Synchrony and tail-dependent synchrony have different effects on the stability of terrestrial and freshwater communities


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Abstract

Global change alters the stability of biological communities by affecting species richness and how species covary through time (i.e., synchrony). There are few large-scale empirical tests of stability-diversity-synchrony relationships and those mostly focus on the terrestrial realm. Moreover, the effect of synchrony is largely unknown when species only covary at either high or low extremes of abundance (i.e., tail-dependent synchrony), a common phenomenon in ecological communities. Here, we synthesized long-term community time-series data (20+ years of species’ abundances/biomass for 2,668 communities across 7 taxonomic groups) from both terrestrial and freshwater realms and explored how the relationships among richness, synchrony, and stability vary across realms. We also investigated the effect of tail-dependent synchrony on stability across 714 freshwater and 1,954 terrestrial communities. For terrestrial communities, we found a positive diversity-stability relationship and that the tail-dependent synchrony was a more important determinant of stability than the traditional measure of overall synchrony (i.e., based on the covariation of all species). For freshwater communities, only overall synchrony explained some variation in stability. Assessing tail-dependent synchrony can improve our ability to understand why stability varies across different ecosystems and thereby our inferences about the causes of human-mediated biodiversity loss.
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Abstract:

Global change alters the stability of biological communities by affecting species richness and how species covary through time (i.e., synchrony). There are few large-scale empirical tests of stability-diversity-synchrony relationships and those mostly focus on the terrestrial realm. Moreover, the effect of synchrony is largely unknown when species only covary at either high or low extremes of abundance (i.e., tail-dependent synchrony), a common phenomenon in ecological communities. Here, we synthesized long-term community time-series data (20+ years of species’ abundances/biomass for 2,668 communities across 7 taxonomic groups) from both terrestrial and freshwater realms and explored how the relationships among richness, synchrony, and stability vary across realms. We also investigated the effect of tail-dependent synchrony on stability across 714 freshwater and 1,954 terrestrial communities. For terrestrial communities, we found a positive diversity-stability relationship and that the tail-dependent synchrony was a more important determinant of stability than the traditional measure of overall synchrony (i.e., based on the covariation of all species). For freshwater communities, only overall synchrony explained some variation in stability. Assessing tail-dependent synchrony can improve our ability to understand why stability varies across different ecosystems and thereby our inferences about the causes of human-mediated biodiversity loss.
Introduction

Temporal synchrony of communities, the tendency for multiple species to fluctuate synchronously through time at the same site, can strongly influence the persistence of populations in the face of environmental variability (Yachi & Loreau 1999; Valencia et al. 2020). Communities are more likely to persist in variable environments when species have low synchrony and respond differently to environmental perturbations, making a community more stable (Yachi & Loreau 1999; Craven et al. 2018). In contrast, high synchrony, where species respond similarly to environmental change, can increase the variability in total community biomass making a community less stable (Loreau & de Mazancourt 2008). Additionally, species can have similar threshold-like responses to environmental changes (Walter et al. 2022), such as high mortality beyond a temperature threshold (Bragazza 2008) or high productivity beyond a resource threshold (Interlandi & Kilham 2001). In such cases, species can become synchronous when they have either simultaneously low abundance or simultaneously high abundance, and thus are strongly correlated only in their extreme abundances (Figure 1). For example, when plant species are synchronously rare (i.e., having low abundance) in drought conditions, traditional measures of synchrony will underestimate extinction risk in the community (Ghosh et al. 2021). Alternatively, when pest species are synchronously abundant, due to shared phenological responses to temperature thresholds (Ghosh et al. 2020b), an assessment of synchrony at the extremes can help identify risks to crop production.

Synchrony at the extremes (also referred to as tail-dependent synchrony (Ghosh et al. 2020b, 2021; Walter et al. 2022)) has been routinely overlooked in previous analyses of community dynamics, even though it is central to understanding how species richness influences stability (Ghosh et al. 2021). Stability, the inverse of temporal variability of the sum of species’ abundances (or biomass) in a community (McCann 2000; Pennekamp et al. 2018), often increases with species richness and
decreases with overall synchrony. A positive relationship between richness and stability can result from statistical averaging of multiple independent population time series, a phenomenon known as the portfolio effect (Doak et al. 1998; Cottingham et al. 2001). Alternatively, a negative relationship between stability and synchrony can result from differential population responses of species to environmental change, i.e., the insurance hypothesis (Naeem & Li 1997; Yachi & Loreau 1999). Typically, overall synchrony is measured using pairwise covariances among all species (Peterson 1975; Loreau & de Mazancourt 2008), but these metrics do not account for potential correlations between species when both have either simultaneously low or high abundance relative to their mean abundance over time. Here, we explicitly consider how pairwise correlations can emerge between species when they have simultaneously either high or low abundances (Figure 1a, b). This approach, which uses time series of ranked abundances to quantify tail-dependent synchrony (Ghosh et al. 2020a) (see Materials & Methods), complements traditional overall measures of synchrony and provides additional insight into the relationship between synchrony and stability. For instance, measuring overall synchrony for a grassland community that is repeatedly exposed to droughts would be unlikely to account for co-variation in drought-dependence among grassland species, and thereby potentially overestimate the stability of the community. An overestimate of stability is, in fact, a general outcome of ignoring synchrony that can emerge at the extremes of species abundances (Ghosh et al. 2021). Integrating tail-dependent synchrony into the ecological theory of community stability thus provides a broader perspective on synchrony and novel insight into how community stability will vary across time and space.

Here, we evaluate the influence of richness, overall synchrony, and tail-dependent synchrony on community stability using time series across multiple taxonomic groups from 2,668 communities
in freshwater (n=714) and terrestrial (n=1,954) realms. We considered the two realms independently as it is well recognized that the process underlying biodiversity dynamics may differ within (i.e., among taxa) and across realms (Blowes et al. 2019; Antão et al. 2020; van Klink et al. 2020). Previous work has suggested that (i) differences in the extent of niche packing of species along environmental gradients can contribute to differences in overall richness among realms (e.g. between marine and terrestrial systems) (May et al. 1994; Mora et al. 2011; Grosberg et al. 2012), (ii) underlying drivers of biodiversity loss can differ among terrestrial, freshwater, and marine systems (Jaureguiberry et al. 2022), and (iii) contrasting physical (e.g. light attenuation), chemical (e.g. nutritional quality), and habitat properties (e.g. connectivity) of ecosystems can lead to different expected biodiversity responses to environmental change (Mcfadden et al. 2023). Using data from both freshwater and terrestrial realms we evaluate how richness, overall synchrony, and tail-dependent synchrony influence community stability (Tilman et al. 1998; McCann 2000; Cottingham et al. 2001; Loreau & de Mazancourt 2013) between realms.

Materials & Methods

Data processing: We compiled long-term (a minimum of 20 years sampled) community time series data across 7 taxa (terrestrial birds: n=1,259, invertebrates: n=124, plants: n=435, and mammals: n=136, freshwater fish: n=587, invertebrates: n=112, and phytoplankton: n=15) from the terrestrial (n=1,954) and freshwater (n=714) realms, using several databases (e.g., BioTIME (BioTIME Consortium 2018; Dornelas et al. 2018), RivFISHTIME (Comte et al. 2021), Breeding Bird Survey (Pardieck et al. 2020), SLU database (MVM-Start 2020)), NZ Freshwater Fish Database (NIWA 2016), Long Term Resource Monitoring Program database (Upper Midwest Environmental Sciences Center 2016)), and other studies (Beven 1976; Kendeigh 1982; Williamson 1983, 1987; Hall 1984; Vickery & Nudds 1984; Moore 1991; Gibbons et al. 1993;

There are very few (<40) long-term datasets available from the marine realm (source: public database BioTIME), so we excluded marine systems from our analysis. A total of 242 study IDs for 2,668 communities have been included in this analysis (see Table S1). Eighty-five percent of the communities recorded abundance data (240 studies, 2,267 communities). Fifteen percent of the communities, all representing plant taxa, recorded biomass data instead (2 studies, 401 communities). It is common for plant studies to use biomass, density or cover in place of abundance (Chiarucci et al. 1999; Larocque 2016), so we retained studies recording abundance or biomass in our analysis. Most of the data were identified at the species level. When species-level identification was not confidently available throughout the sampling periods (mainly for freshwater invertebrates, zooplankton, and phytoplankton), higher taxonomic level aggregation
was performed. Following previous analyses of community stability that focused on common over rare species (Sasaki & Lauenroth 2011; Thibaut & Connolly 2013; Valencia et al. 2020), we only included species that were present in at least 70% of the sampling time points.

To mitigate bias associated with differences in sampling effort across realms and taxonomic groups, we conducted repeated analyses with subsampled communities from our entire dataset without replacement (Figure S1). First, we selected a more balanced pool of 1,768 communities across realms (terrestrial: freshwater = 60:40) by stratified random sampling across 70 strata for birds from the BBS database which was more dominant in the initial dataset (n=1,227). We reduced this BBS dataset (Pardieck et al. 2020) to ~27% (n=327) via randomly sampling data points from each stratum proportional to the stratum area. Next, we selected a more balanced pool across taxa by sampled randomly (without replacement) 15 communities for each of 7 taxa, and for 100 replicates. As phytoplankton were only recorded for 15 communities, they were always included in 105 community pools in all 100 replicates. Figure S1 depicts the rarefaction scheme of data included in this study. We analyzed our model for the 100 replicates and presented the summarized results.

Synthesizing data from different databases also requires caution, as we need to ensure consistency in sampling effort and minimization of sampling errors. To address this issue, we first aggregated annual data considering months that were sampled consistently throughout the whole period for each study and with a minimum sampling period of 20 years. Second, in particular for Breeding Bird Survey dataset (Pardieck et al. 2020), we considered data for year 1997 onwards to have consistent quality-control for each sampling event (with “RunType code”=1 that ensures data were collected consistent with all standardBBS criteria). Third, there may be uncertainty due to different types of sampling protocols - e.g., electrofishing vs. gillnet use for RivFishTIME
database. But, as we did not have full information about the sampling protocol for all the dataset included in this analysis, we considered a random effect in our modeling based on the types of taxa and plots nested within a given study sites (e.g., study sites are analogous to strata for BBS dataset and to hydrobasins for RivFishTIME).

To further evaluate how poor sampling effort could affect our estimates of tail-dependent synchrony, we simulated a scenario of the true pattern versus observed pattern of a species’ abundance distribution (Figure S2). In the simulation, we introduced a known amount of undersampling (e.g., 20%, 40%, or 80%) to the true pattern and reran our analysis (Figure S2, Section S1). The most common scenario in empirical datasets is that species occurrences will be missing (i.e. undersampled) because they are synchronously scarce (shown in highlights, Figure S2) for some years. We find that if data are undersampled by 20% of those years, then that would have a negligible effect on the tail-asymmetry estimates (i.e., Figure S2, h and n both have the same tail-asymmetry value). In contrast, if one missed 80% of those years then that would lead to 60% error in the estimates (i.e., Figure S2, l compared to Figure S2, h). Actual sampling completeness is unknown and varies across taxa and time. However, assuming that in most cases sampling was relatively complete (only 20 to 40 percent missing) then our results would still provide useful and consistent interpretations. Nonetheless, to account for variation in sampling completeness we introduced some randomness for each study in the modeling (see Hierarchical Bayesian modeling below).

**Data summary statistics:** Stability was nearly three times higher in terrestrial than freshwater communities (terrestrial: median=3.52, n=1,954, interquartile-range - IQR =2.93; freshwater: median= 1.13, n=714, IQR= 0.62). Terrestrial communities had higher species richness (median=36, IQR=28) compared to freshwater communities (median=4, IQR=6). Our terrestrial
communities also had four times lower levels of overall synchrony than in freshwater communities (terrestrial: median=0.16, IQR=0.16; freshwater: median=0.52, IQR=0.29), and tail-dependent synchrony was seventy-five times higher in terrestrial (median=9.06, IQR=10.9) than in freshwater communities (median=0.12, IQR=0.65). A visual representation of raw data distribution is depicted in Figure S3.

Quantifying community stability, overall synchrony, and tail-dependent synchrony:

To measure community stability, we used the abundance (or biomass if abundance was not available) time series of $N$ species in a community that was sampled for $T \geq 20$ years. Total community abundance (or biomass) was the sum of individual species time series ($m_i$), and represented as $M = \sum_{i=1}^{n} m_i$. Community stability ($S$) was then computed by taking the ratio of the median and the interquartile range ($IQR$), instead of the mean and standard deviation ($sd$), for the total community-abundance (or biomass) time series, i.e., $S = \frac{\text{median}(M)}{\text{IQR}(M)}$. The choice of this metric was made based on the fact that the usual definition of stability ($= \frac{\text{mean}(M)}{\text{sd}(M)}$) is sensitive to extreme values when the temporal distribution of the data is not gaussian/normal (Altman & Bland 1994) (see Figure S4). Therefore, if species are synchronous at the extremes (e.g., as shown in (Ghosh et al. 2021)), total abundance (or biomass, $M$) could be skewed and thus, a non-biased estimator for stability is preferred.

We measured overall synchrony using a standard covariance-based metric (i.e., Loreau-de Mazancourt synchrony (Loreau & de Mazancourt 2008)) and a new community-level correlation metric. The Loreau-de Mazancourt synchrony (Loreau & de Mazancourt 2008) (LMS) is the ratio of the variance in total community abundance (or biomass) time series compared to the one with species in the community in perfect synchrony. LMS is recommended over the classic variance
ratio approach (Thibaut & Connolly 2013) and quantified as $\sum_{ij} v_{ij} / (\sum_i \sqrt{v_{ii}})^2$, where $v_{ij}$ is the covariance between species $i$ and $j$, and $v_{ii}$ is the variance in $i^{th}$ species time series. Community-level correlation is a rank-based measure using the Spearman correlation for each possible pairwise combination of species time series (total $N(N-1)/2$ combinations are possible). We classified pairwise correlations between species to be either independent (no correlation), synchronous (positive correlation), or asynchronous (negative correlation). We computed the community-level correlation ($c$) by taking the sum of all significant pairwise between-species correlations and dividing the sum by $N(N-1)/2$. This community-level correlation ($c$) was used as an alternative measure of overall synchrony to test the robustness of our findings. Our results were qualitatively similar using these two metrics (Figures S5, S6), therefore, we retained LMS as it is commonly used in the literature and thus, facilitates comparison to other work.

To measure tail-dependent synchrony, we followed three steps. First, we made a copula plot (Nelsen 2007; Ghosh et al. 2020a) with each positively correlated species pair - where each species time series was ranked (in increasing order) independently and divided by $(T+1)$ so that they fell within a unit box (0,1), we called this scatter plot of a bivariate copula as a “normalized rank plot” (e.g. see Fig 1a in the main text). We used a ranked time series instead of the raw data because ranking makes the marginals of the bivariate distribution uniform, and extracts separately dependence between two variables at their extreme values (i.e., the tail-dependence, for details see (Sklar 1959; Nelsen 2007; Joe 2014)). As a result, the rank of one species is related to the rank of the other species. When the ranks of both species matched, they were closely associated and were considered synchronous. If there was more association between lower ranks (i.e., when both species had low abundance as in Fig 1a, top panel) - a strong tail appeared in the lower half of the diagonal line $y = -x + I$ (i.e., below a 50% threshold). Conversely, if there was greater
association between higher ranks (i.e., when both species were highly abundant as in Fig 1a, bottom panel) - a strong tail appeared in the upper half of the diagonal line $y = -x + 1$ (i.e., above the 50% threshold). Second, we computed a partial Spearman correlation (Ghosh et al. 2020a) for the lower half ($\text{Cor}_l$) and upper half ($\text{Cor}_u$) of the copula plot. In Fig 1a, top panel, $\text{Cor}_l$ is greater than $\text{Cor}_u$, i.e., the data points below the diagonal line $y = -x + 1$ of the normalized rank plot contribute more to the total Spearman correlation of all the data points. In contrast, in Fig 1a, bottom panel, $\text{Cor}_u$ is greater than $\text{Cor}_l$ and the points lying above the diagonal line contribute more to the total Spearman correlation. Third, we quantified total tail asymmetry as, $T_A = \sum |\text{Cor}_l - \text{Cor}_u|_ij$, where the sum was for any two dissimilar species $i$ and $j$ such that $i < j$, $i = 1, ..., N$, $j=1, ..., N$. This is the measure of net tail dependence for all possible dissimilar and synchronous species pairs from the community - which we termed as tail-dependent synchrony for a community. Further, to determine the relative importance of synchrony at lower and upper extremes on stability we split total tail asymmetry into its two counterparts. We defined lower tail-dependent synchrony (i.e., synchrony when species were simultaneously rare) as $L = \sum (\text{Cor}_l - \text{Cor}_u)_{ij}$ for those species-pair when $\text{Cor}_l > \text{Cor}_u$ and upper tail-dependent synchrony (i.e., synchrony when species were simultaneously common) as $U = \sum (\text{Cor}_u - \text{Cor}_l)_{ij}$ for those species-pair when $\text{Cor}_l < \text{Cor}_u$. Here, we only considered positively correlated (aka synchronous) species-pairs in our calculation of tail-dependent synchrony (see section S2 for details).

To calculate total tail asymmetry ($T_A$) a threshold is needed. We used a 50% threshold when we computed the dependence at the extremes (i.e., L or U). Choosing a more conservative threshold (e.g., 75%) would require longer time series for the community. The 50% threshold yielded 2,668 communities with a minimum of 20 years sampled (i.e., 20 data points at least for our copula plot); however, when we increased the threshold to 75%, the sample size reduced drastically to 41...
communities (with a minimum of 40 years of data points). From these 41 communities we
subsequently excluded 6 that had no synchrony and used the remaining 35 communities to
compare the metrics L and U using both 50% and 75% thresholds. For these 35 communities, we
found strong correlations between the two thresholds (Spearman correlations >0.9, p-values
<0.001). Overall, this analysis suggests that our findings would be qualitatively similar irrespective
of the choice of threshold.

**Hierarchical Bayesian modeling:** We built a hierarchical multi-group mixed-effect Bayesian
model, considering all factors together. Richness, overall synchrony, and tail-dependent synchrony
were fixed effects. Realm, which was a categorical variable with two levels (terrestrial versus
freshwater), was considered as an interactive fixed effect. This setup allowed us to compare the
path estimates for stability-driver relationships between terrestrial and freshwater systems. Finally,
taxa and plots nested within the study sites for different taxa (7 broad taxonomic groups in total:
birds, fish, terrestrial and freshwater plants, terrestrial mammals, terrestrial and freshwater
invertebrates) were added as random effects (i.e., intercepts). We ran simple and complex versions
of this model for 100 replicates (as shown in Figure S1). The simple version depicted in Figure 1C
and Figure 2, included direct paths between each variable and stability. To evaluate model
performance, we compared the eight possible combinations of stability-driver relationships: (i)
richness, (ii) richness and LM synchrony, (iii) richness and total tail-asymmetry, (iv) richness, LM
synchrony, and total tail-asymmetry, with and without the realm effect (Figures S7, S8). The
complex version considered both the direct and indirect effects of richness on stability by including
two extra paths: richness to tail-dependent synchrony and richness to overall synchrony (Figures
S5: LM synchrony, Figure S6: community-level correlation). Bayesian analyses were performed
in R-software using the brm() function from the ‘brms’ package (Bürkner 2023) after data
standardization (zero mean, unit standard deviation) to compare coefficients for different types of
predictors on the same scale. As multi-collinearity can lead to path estimates >1, we checked if
there are any collinearity issues regarding the driver variables we chose. In this respect, we found
that the variation inflation factor (VIF) was acceptable for our model (Figure S9: VIF <2 for the
model with whole and subsetted data; <5 for 98 replicates, between 5 to 5.5 for 2 replicates). A
VIF greater than 10 (or >5 if being conservative) is usually considered as an indicator of
multicollinearity (Vittinghoff et al. 2005; James et al. 2013). For each of 100 replicates, we
followed this procedure: we used 16,000 total iterations with 75% warmup on each of four chains
(starting with randomized initialization) to fit the parameters of a gaussian distribution with weakly
informative priors, where every fourth sample was drawn using NUTS sampling from post-
warmup samples to avoid auto-correlation. Convergence was assured by checking Rhat = 1
(potential scale reduction factor on split chains) and significance was assessed on a 95% CI scale.
Comparison among model performances was computed using the compare_performance()
function from the ‘performance’ R-package (Lüdecke et al. 2021).

Results & Discussion

Tail-dependent synchrony (when species have simultaneously low or high abundance; Figure 1)
explained significant variation in stability of terrestrial communities and had a better explanatory
power than overall synchrony (Figure 2a, Figure S10). In particular, upper tail-dependent
synchrony (i.e., synchrony when species were common) had a stronger impact on terrestrial
stability than lower tail-dependent synchrony (Figure S11). This finding is consistent with previous
research (Valencia et al. 2020) indicating synchrony among dominant species is important for
terrestrial stability. In contrast to the terrestrial realm, only overall synchrony, and not tail-
dependent synchrony, explained variation in freshwater stability (Figure 2b, Figure S10).
Richness had a strong positive influence on the stability of terrestrial systems, yielding the most extensive empirical support for this relationship to date and confirming past plant-community based studies (Tilman et al. 2006; Valencia et al. 2020) (Figure 2a). We found that in both freshwater and terrestrial systems richness was positively associated with tail-dependent synchrony and negatively associated with overall synchrony (Figure S5). Importantly, however, terrestrial richness influenced stability directly and also indirectly via affecting both types of synchrony (Figure S5a), whereas freshwater richness had no direct effect on stability, but indirectly influenced stability mainly via the effects on overall synchrony (Figure S5b). Overall, our analysis of a taxonomically diverse set of communities from freshwater and terrestrial systems confirms the importance of richness for stability, and additionally provides novel insight into the effects of different types of synchrony on stability (McCann 2000; Xu et al. 2021).

Overall synchrony and tail-dependent synchrony revealed different insights about the stability of ecological communities. First, not only do our results confirm that richness is an important driver of stability in terrestrial communities, but they also reveal that over a broad gradient of richness measures of overall synchrony explained little variation in the stability of freshwater and terrestrial communities (Figure 3a). When tail-dependent synchrony is not considered, we overestimate the stability of terrestrial and freshwater communities (Figure 3a). Furthermore, these overestimates of stability increase with increasing species richness (Figure 3a). Second, our analysis recovers the expected negative relationship between stability and overall synchrony for freshwater communities (Figure 3b, right panel) and between stability and tail-dependent synchrony for terrestrial communities (Figure 3b, left panel). In terrestrial systems, our analysis reveals that stability is strongly dependent on tail-dependent synchrony rather than overall synchrony. This result is particularly clear in species-poor communities where the stability of terrestrial systems
drops below that of freshwater systems (Figure 3b, compare two pink dots and note the different y-axes’ ranges).

The realm-dependence of some of our conclusions (e.g. Figure 2, Figure 3, Figure S7) could stem from realm-specific differences in physical and environmental characteristics (Thackeray et al. 2010; Forster et al. 2012). For example, recent work suggests greater climate fluctuations in terrestrial systems lead to greater physiological stress across multiple species (Jørgensen et al. 2022), with potential consequences for synchrony occurring at the extremes of species’ population abundance. However, because our dataset has relatively few species-rich freshwater communities (See Data summary statistics) our ability to detect the effects of tail-dependent synchrony is likely greater in terrestrial communities. Nevertheless, our analyses suggest that realm-specific characteristics could differentially shape relationships between temporal synchrony and stability.

Overall, our results emphasize the importance of tail-dependent synchrony as a potential determinant of community stability. The greater explanatory power of tail-dependent synchrony than overall synchrony on stability in terrestrial communities (Figure 2, Figure S8), adds new insight into decades of research that has consistently identified species richness and overall synchrony as the key determinants of community stability (Tilman et al. 1998; McCann 2000; Cottingham et al. 2001; Loreau & de Mazancourt 2013). The prevalence of tail-dependent synchrony in natural communities (Ghosh et al. 2020b, 2021; Walter et al. 2022) suggests that measuring only overall synchrony may oversimplify complex community dynamics. Hence, developing a broader view of synchrony can provide a more detailed and accurate assessment of community dynamics given ongoing global environmental change.

As the frequency of extreme environmental conditions is projected to increase in the coming
decades (Fischer et al. 2021), therefore, species will likely find themselves either at the edge or beyond their physiological tolerance limit (Khaliq et al. 2014; Buckley & Huey 2016). Such threshold-like biological responses of populations are often observed in response to environmental fluctuations in general (Brown & Brown 1998; Bragazza 2008), and to extreme climatic events in particular (Ummenhofer & Meehl 2017). In such scenarios, measures of tail-dependent synchrony will help elucidate the influence of extreme environmental events on community dynamics and gauge the severity of community responses to extreme events. As a result, continuing to focus on overall synchrony may underestimate both the interspecific diversity of population responses to environmental change and the susceptibility of communities to ongoing disturbances (Walter et al. 2022).

In sum, considering both overall synchrony and tail-dependent synchrony will help disentangle relationships between species richness, environmental change, and community stability as they provide complementary yet critical information for conservation planning (Maxwell et al. 2019). Overall synchrony can be used to assess the susceptibility of an entire community to environmental change, while tail-dependent synchrony focuses on the impact of those species that either benefit (become simultaneously abundant) or suffer (become simultaneously scarce) in response to such environmental change. Until now, it has not been appreciated that tail-dependent synchrony can have strong impacts on the stability of higher levels of biological organization – i.e., the community. Given concerns about ecosystems being pushed beyond their capacity to sustain humanity (Wang-Erlandsson et al. 2022), it is essential to integrate our understanding of the importance of tail-dependent synchrony for community stability into wise decision making for both ecosystem conservation and restoration.
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Figure 1: Incorporating tail-dependent synchrony into ecological stability analysis. (a) Tail-dependent synchrony could occur in either tail of species’ ranks if they have simultaneously low abundances (more synchrony between lower ranks makes lower tail-dependence, top panel) or simultaneously high abundances (more synchrony between higher ranks makes upper tail-dependence, bottom panel); (b) Quantifying tail-dependent synchrony for a community (see Materials & Methods) as total tail asymmetry, \( T_A \). For each positively correlated species pair, lower tail-dependence and upper tail-dependence were measured using the partial Spearman correlation approach (Ghosh et al. 2020a), and total tail asymmetry was defined as the sum of their absolute differences; (c) a schematic diagram showing a model for stability-synchrony-diversity relationships that could vary across terrestrial vs. freshwater realm.
Figure 2: Drivers of stability vary across realms. (a) Richness and both types of synchrony explained the variation in terrestrial community stability, (b) whereas for freshwater communities, overall synchrony was more important. Numbers by the arrows (bold for significant) are the average of 100 median estimates (representing the 100 replicates as shown in see Figures S1c and S10). For each run, we took the median of 4,000 posterior samples. Italicized numbers within the parentheses indicate how many times, out of 100 runs, the median was significantly different than zero (based on 95% CI**). Solid arrows indicate significant effects, whereas a dashed arrow indicates none of the 100 medians were significantly different than zero. $b_0$ is the intercept used in the hierarchical mixed-effect Bayesian analysis.
Figure 3: Tail-dependent synchrony matters for estimating richness effects on stability (a) and uncovering the effects of synchrony on stability (b). We show here the conditional plots with the posterior estimates from the hierarchical Bayesian model (as shown in Figure 2) conditioning on any two of these variables: overall synchrony (LMS), tail-dependent synchrony (T_A), and species richness (R). (a) Stability increases with richness in terrestrial communities, but for freshwater communities, stability decreases with richness, irrespective of the values of overall synchrony (LMS) and tail-dependent synchrony (T_A). But if we ignore the contribution of the tail-dependent
synchrony, terrestrial stability would be overestimated and freshwater stability would be underestimated. (b) For the terrestrial realm, stability shows a nonlinear decrease with increasing tail-dependent synchrony. The effect of richness was also stronger for terrestrial stability. For the freshwater community, stability decreases with increasing overall synchrony, but the changes due to changes in richness or tail-dependent synchrony are much smaller compared to the terrestrial realm (compare the y-axes). For the species-poor community (R=4), the destabilizing effect of tail-dependent synchrony is so strong that the terrestrial community becomes less stable (-8.21) than the freshwater one (-7.55) beyond a certain threshold (compare the pink dots from both panels, note different y-axes ranges).

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