

Title: 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.

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;

153 Standley *et al.* 1996; Stone *et al.* 1997; Merritt 1999; Gaston & Blackburn 2000; Holmes & Sherry
 154 2001; Enemar *et al.* 2004; NCEAS 10241 : Zilov: The 60-year data set of plankton dynamics in
 155 Lake Baikal *et al.* 2006; Svensson 2006; Bê che & Resh 2007; Bêche & Resh 2007; Friggens 2008;
 156 Rudstam 2008a, b; Rudstam & Jackson 2008a, b; Ernest *et al.* 2009; Day 2010; Lack 2010;
 157 Magnuson, J., S. Carpenter, and E. Stanley 2010; McLarney *et al.* 2010; Svensson *et al.* 2010;
 158 Zachmann *et al.* 2010; Lter 2011a, b; Wagner *et al.* 2011; Animal Demography Unit 2012; Harmon
 159 M & Franklin 2012; HawkCount 2012; HMANA 2012; Magnuson *et al.* 2012; Center for
 160 Limnology & Lter 2013; Sers 2013; Vasseur *et al.* 2014; Lightfoot 2015, 2016; Thackeray *et al.*
 161 2015; Gross 2016; Hartnett, D.C. & Collins, S.L. 2016; Joern 2016; Kaufman 2016; Sandercock
 162 2016; Willig, M. R. & Bloch, C. P. 2016; Carpenter, S., J. Kitchell, J. Cole, and M. Pace 2017;
 163 Landis 2018; “Finnish electrofishing register Hertta” 2019, “The Missouri Coteau Wetland
 164 Ecosystem Observatory” 2020; Blowes *et al.* 2019; Pomati *et al.* 2019; UK Environmental Agency
 165 2019; McLean *et al.* 2021).

166 There are very few (<40) long-term datasets available from the marine realm (source: public
 167 database BioTIME), so we excluded marine systems from our analysis. A total of 242 study IDs
 168 for 2,668 communities have been included in this analysis (see Table S1). Eighty-five percent of
 169 the communities recorded abundance data (240 studies, 2,267 communities). Fifteen percent of the
 170 communities, all representing plant taxa, recorded biomass data instead (2 studies, 401
 171 communities). It is common for plant studies to use biomass, density or cover in place of
 172 abundance (Chiarucci *et al.* 1999; Larocque 2016), so we retained studies recording abundance or
 173 biomass in our analysis. Most of the data were identified at the species level. When species-level
 174 identification was not confidently available throughout the sampling periods (mainly for
 175 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 we 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 (≥ 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., $S = median(M)/IQR(M)$. The choice of this metric was made based on the fact that the usual definition of stability ($= mean(M)/sd(M)$) 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 $\sum_{i,j} v_{ij} / (\sum_i \sqrt{v_{ii}})^2$, 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 $y = -x + 1$ (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 (Cor_l) and upper half (Cor_u) of the copula plot. In Fig 1a, top panel, Cor_l is greater than 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, Cor_u is greater than Cor_l and the points lying above the diagonal line contribute more to the total Spearman correlation. Third, we quantified total tail asymmetry as, $T_A = \sum |Cor_l - Cor_u|_{ij}$, where the sum was for any two dissimilar species i and j such that $i < j$, $i = 1, \dots, N$, $j = 1, \dots, N$. 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 $L = \sum (Cor_l - Cor_u)_{ij}$ for those species-pair when $Cor_l > Cor_u$ and upper tail-dependent synchrony (i.e., synchrony when species were simultaneously common) as $U = \sum (Cor_u - Cor_l)_{ij}$ for those species-pair when $Cor_l < Cor_u$. 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 subsetting 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 $\hat{R} = 1$ (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 (Lüdtke *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

359 drops below that of freshwater systems (Figure 3b, compare two pink dots and note the different
360 y-axes' ranges).

361 The realm-dependence of some of our conclusions (e.g. Figure 2, Figure 3, Figure S7) could stem
362 from realm-specific differences in physical and environmental characteristics (Thackeray *et al.*
363 2010; Forster *et al.* 2012). For example, recent work suggests greater climate fluctuations in
364 terrestrial systems lead to greater physiological stress across multiple species (Jørgensen *et al.*
365 2022), with potential consequences for synchrony occurring at the extremes of species' population
366 abundance. However, because our dataset has relatively few species-rich freshwater communities
367 (See *Data summary statistics*) our ability to detect the effects of tail-dependent synchrony is likely
368 greater in terrestrial communities. Nevertheless, our analyses suggest that realm-specific
369 characteristics could differentially shape relationships between temporal synchrony and stability.

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

380 As the frequency of extreme environmental conditions is projected to increase in the coming

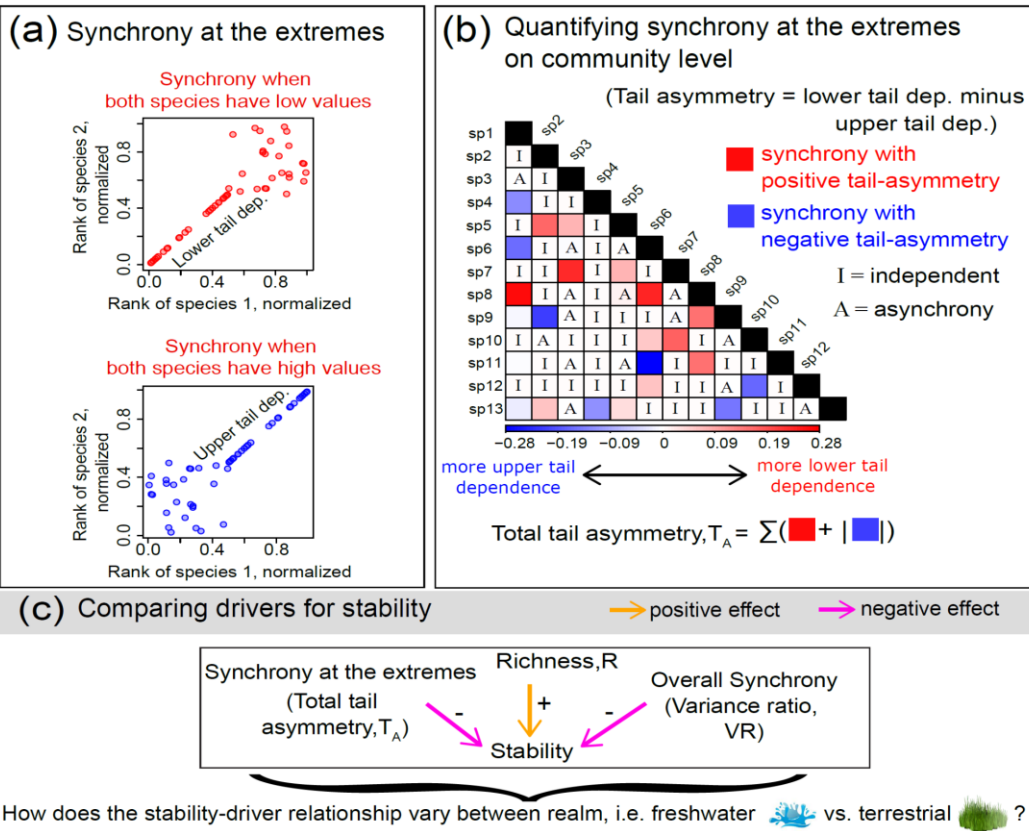
decades (Fischer *et al.* 2021), therefore, species will likely find themselves either at the edge or beyond their physiological tolerance limit (Khaliq *et al.* 2014; Buckley & Huey 2016). Such threshold-like biological responses of populations are often observed in response to environmental fluctuations 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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Incorporating synchrony at the extremes into ecological stability analysis



428 How does the stability-driver relationship vary between realm, i.e. freshwater vs. terrestrial ?

429 **Figure 1:** Incorporating tail-dependent synchrony into ecological stability analysis. (a) Tail-
430 dependent synchrony could occur in either tail of species' ranks if they have simultaneously low
431 abundances (more synchrony between lower ranks makes lower tail-dependence, top panel) or
432 simultaneously high abundances (more synchrony between higher ranks makes upper tail-
433 dependence, bottom panel); (b) Quantifying tail-dependent synchrony for a community (see
434 *Materials & Methods*) as total tail asymmetry, T_A . For each positively correlated species pair,
435 lower tail-dependence and upper tail-dependence were measured using the *partial Spearman*
436 *correlation* approach (Ghosh *et al.* 2020a), and total tail asymmetry was defined as the sum of
437 their absolute differences; (c) a schematic diagram showing a model for stability-synchrony-
438 diversity relationships that could vary across terrestrial vs. freshwater realm.

Drivers of stability vary across realms

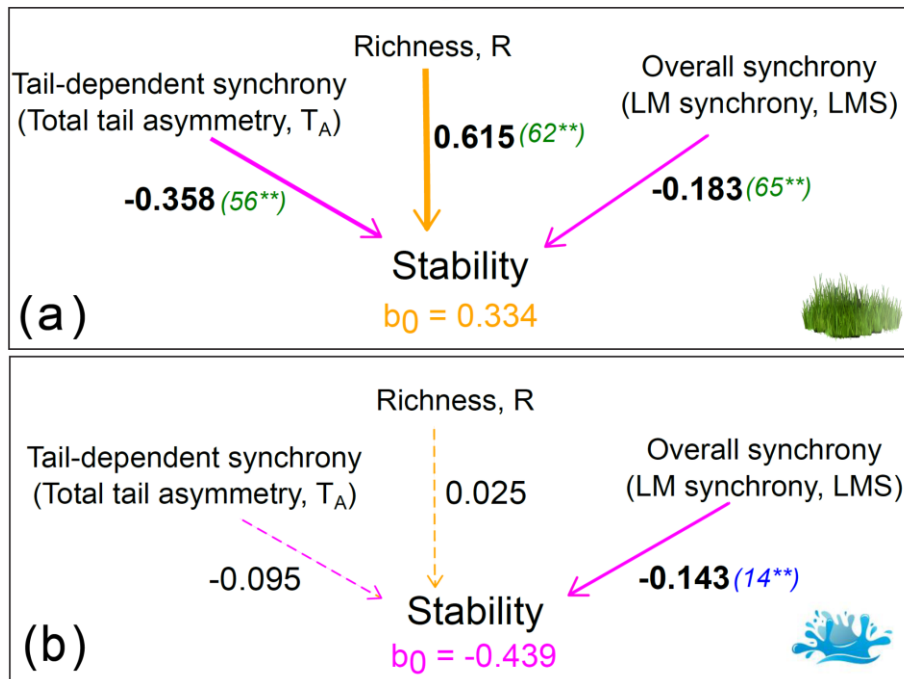
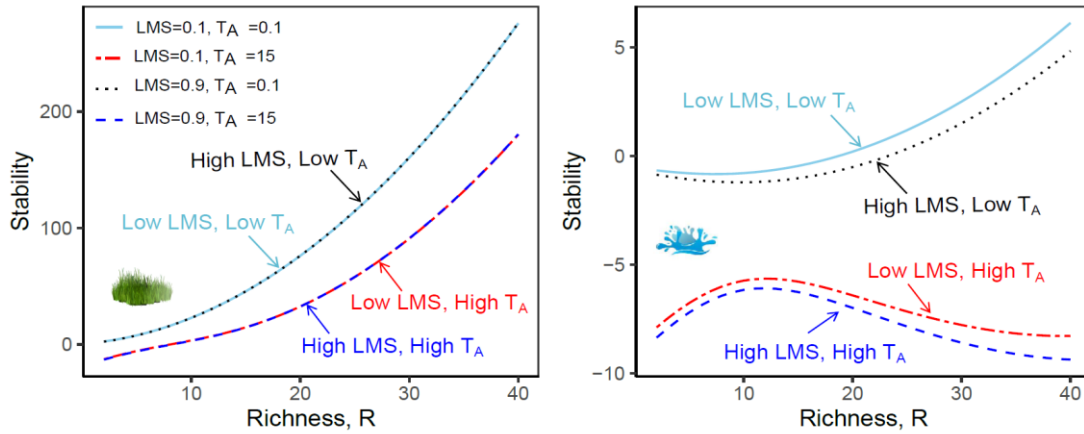


Figure 2: Drivers of stability vary across realms. (a) Richness and both types of synchrony explained the variation in terrestrial community stability, (b) whereas for freshwater communities, overall synchrony was more important. Numbers by the arrows (bold for significant) are the average of 100 median 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.

(a) Stability is overestimated for terrestrial and freshwater communities when ignoring tail-dependent synchrony
 Scenarios with varying synchrony (overall synchrony = LMS, Tail-dependent synchrony = T_A)



(b) The negative impacts of tail-dependent synchrony (terrestrial) and overall synchrony (freshwater) on stability
 Scenarios with varying richness (= R)

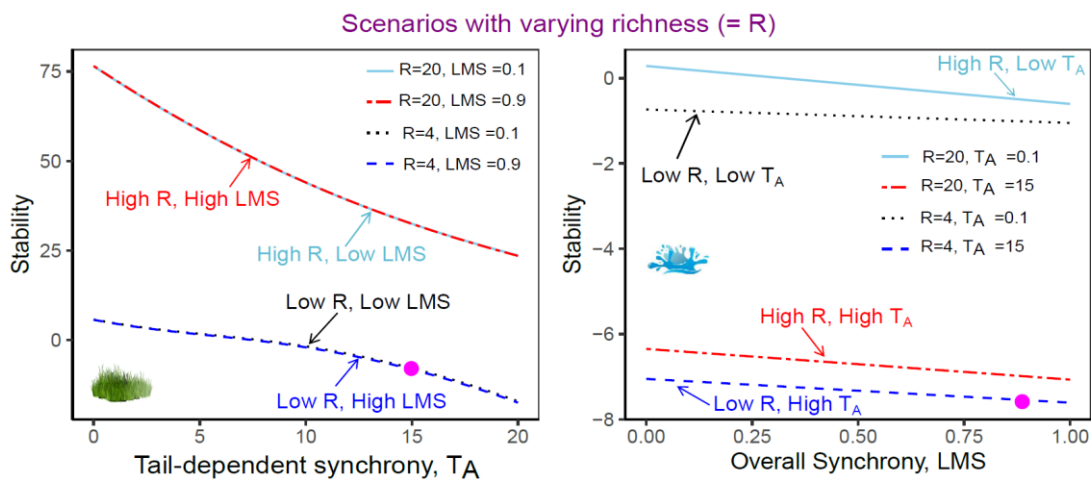


Figure 3: Tail-dependent synchrony matters for estimating richness effects on stability (a) and uncovering the effects of synchrony on stability (b). We show here the conditional plots with the posterior estimates from the hierarchical Bayesian model (as shown in Figure 2) conditioning on any two of 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).

References

- Altman, D.G. & Bland, J.M. (1994). Quartiles, quintiles, centiles, and other quantiles. *BMJ*, 309, 996.
- Animal Demography Unit. (2012). “Coordinated Waterbird Counts (CWAC) - AfrOBIS”. Available at <http://www.iobis.org/>, accessed 2012.
- Antão, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E., *et al.* (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nat Ecol Evol*, 4, 927–933.
- Bêche, L.A. & Resh, V.H. (2007). Biological traits of benthic macroinvertebrates in California mediterranean-climate streams: long-term annual variability and trait diversity patterns. *Fundam. Appl. Limnol.*, 169, 1–23.
- Bêche, L.A. & Resh, V.H. (2007). Short-term climatic trends affect the temporal variability of

480 macroinvertebrates in California “Mediterranean” streams. *Freshw. Biol.*, 52, 2317–2339.

481 Beven, G. (1976). Changes in breeding bird populations of an oak-wood on Bookham Common,
 482 Surrey, over twenty-seven years. *Lond. Nat.*, 55, 23–42.

483 BioTIME Consortium. (2018). BioTIME, available at <https://zenodo.org/record/5026943>.

484 Blowes, S.A., Supp, S.R., Antão, L.H., Bates, A., Bruelheide, H., Chase, J.M., *et al.* (2019). The
 485 geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366, 339–
 486 345.

487 Bragazza, L. (2008). A climatic threshold triggers the die-off of peat mosses during an extreme
 488 heat wave. *Global Change Biology*.

489 Brown, C.R. & Brown, M.B. (1998). Intense natural selection on body size and wing and tail
 490 asymmetry in cliff swallows during severe weather. *Evolution*, 52, 1461–1475.

491 Buckley, L.B. & Huey, R.B. (2016). Temperature extremes: geographic patterns, recent changes,
 492 and implications for organismal vulnerabilities. *Glob. Chang. Biol.*, 22, 3829–3842.

493 Bürkner. (2023). *brms: An R package for Bayesian multilevel models using Stan*.

494 Carpenter, S., J. Kitchell, J. Cole, and M. Pace. (2017). Cascade Project at North Temperate
 495 Lakes LTER Core Data Zooplankton 1984 - 2016.

496 Center for Limnology & Lter, N. (2013). North Temperate Lakes LTER: Zooplankton - Trout
 497 Lake Area 1982 - current.

498 Chiarucci, A., Wilson, J.B., Anderson, B.J. & Dominicis, V. (1999). Cover versus biomass as an
 499 estimate of species abundance: does it make a difference to the conclusions? *J. Veg. Sci.*,
 500 10, 35–42.

501 Comte, L., Carvajal-Quintero, J., Tedesco, P.A., Giam, X., Brose, U., Erős, T., *et al.* (2021).
 502 RivFishTIME: A global database of fish time-series to study global change ecology in

503 riverine systems. *Global Ecology and Biogeography*.

504 Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal
505 variability of ecological systems. *Ecol. Lett.*, 4, 72–85.

506 Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., *et al.* (2018).
507 Multiple facets of biodiversity drive the diversity–stability relationship. *Nature Ecology &*
508 *Evolution*, 2, 1579–1587.

509 Day, F. (2010). “Long-term N-fertilized vegetation plots on Hog Island, Virginia Coastal Barrier
510 Islands, 1992-2014.” Virginia Coast Reserve Long-Term Ecological Research Project.
511 Available at: [http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-](http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.106)
512 [vcr.106](http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.106), accessed 2013.

513 Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O’Malley, R.E. & Thomson, D. (1998).
514 The statistical inevitability of stability-diversity relationships in community ecology. *Am.*
515 *Nat.*, 151, 264–276.

516 Dornelas, M., Antão, L.H., Moyes, F., Bates, A.E., Magurran, A.E., Adam, D., *et al.* (2018).
517 BioTIME: A database of biodiversity time series for the Anthropocene. *Glob. Ecol.*
518 *Biogeogr.*, 27, 760–786.

519 Enemar, A., Sjöstrand, B., Andersson, G. & Von Proschwitz, T. (2004). The 37-year dynamics
520 of a subalpine passerine bird community, with special emphasis on the influence of
521 environmental temperature and Epirrita autumnata cycles. *Ornis Svec.*, 14, 63–106.

522 Ernest, S.K.M., Valone, T.J. & Brown, J.H. (2009). Long-term monitoring and experimental
523 manipulation of a Chihuahuan Desert ecosystem near Portal, Arizona, USA. *Ecology*, 90,
524 1708–1708.

525 Finnish electrofishing register Hertta. (2019). Available at

526 https://wwwp2.ymparisto.fi/koekalastus_sahko/yhteinen/Login.aspx?ReturnUrl=%2fkoekal
527 [astus_sahko](https://wwwp2.ymparisto.fi/koekalastus_sahko/yhteinen/Login.aspx?ReturnUrl=%2fkoekal). Available at:
528 https://wwwp2.ymparisto.fi/koekalastus_sahko/yhteinen/Login.aspx?ReturnUrl=%2fkoekal
529 [astus_sahko](https://wwwp2.ymparisto.fi/koekalastus_sahko/yhteinen/Login.aspx?ReturnUrl=%2fkoekal). Last accessed 2019.

530 Fischer, E.M., Sippel, S. & Knutti, R. (2021). Increasing probability of record-shattering climate
531 extremes. *Nat. Clim. Chang.*, 11, 689–695.

532 Forster, J., Hirst, A.G. & Atkinson, D. (2012). Warming-induced reductions in body size are
533 greater in aquatic than terrestrial species. *Proc. Natl. Acad. Sci. U. S. A.*, 109, 19310–19314.

534 Friggens, M. (2008). “Sevilleta LTER Small Mammal Population Data”, Albuquerque, NM:
535 Sevilleta Long Term Ecological Research Site Database: SEV008. Available at:
536 <http://sev.lternet.edu/data/sev-8>, accessed 2012.

537 Gaston, K.J. & Blackburn, T.M. (Eds.). (2000). Pattern and Process in Macroecology.

538 Ghosh, S., Cottingham, K.L. & Reuman, D.C. (2021). Species relationships in the extremes and
539 their influence on community stability. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 376,
540 20200343.

541 Ghosh, S., Sheppard, L.W., Holder, M.T., Loecke, T.D., Reid, P.C., Bever, J.D., *et al.* (2020a).
542 Copulas and their potential for ecology. In: *Advances in Ecological Research*. Elsevier, pp.
543 409–468.

544 Ghosh, S., Sheppard, L.W., Reid, P.C. & Reuman, D. (2020b). A new approach to interspecific
545 synchrony in population ecology using tail association. *Ecol. Evol.*, 10, 12764–12776.

546 Gibbons, D.W., Reid, J.B. & Chapman, R.A. (1993). The New Atlas of Breeding Birds of Britain
547 and Ireland 1988-91: Poyser.

548 Grosberg, R.K., Vermeij, G.J. & Wainwright, P.C. (2012). Biodiversity in water and on land.

549 *Curr. Biol.*, 22, R900–3.

550 Gross, K. (2016). Plant Community and Ecosystem Responses to Long-term Fertilization &
551 Disturbance at the Kellogg Biological Station, Hickory Corners, MI (1989 to 2014).

552 Hall, G.A. (1984). A Long-Term Bird Population Study in an Appalachian Spruce Forest. *Wilson*
553 *Bull.*, 96, 228–240.

554 Harmon M & Franklin. (2012). “Long-term growth, mortality and regeneration of trees in
555 permanent vegetation plots in the Pacific Northwest, 1910 to present.” Long-Term
556 Ecological Research. Forest Science Data Bank, Corvallis. Available at:
557 <http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TV010>, accessed 2012.

558 Hartnett, D.C. & Collins, S.L. (2016). PVC02 Plant Species Composition on Selected
559 Watersheds at Konza Prairie. Environmental Data Initiative. Available at:
560 <http://dx.doi.org/10.6073/pasta/7b6df00de4d0fcecfd344c02de9f9c62>, accessed 2017.

561 HawkCount. (2012). *HawkCount Database*. Available at: <https://www.hawkcount.org/>. Last
562 accessed 2012.

563 HMANA. (2012). “Hawk Migration Association of North America (HMANA).” Available at:
564 <http://www.hmana.org/>, accessed 2012.

565 Holmes, R.T. & Sherry, T.W. (2001). Thirty-year bird population trends in an unfragmented
566 temperate deciduous forest: importance of habitat change. *Auk*.

567 Interlandi, S.J. & Kilham, S.S. (2001). Limiting resources and the regulation of diversity in
568 phytoplankton communities. *Ecology*, 82, 1270–1282.

569 James, G., Witten, D., Hastie, T. & Tibshirani, R. (2013). *An Introduction to Statistical*
570 *Learning: with Applications in R*. Springer Science & Business Media.

571 Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., *et al.*

572 (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Sci Adv*, 8,
 573 eabm9982.

574 Joe, H. (2014). *Dependence Modeling with Copulas*. CRC Press.

575 Joern, A. (2016). CGR02 Sweep Sampling of Grasshoppers on Konza Prairie LTER watersheds
 576 (1982-present). Environmental Data Initiative. Available at:
 577 <http://dx.doi.org/10.6073/pasta/7060b2c244229a37e3bfc8c18f14ad02>, accessed 2016.

578 Jørgensen, L.B., Ørsted, M., Malte, H., Wang, T. & Overgaard, J. (2022). Extreme escalation of
 579 heat failure rates in ectotherms with global warming. *Nature*, 611, 93–98.

580 Kaufman, D.W. (2016). *Seasonal summary of numbers of small mammals on 14 LTER traplines*
 581 *in prairie habitats at Konza Prairie. Konza Prairie Long-Term Ecological Research.*
 582 Available at: [http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-](http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-mammals-14-lter-traplines-prairie-habitats-konza)
 583 [mammals-14-lter-traplines-prairie-habitats-konza](http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-mammals-14-lter-traplines-prairie-habitats-konza), accessed 2016. Last accessed 2016.

584 Kendeigh, S.C. (1982). *Bird Populations in East Central Illinois: Fluctuations, Variations, and*
 585 *Development Over a Half-century*. University of Illinois Press.

586 Khaliq, I., Hof, C., Prinzing, R., Böhning-Gaese, K. & Pfenninger, M. (2014). Global variation
 587 in thermal tolerances and vulnerability of endotherms to climate change. *Proc. Biol. Sci.*,
 588 281, 20141097.

589 van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020).
 590 Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances.
 591 *Science*, 368, 417–420.

592 Lack, P. (2010). *The Atlas of Wintering Birds in Britain and Ireland*. A&C Black.

593 Landis, D. (2018). Insect Population Dynamics on the Main Cropping System Experiment at the
 594 Kellogg Biological Station, Hickory Corners, MI (1989 to 2017).

595 Larocque, G.R. (2016). *Ecological Forest Management Handbook*. CRC Press.

596 Lightfoot, D. (2015). Long-term core site grasshopper dynamics for the Sevilleta national
597 wildlife refuge, New Mexico (1992-2013).

598 Lightfoot, D. (2016). “Small Mammal Exclosure Study (SMES)”. Sevilleta Long Term
599 Ecological Research Program. Available at: [http://sev.lternet.edu/content/small-mammal-](http://sev.lternet.edu/content/small-mammal-exclosure-study-smes-0)
600 [exclosure-study-smes-0](http://sev.lternet.edu/content/small-mammal-exclosure-study-smes-0), accessed 2016.

601 Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: neutral and
602 nonneutral community dynamics in fluctuating environments. *Am. Nat.*, 172, E48–66.

603 Loreau, M. & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of
604 underlying mechanisms. *Ecol. Lett.*, 16 Suppl 1, 106–115.

605 Lter, N. (2011a). “North Temperate Lakes LTER: Phytoplankton - Madison Lakes Area 1995 -
606 current.” North Temperate Lakes Long Term Ecological Research Program, Center for
607 Limnology, University of Wisconsin-Madison. Available at:
608 [https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-madison-](https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-madison-lakes-area-1995-current)
609 [lakes-area-1995-current](https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-madison-lakes-area-1995-current), accessed 2013.

610 Lter, N. (2011b). “North Temperate Lakes LTER: Zooplankton–Madison Lakes Area 1997–
611 current.” North Temperate Lakes Long Term Ecological Research Program, Center for
612 Limnology, University of Wisconsin-Madison. Available at:
613 [http://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplanktonmadison-](http://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplanktonmadison-lakes-area-1997-current)
614 [lakes-area-1997-current](http://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplanktonmadison-lakes-area-1997-current), accessed 2013 (2011).

615 Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. (2021). performance: An
616 R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open*
617 *Source Software*.

618 Magnuson, J.J., Carpenter, S.R. & Stanley, E.H. (2012). North Temperate Lakes LTER: Fish
 619 Abundance 1981 - current, North Temperate Lakes Long Term Ecological Research
 620 program, NSF. Center for Limnology, University of Wisconsin-Madison. Available at
 621 [https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-fish-abundance-1981-](https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-fish-abundance-1981-current)
 622 [current.](https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-fish-abundance-1981-current)
 623 Magnuson, J., S. Carpenter, and E. Stanley. (2010). North Temperate Lakes LTER: Benthic
 624 Macroinvertebrates 1981 - current, ver 34.
 625 Maxwell, S.L., Butt, N., Maron, M., McAlpine, C.A., Chapman, S., Ullmann, A., *et al.* (2019).
 626 Conservation implications of ecological responses to extreme weather and climate events.
 627 *Divers. Distrib.*, 25, 613–625.
 628 May, R.M., Godfrey, J., Beddington, J.R., Cushing, D.H., May, R.M. & Steele, J.H. (1994).
 629 Biological diversity: differences between land and sea. *Philos. Trans. R. Soc. Lond. B Biol.*
 630 *Sci.*, 343, 105–111.
 631 McCann, K.S. (2000). The diversity–stability debate. *Nature*, 405, 228–233.
 632 McFadden, Sendek, Brosse & Bach. (2023). Linking human impacts to community processes in
 633 terrestrial and freshwater ecosystems. *Ecology Letters*, 26, 203–218.
 634 McLarney, W.O., Meador, J. & Chamblee, J. (2010). Upper Little Tennessee River
 635 biomonitoring program database. Coweeta Long Term Ecological Research Program.
 636 McLean, K.I., Mushet, D.M., Newton, W.E. & Sweetman, J.N. (2021). Long-term multidecadal
 637 data from a prairie-pothole wetland complex reveal controls on aquatic-macroinvertebrate
 638 communities. *Ecol. Indic.*, 126, 107678.
 639 Merritt, J. (1999). Long Term Mammal Data from Powdermill Biological Station 1979-1999.
 640 Environmental Data Initiative. Available at:

641 <http://dx.doi.org/10.6073/pasta/83c888854e239a79597999895bb61cfe>, accessed 2016.
 642 Moore, N.W. (1991). The development of dragonfly communities and the consequences of
 643 territorial behaviour: a 27 year study on small ponds at Woodwalton Fen, Cambridgeshire,
 644 United Kingdom. NERC Centre for Population Biology, Imperial College. The Global
 645 Population Dynamics Database Version 2.0. Available at:
 646 <http://www3.imperial.ac.uk/cpb/databases/gpdd>, accessed 2012. *Odonatologica*, 20, 203–
 647 231.
 648 Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011). How Many Species Are
 649 There on Earth and in the Ocean? *PLoS Biol.*, 9, e1001127.
 650 MVM-Start, M. (2020). *Miljödata MVM - Start. Miljödata MVM - Start*. Available at:
 651 <https://miljodata.slu.se/mvm/Default.aspx>. Last accessed 2020.
 652 Naeem, S. & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390, 507–509.
 653 NCEAS 10241 : Zilov: The 60-year data set of plankton dynamics in Lake Baikal, National
 654 Center for Ecological Analysis and Synthesis & Izmet'seva, L. (2006). Lake Baikal
 655 Plankton.
 656 Nelsen, R.B. (2007). *An Introduction to Copulas*. Springer Science & Business Media.
 657 NIWA. (2016). “*The New Zealand Freshwater Fish Database*”. Available at:
 658 <https://www.niwa.co.nz/our-services/online-services/freshwater-fish-database>, accessed
 659 2016. Last accessed 2016.
 660 Pardieck, K.L., Ziolkowski, D.J., Lutmerding, M. & Aponte, V.I. (2020). North American
 661 Breeding Bird Survey Dataset 1966–2019: US Geological Survey data release. 2020. DOI:
 662 <https://doi.org/10.5066>.
 663 Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y., *et al.* (2018).

664 Biodiversity increases and decreases ecosystem stability. *Nature*, 563, 109–112.

665 Peterson, C.H. (1975). Stability of Species and of Community for the Benthos of two Lagoons.

666 *Ecology*, 56, 958–965.

667 Pomati, F., Shurin, J.B., Andersen, K.H., Tellenbach, C. & Barton, A.D. (2019). Interacting

668 Temperature, Nutrients and Zooplankton Grazing Control Phytoplankton Size-Abundance

669 Relationships in Eight Swiss Lakes. *Front. Microbiol.*, 10, 3155.

670 R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation

671 *for Statistical Computing, Vienna, Austria*. URL <https://www.R-project.org/>.

672 Rudstam, L. (2008a). *Zooplankton survey of Oneida Lake, New York, 1964 – 2012, KNB Data*

673 *Repository*. Available at: <https://knb.ecoinformatics.org/#view/kgordon.17.56>. Available at:

674 <https://knb.ecoinformatics.org/#view/kgordon.17.56>. Last accessed 2016.

675 Rudstam, L.G. (2008b). Phytoplankton in Oneida Lake, New York, 1975 -- present. Knowledge

676 Network for Biocomplexity. kgordon.31.64.

677 Rudstam, L.G. & Jackson, J.R. (2008a). Bottom trawl surveys from Oneida Lake, NY, 1958 to

678 present. Knowledge Network for Biocomplexity. kgordon.19.98.

679 Rudstam, L.G. & Jackson, J.R. (2008b). Gill net survey of fishes of Oneida Lake, NY, 1957 –

680 2010, kgordon.14.129.

681 Sandercock, B.K. (2016). “Variable distance line-transect sampling of bird population numbers

682 in different habitats on Konza Prairie (1981 - 2009)”. Konza Prairie Long Term Ecological

683 Research Program. Available at:

684 <http://www.konza.ksu.edu/knz/pages/data/KnzEntity.aspx?id=CBP011>, accessed 2016.

685 Sasaki, T. & Lauenroth, W.K. (2011). Dominant species, rather than diversity, regulates

686 temporal stability of plant communities. *Oecologia*, 166, 761–768.

687 Sers, B. (2013). Swedish Electrofishing RegiSter--SERS. Swedish University of Agricultural
688 Sciences (SLU), Department of Aquatic Resources.

689 Sklar, M. (1959). Fonctions de repartition a n dimensions et leurs marges. *Publ. Inst. Statist.*
690 *Univ. Paris*, 8, 229–231.

691 Standley, P., Bucknell, N.J., Swash, A. & Collins, I.D. (1996). *The Birds of Berkshire. Berkshire*
692 *Atlas Group*.

693 Stone, B.H., Sears, J., Cranswick, P.A. & Gregory, R.D. (1997). Population estimates of birds in
694 Britain and in the United Kingdom. *Br. Birds*, 90, 1–22.

695 Svensson, S. (2006). Species composition and population fluctuations of alpine bird communities
696 during 38 years in the Scandinavian mountain range. *Ornis Svec.*, 16, 183–210.

697 Svensson, S., Thorner, A.M. & Nyholm, N.E.I. (2010). Species trends, turnover and composition
698 of a woodland bird community in southern Sweden during a period of fifty-seven years.
699 *Ornis Svec.*, 20.

700 Thackeray, S.J., De Ville, M.M., Fletcher, J.M., James, J.B., Maberly, S.C., Mackay, E.B., *et al.*
701 (2015). Cumbrian Lakes plankton and fish data (1940 to 2013).

702 Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., *et al.* (2010).
703 Trophic level asynchrony in rates of phenological change for marine, freshwater and
704 terrestrial environments. *Glob. Chang. Biol.*, 16, 3304–3313.

705 *The Missouri Coteau Wetland Ecosystem Observatory*. (2020). . Available at:
706 <https://www.sciencebase.gov/catalog/item/52f0ffd9e4b0f941aa181fc6>. Last accessed 24
707 July 2023.

708 Thibaut, L.M. & Connolly, S.R. (2013). Understanding diversity-stability relationships: towards
709 a unified model of portfolio effects. *Ecol. Lett.*, 16, 140–150.

710 Tilman, D., Lehman, C.L. & Bristow, C.E. (1998). Diversity-stability relationships: statistical
 711 inevitability or ecological consequence? *Am. Nat.*, 151, 277–282.

712 Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a
 713 decade-long grassland experiment. *Nature*, 441, 629–632.

714 UK Environmental Agency. (2019). NFPD: Freshwater fish survey relational datasets.

715 Ummenhofer, C.C. & Meehl, G.A. (2017). Extreme weather and climate events with ecological
 716 relevance: a review. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 372.

717 Upper Midwest Environmental Sciences Center. (2016). *Long Term Resource Monitoring*
 718 *Program. USGS - U.S. Geological Survey - Upper Midwest Environmental Sciences Center.*
 719 Available at: https://www.umesc.usgs.gov/data_library/fisheries/fish1_query.shtml. Last
 720 accessed 2019.

721 Valencia, E., de Bello, F., Galland, T., Adler, P.B., Lepš, J., E-Vojtkó, A., *et al.* (2020).
 722 Synchrony matters more than species richness in plant community stability at a global scale.
 723 *Proc. Natl. Acad. Sci. U. S. A.*, 117, 24345–24351.

724 Vasseur, D.A., Fox, J.W., Gonzalez, A., Adrian, R., Beisner, B.E., Helmus, M.R., *et al.* (2014).
 725 Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems.
 726 *Proc. Biol. Sci.*, 281, 20140633.

727 Vickery, W.L. & Nudds, T.D. (1984). Detection of density-dependent effects in annual duck
 728 censuses. *Ecology*, 65, 96–104.

729 Vittinghoff, E., Glidden, D.V., Shiboski, S.C. & McCulloch, C.E. (2005). *Regression Methods in*
 730 *Biostatistics*. Springer New York.

731 Wagner, R., Marxsen, J., Zwick, P. & Cox, E.J. (2011). *Central European Stream Ecosystems:*
 732 *The Long Term Study of the Breitenbach*. John Wiley & Sons.

733 Walter, J.A., Castorani, M.C.N., Bell, T.W., Sheppard, L.W., Cavanaugh, K.C. & Reuman, D.C.
 734 (2022). Tail-dependent spatial synchrony arises from nonlinear driver-response
 735 relationships. *Ecol. Lett.*, 25, 1189–1201.

736 Wang-Erlandsson, L., Tobian, A., van der Ent, R.J., Fetzer, I., te Wierik, S., Porkka, M., *et al.*
 737 (2022). A planetary boundary for green water. *Nature Reviews Earth & Environment*, 1–13.

738 Williamson, M. (1983). The Land-Bird Community of Skokholm: Ordination and Turnover.
 739 *Oikos*, 41, 378–384.

740 Williamson, M. (1987). Are communities ever stable? *Symposium of the British Ecological*
 741 *Society*, 26, 353–371.

742 Willig, M. R. & Bloch, C. P. (2016). “El Verde Grid long-term invertebrate data: Luquillo Long
 743 Term Ecological Research Site Database: Data Set 107”. Available
 744 at:<http://luq.lternet.edu/data/luqmetadata107/7427>, accessed 2016.

745 Xu, Q., Yang, X., Yan, Y., Wang, S., Loreau, M. & Jiang, L. (2021). Consistently positive effect
 746 of species diversity on ecosystem, but not population, temporal stability. *Ecol. Lett.*, 24,
 747 2256–2266.

748 Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating
 749 environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.*, 96, 1463–1468.

750 Zachmann, L., Moffet, C. & Adler, P. (2010). Mapped quadrats in sagebrush steppe: long-term
 751 data for analyzing demographic rates and plant–plant interactions. *Ecology*, 91, 3427–3427.