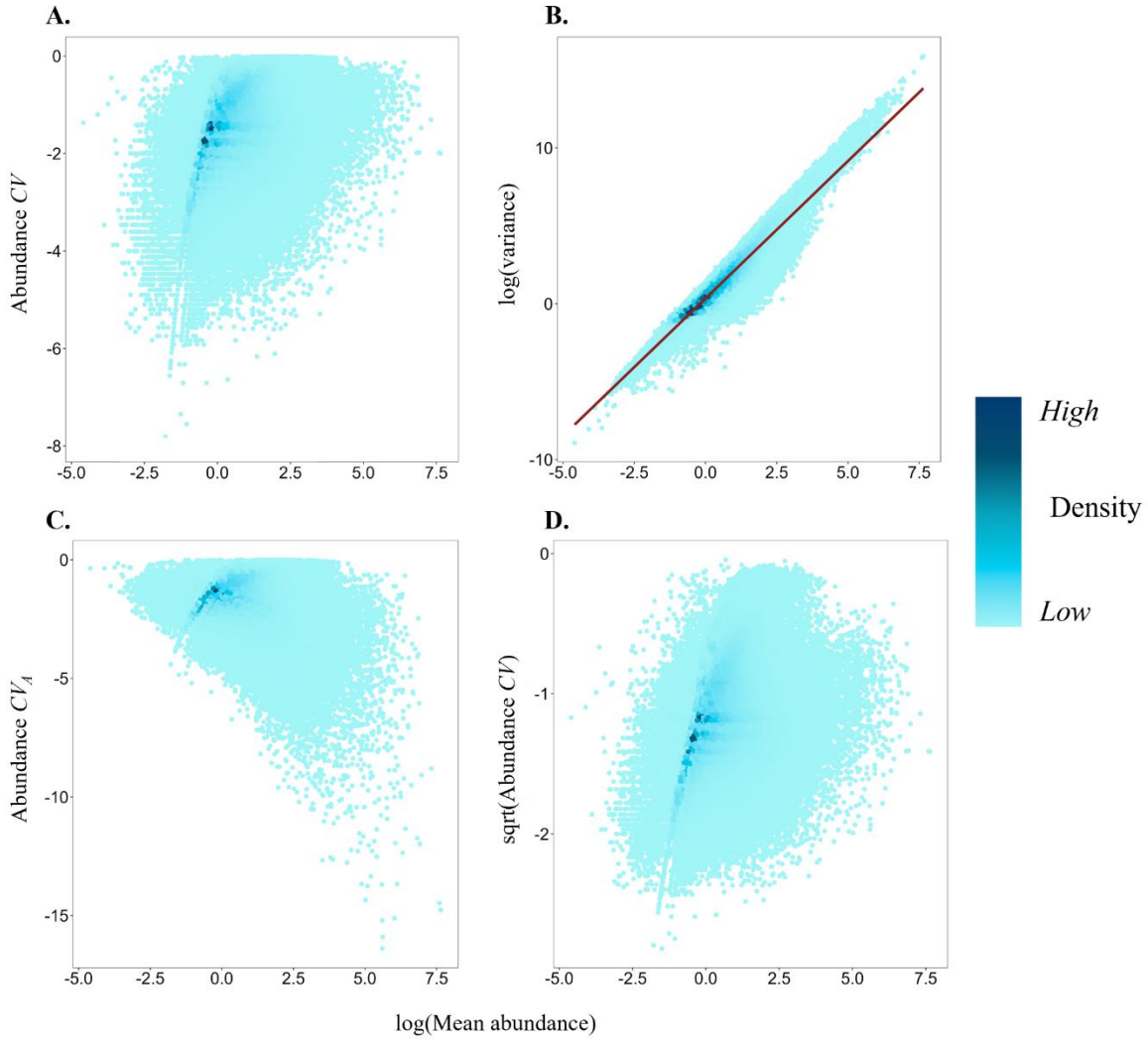

Figure S2. Taylor's power law (TPL) can bias estimates of coefficient of variation (*CV*) obtained for more abundant populations, thus affecting assessments of population- and assemblage-level stability. Visualisation of **(A)** the relationship between *CV* and mean estimates computed across population abundance time-series; **(B)** the log-log relationship between sample variances and means, with the solid line reflecting the grand-mean pattern modelled across 30 rarefaction iterations, with error displayed as 95% CIs; **(C)** the relationship between adjusted *CV* (CV_A) estimates computed using the Power Law Residuals (POLAR) approach and sample means; and **(D)** the relationship between square-root-transformed abundance *CV* estimates and sample means Note that *CV* and CV_A are shown on a reversed scale such that higher values reflect greater stability. Point colour reflects the density of overlapping points across all panels.

Appendix S3: The effect of time-series length on measures of stability

We report a nonlinear association between time-series length and estimates of population- and assemblage-level stability (Fig. S3). To address any signal arising from the duration of a biodiversity time series in subsequent estimates of stability (*115*), we assessed the relationship between our derived estimates of population- and assemblage-level stability and the length of the abundance time series used to compute them. Our assessment of these patterns entailed using polynomial models parameterised using uninformed priors to quantify the relationship between our transformed population- and assemblage-level adjusted *CV* estimates and the number of years covered by the corresponding abundance time series. A nonlinear approach was favoured over a linear approach following assessment of ELPD estimates derived from preliminary LOO comparisons of the two forms. Our models included assemblage identity as a random effect and involved Monte Carlo resampling; each model was repeated across 10% data subsamples extracted for each of our 30 rarefied data samples, with each repetition comprising a single chain of 2000 iterations. At first glance, our models indicate that time-series length has a positive effect on population- and assemblage-level stability (Fig. S3). However, caution is necessary when interpreting this relationship, as further visual inspection suggests possible overfitting at higher time-series durations due to a relative lack of data. Most of the abundance time series underlying our sample of population and assemblage stability estimates span < 10 to 15 years. Across these shorter time series, our fitted curves initially show a negligible decline in population- and assemblage-level stability with increasing time series duration (Fig. S3). Subsequently, the length of the time series underlying our data sample is unlikely to be significantly biasing our computation of population- and assemblage-level stability nor the analyses we present using these data.

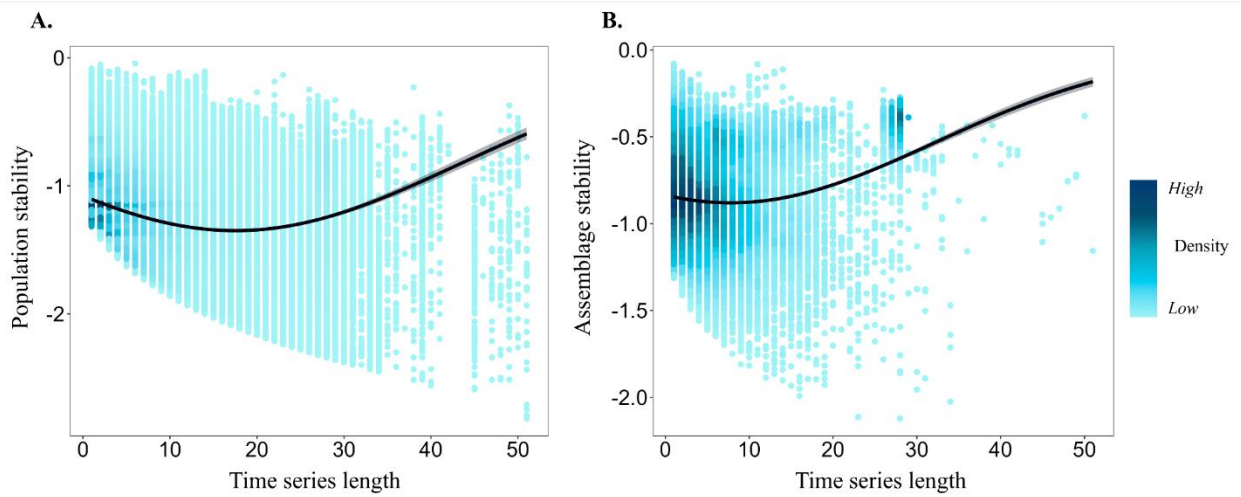

Figure S3. Time series length has a negligible effect on population- and assemblage-level stability. The relationship between the length of a time series (*i.e.*, number of years surveyed) and temporal variation in **(A)** population abundance and **(B)** total assemblage abundance. Across both panels, the solid black line represents the grand-mean pattern in time-series length and stability modelled across 30 rarefaction iterations, with error displayed as 95% CIs. Point colour reflects the density of overlapping points across each plot.