# 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.

1    **Title:** Synchrony and tail-dependent synchrony have different effects on the stability of terrestrial

2    and freshwater communities

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66 diversity-synchrony relationships and those mostly focus on the terrestrial realm. Moreover, the

67 effect of synchrony is largely unknown when species only covary at either high or low extremes

68 of abundance (i.e., tail-dependent synchrony), a common phenomenon in ecological communities.

69 Here, we synthesized long-term community time-series data (20+ years of species'

70 abundances/biomass for 2,668 communities across 7 taxonomic groups) from both terrestrial and

71 freshwater realms and explored how the relationships among richness, synchrony, and stability

72 vary across realms. We also investigated the effect of tail-dependent synchrony on stability across

73 714 freshwater and 1,954 terrestrial communities. For terrestrial communities, we found a positive

74 diversity-stability relationship and that the tail-dependent synchrony was a more important

75 determinant of stability than the traditional measure of overall synchrony (i.e., based on the

76 covariation of all species). For freshwater communities, only overall synchrony explained some

77 variation in stability. Assessing tail-dependent synchrony can improve our ability to understand

78 why stability varies across different ecosystems and thereby our inferences about the causes of

79 human-mediated biodiversity loss.

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**Introduction**

85 Temporal synchrony of communities, the tendency for multiple species to fluctuate synchronously

86 through time at the same site, can strongly influence the persistence of populations in the face of

87 environmental variability (Yachi & Loreau 1999; Valencia *et al.* 2020). Communities are more

88 likely to persist in variable environments when species have low synchrony and respond differently

89 to environmental perturbations, making a community more stable (Yachi & Loreau 1999; Craven

90 *et al.* 2018). In contrast, high synchrony, where species respond similarly to environmental change,

91 can increase the variability in total community biomass making a community less stable (Loreau

92 & de Mazancourt 2008). Additionally, species can have similar threshold-like responses to

93 environmental changes (Walter *et al.* 2022), such as high mortality beyond a temperature threshold

94 (Bragazza 2008) or high productivity beyond a resource threshold (Interlandi & Kilham 2001). In

95 such cases, species can become synchronous when they have either simultaneously low abundance

96 or simultaneously high abundance, and thus are strongly correlated only in their extreme

97 abundances (Figure 1). For example, when plant species are synchronously rare (i.e., having low

98 abundance) in drought conditions, traditional measures of synchrony will underestimate extinction

99 risk in the community (Ghosh *et al.* 2021). Alternatively, when pest species are synchronously

100 abundant, due to shared phenological responses to temperature thresholds (Ghosh *et al.* 2020b),

101 an assessment of synchrony at the extremes can help identify risks to crop production.

102 Synchrony at the extremes (also referred to as tail-dependent synchrony (Ghosh *et al.* 2020b, 2021;

103 Walter *et al.* 2022)) has been routinely overlooked in previous analyses of community dynamics,

104 even though it is central to understanding how species richness influences stability (Ghosh *et al.*

105 2021). Stability, the inverse of temporal variability of the sum of species' abundances (or biomass)

106 in a community (McCann 2000; Pennekamp *et al.* 2018), often increases with species richness and

107     decreases with overall synchrony. A positive relationship between richness and stability can result

108     from statistical averaging of multiple independent population time series, a phenomenon known

109     as the portfolio effect (Doak *et al.* 1998; Cottingham *et al.* 2001). Alternatively, a negative

110     relationship between stability and synchrony can result from differential population responses of

111     species to environmental change, i.e., the insurance hypothesis (Naeem & Li 1997; Yachi &

112     Loreau 1999). Typically, overall synchrony is measured using pairwise covariances among all

113     species (Peterson 1975; Loreau & de Mazancourt 2008), but these metrics do not account for

114     potential correlations between species when both have either simultaneously low or high

115     abundance relative to their mean abundance over time. Here, we explicitly consider how pairwise

116     correlations can emerge between species when they have simultaneously either high or low

117     abundances (Figure 1a, b). This approach, which uses time series of ranked abundances to quantify

118     tail-dependent synchrony (Ghosh *et al.* 2020a) (see ***Materials & Methods***), complements

119     traditional overall measures of synchrony and provides additional insight into the relationship

120     between synchrony and stability. For instance, measuring overall synchrony for a grassland

121     community that is repeatedly exposed to droughts would be unlikely to account for co-variation in

122     drought-dependence among grassland species, and thereby potentially overestimate the stability

123     of the community. An overestimate of stability is, in fact, a general outcome of ignoring synchrony

124     that can emerge at the extremes of species abundances (Ghosh *et al.* 2021). Integrating tail-

125     dependent synchrony into the ecological theory of community stability thus provides a broader

126     perspective on synchrony and novel insight into how community stability will vary across time

127     and space.

128     Here, we evaluate the influence of richness, overall synchrony, and tail-dependent synchrony on

129     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

176   was performed. Following previous analyses of community stability that focused on common over

177   rare species (Sasaki & Lauenroth 2011; Thibaut & Connolly 2013; Valencia *et al.* 2020), we only

178   included species that were present in at least 70% of the sampling time points.

179   To mitigate bias associated with differences in sampling effort across realms and taxonomic

180   groups, we conducted repeated analyses with subsampled communities from our entire dataset

181   without replacement (Figure S1). First, we selected a more balanced pool of 1,768 communities

182   across realms (terrestrial: freshwater = 60:40) by stratified random sampling across 70 strata for

183   birds from the BBS database which was more dominant in the initial dataset (n=1,227). We

184   reduced this BBS dataset (Pardieck *et al.* 2020) to ~27% (n=327) via randomly sampling data

185   points from each stratum proportional to the stratum area. Next, we selected a more balanced pool

186   across taxa by sampled randomly (without replacement) 15 communities for each of 7 taxa, and

187   for 100 replicates. As phytoplankton were only recorded for 15 communities, they were always

188   included in 105 community pools in all 100 replicates. Figure S1 depicts the rarefaction scheme

189   of data included in this study. We analyzed our model for the 100 replicates and presented the

190   summarized results.

191   Synthesizing data from different databases also requires caution, as we need to ensure consistency

192   in sampling effort and minimization of sampling errors. To address this issue, we first aggregated

193   annual data considering months that were sampled consistently throughout the whole period for

194   each study and with a minimum sampling period of 20 years. Second, in particular for Breeding

195   Bird Survey dataset (Pardieck *et al.* 2020), we considered data for year 1997 onwards to have

196   consistent quality-control for each sampling event (with "RunType code"=1 that ensures data were

197   collected consistent with all standardBBS criteria). Third,  there may be  uncertainty due to

198   different types of sampling protocols - e.g., electrofishing vs. gillnet use for RivFishTIME

199    database. But, as we did not have full information about the sampling protocol for all the dataset

200    we included in this analysis, we considered a random effect in our modeling based on the types of

201    taxa and plots nested within a given study sites (e.g., study sites are analogous to strata for BBS

202    dataset and to hydrobasins for RivFishTIME).

203    To further evaluate how poor sampling effort could affect our estimates of tail-dependent

204    synchrony, we simulated a scenario of the true pattern versus observed pattern of a species'

205    abundance distribution (Figure S2). In the simulation, we introduced a known amount of

206    undersampling (e.g., 20%, 40%, or 80%) to the true pattern and reran our analysis (Figure S2,

207    Section S1). The most common scenario in empirical datasets is that species occurrences will be

208    missing (i.e. undersampled) because they are synchronously scarce (shown in highlights, Figure

209    S2) for some years. We find that if data are undersampled by 20% of those years, then that would

210    have a negligible effect on the tail-asymmetry estimates (i.e., Figure S2, h and n both have the

211    same tail-asymmetry value). In contrast, if one missed 80% of those years then that would lead to

212    60% error in the estimates (i.e., Figure S2, l compared to Figure S2, h). Actual sampling

213    completeness is unknown and varies across taxa and time. However, assuming that in most cases

214    sampling was relatively complete (only 20 to 40 percent missing) then our results would still

215    provide useful and consistent interpretations.  Nonetheless, to account for variation in sampling

216    completeness we introduced some randomness for each study in the modeling (see *Hierarchical*

217    *Bayesian modeling* below).

218    *Data summary statistics:* Stability was nearly three times higher in terrestrial than freshwater

219    communities (terrestrial: median=3.52, n=1,954, interquartile-range - IQR =2.93; freshwater:

220    median= 1.13, n=714, IQR= 0.62). Terrestrial communities had higher species richness

221    (median=36, IQR=28) compared to freshwater communities (median=4, IQR=6). Our terrestrial

222    communities also had four times lower levels of overall synchrony than in freshwater communities

223    (terrestrial: median=0.16, IQR=0.16; freshwater: median=0.52, IQR=0.29), and tail-dependent

224    synchrony was seventy-five times higher in terrestrial (median=9.06, IQR=10.9) than in freshwater

225    communities (median=0.12, IQR=0.65). A visual representation of raw data distribution is

226    depicted in Figure S3.

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

228    To measure community stability, we used the abundance (or biomass if abundance was not

229    available) time series of $N$ species in a community that was sampled for $T$ ($\geq 20$) years. Total

230    community abundance (or biomass) was the sum of individual species time series ($m_i$), and

231    represented as $M = \sum_{i=1}^{n} m_i$. Community stability ($S$) was then computed by taking the ratio of

232    the median and the interquartile range ($IQR$), instead of the mean and standard deviation ($sd$), for

233    the total community-abundance (or biomass) time series, i.e., $S = median(M)/IQR(M)$. The

234    choice of this metric was made based on the fact that the usual definition of stability ($=$

235    $mean(M)/sd(M)$) is sensitive to extreme values when the temporal distribution of the data is not

236    gaussian/ normal (Altman & Bland 1994) (see Figure S4). Therefore, if species are synchronous

237    at the extremes (e.g., as shown in (Ghosh *et al.* 2021)), total abundance (or biomass, $M$) could be

238    skewed and thus, a non-biased estimator for stability is preferred.

239    We measured overall synchrony using a standard covariance-based metric (i.e., Loreau-de

240    Mazancourt synchrony (Loreau & de Mazancourt 2008)) and a new community-level correlation

241    metric. The Loreau-de Mazancourt synchrony (Loreau & de Mazancourt 2008) (LMS) is the ratio

242    of the variance in total community abundance (or biomass) time series compared to the one with

243    species in the community in perfect synchrony. LMS is recommended over the classic variance

244  ratio approach (Thibaut & Connolly 2013) and quantified as $\sum_{i,j} v_{ij} / (\sum_i \sqrt{v_{ii}})^2$, where $v_{ij}$ is the

245  covariance between species $i$ and $j$, and $v_{ii}$ is the variance in $i^{\text{th}}$ species time series. Community-

246  level correlation is a rank-based measure using the Spearman correlation for each possible pairwise

247  combination of species time series (total *N(N-1)/2* combinations are possible). We classified

248  pairwise correlations between species to be either independent (no correlation), synchronous

249  (positive correlation), or asynchronous (negative correlation). We computed the community-level

250  correlation (*c*) by taking the sum of all significant pairwise between-species correlations and

251  dividing the sum by *N(N-1)/2*. This community-level correlation (*c*) was used as an alternative

252  measure of overall synchrony to test the robustness of our findings. Our results were qualitatively

253  similar using these two metrics (Figures S5, S6), therefore, we retained LMS as it is commonly

254  used in the literature and thus, facilitates comparison to other work.


255  To measure tail-dependent synchrony, we followed three steps. First, we made a copula plot

256  (Nelsen 2007; Ghosh *et al.* 2020a) with each positively correlated species pair - where each species

257  time series was ranked (in increasing order) independently and divided by $(T + 1)$ so that they fell

258  within a unit box (0,1), we called this scatter plot of a bivariate copula as a "normalized rank plot"

259  (e.g. see Fig 1a in the main text). We used a ranked time series instead of the raw data because

260  ranking makes the marginals of the bivariate distribution uniform, and extracts separately

261  dependence between two variables at their extreme values (i.e., the tail-dependence, for details see

262  (Sklar 1959; Nelsen 2007; Joe 2014) ). As a result, the rank of one species is related to the rank of

263  the other species. When the ranks of both species matched, they were closely associated and were

264  considered synchronous. If there was more association between lower ranks (i.e., when both

265  species had low abundance as in Fig 1a, top panel) - a strong tail appeared in the lower half of the

266  diagonal line $y = -x + 1$ (i.e., below a 50% threshold). Conversely, if there was greater

267    association between higher ranks (i.e., when both species were highly abundant as in Fig 1a,

268    bottom panel) - a strong tail appeared in the upper half of the diagonal line $y = -x + 1$ (i.e., above

269    the 50% threshold). Second, we computed a partial Spearman correlation (Ghosh *et al.* 2020a) for

270    the lower half ($Cor_l$) and upper half ($Cor_u$) of the copula plot. In Fig 1a, top panel, $Cor_l$ is greater

271    than $Cor_u$, i.e., the data points below the diagonal line $y = -x + 1$ of the normalized rank plot

272    contribute more to the total Spearman correlation of all the data points. In contrast, in Fig 1a,

273    bottom panel, $Cor_u$ is greater than $Cor_l$ and the points lying above the diagonal line contribute more

274    to the total Spearman correlation. Third, we quantified total tail asymmetry as, $T_A = \Sigma |Cor_l - Cor_u$

275    $|_{ij}$, where the sum was for any two dissimilar species $i$ and $j$ such that $i < j$, $i = 1, ..., N$, $j = 1, ..., N$.

276    This is the measure of net tail dependence for all possible dissimilar and synchronous species pairs

277    from the community - which we termed as *tail-dependent synchrony* for a community. Further, to

278    determine the relative importance of synchrony at lower and upper extremes on stability we split

279    total tail asymmetry into its two counterparts. We defined lower tail-dependent synchrony (i.e.,

280    synchrony when species were simultaneously rare) as $L = \Sigma(Cor_l - Cor_u)_{ij}$ for those species-pair

281    when $Cor_l > Cor_u$ and upper tail-dependent synchrony (i.e., synchrony when species were

282    simultaneously common) as $U = \Sigma(Cor_u - Cor_l)_{ij}$ for those species-pair when $Cor_l < Cor_u$. Here,

283    we only considered positively correlated (aka synchronous) species-pairs in our calculation of tail-

284    dependent synchrony (see section S2 for details).

285    To calculate total tail asymmetry ($T_A$) a threshold is needed. We used a 50% threshold when we

286    computed the dependence at the extremes (i.e., L or U). Choosing a more conservative threshold

287    (e.g., 75%) would require longer time series for the community. The 50% threshold yielded 2,668

288    communities with a minimum of 20 years sampled (i.e., 20 data points at least for our copula plot);

289    however, when we increased the threshold to 75%, the sample size reduced drastically to 41

290  communities (with a minimum of 40 years of data points). From these 41 communities we

291  subsequently excluded 6 that had no synchrony and used the remaining 35 communities to

292  compare the metrics L and U using both 50% and 75% thresholds. For these 35 communities, we

293  found strong correlations between the two thresholds (Spearman correlations >0.9, p-values

294  <0.001). Overall, this analysis suggests that our findings would be qualitatively similar irrespective

295  of the choice of threshold.

296  ***Hierarchical Bayesian modeling***: We built a hierarchical multi-group mixed-effect Bayesian

297  model, considering all factors together. Richness, overall synchrony, and tail-dependent synchrony

298  were fixed effects.  Realm, which was a categorical variable with two levels (terrestrial versus

299  freshwater), was considered as an interactive fixed effect. This setup allowed us to compare the

300  path estimates for stability-driver relationships between terrestrial and freshwater systems. Finally,

301  taxa and plots nested within the study sites for different taxa (7 broad taxonomic groups in total:

302  birds, fish, terrestrial and freshwater plants, terrestrial mammals, terrestrial and freshwater

303  invertebrates) were added as random effects (i.e., intercepts). We ran simple and complex versions

304  of this model for 100 replicates (as shown in Figure S1). The simple version depicted in Figure 1C

305  and Figure 2, included direct paths between each variable and stability. To evaluate model

306  performance, we compared the eight possible combinations of stability-driver relationships: (i)

307  richness, (ii) richness and LM synchrony, (iii) richness and total tail-asymmetry, (iv) richness, LM

308  synchrony, and total tail-asymmetry, with and without the realm effect (Figures S7, S8). The

309  complex version considered both the direct and indirect effects of richness on stability by including

310  two extra paths: richness to tail-dependent synchrony and richness to overall synchrony (Figures

311  S5: LM synchrony, Figure S6: community-level correlation). Bayesian analyses were performed

312  in R-software using the brm() function from the 'brms' package (Bürkner 2023) after data

313 standardization (zero mean, unit standard deviation) to compare coefficients for different types of

314 predictors on the same scale. As multi-collinearity can lead to path estimates >1, we checked if

315 there are any collinearity issues regarding the driver variables we chose. In this respect, we found

316 that the variation inflation factor (VIF) was acceptable for our model (Figure S9: VIF <2 for the

317 model with whole and subsetted data; <5 for 98 replicates, between 5 to 5.5 for 2 replicates). A

318 VIF greater than 10 (or >5 if being  conservative) is usually considered as an indicator of

319 multicollinearity (Vittinghoff *et al.* 2005; James *et al.* 2013). For each of 100 replicates, we

320 followed this procedure: we used 16,000 total iterations with 75% warmup on each of four chains

321 (starting with randomized initialization) to fit the parameters of a gaussian distribution with weakly

322 informative priors, where every fourth sample was drawn using NUTS sampling from post-

323 warmup samples to avoid auto-correlation. Convergence was assured by checking Rhat = 1

324 (potential scale reduction factor on split chains) and significance was assessed on a 95% CI scale.

325 Comparison among model performances was computed using the compare_performance()

326 function from the 'performance' R-package (Lüdecke *et al.* 2021).

327 **Results & Discussion**

328 Tail-dependent synchrony (when species have simultaneously low or high abundance; Figure 1)

329 explained significant variation in stability of terrestrial communities and had a better explanatory

330 power than overall synchrony (Figure 2a, Figure S10). In particular, upper tail-dependent

331 synchrony (i.e., synchrony when species were common) had a stronger impact on terrestrial

332 stability than lower tail-dependent synchrony (Figure S11). This finding is consistent with previous

333 research (Valencia *et al.* 2020) indicating synchrony among dominant species is important for

334 terrestrial stability. In contrast to the terrestrial realm, only overall synchrony, and not tail-

335 dependent synchrony, explained variation in freshwater stability (Figure 2b, Figure S10).

336     Richness had a strong positive influence on the stability of terrestrial systems, yielding the most

337     extensive empirical support for this relationship to date and confirming past plant-community

338     based studies (Tilman *et al.* 2006; Valencia *et al.* 2020) (Figure 2a). We found that in both

339     freshwater and terrestrial systems richness was positively associated with tail-dependent

340     synchrony and negatively associated with overall synchrony (Figure S5). Importantly, however,

341     terrestrial richness influenced stability directly and also indirectly via affecting both types of

342     synchrony (Figure S5a), whereas freshwater richness had no direct effect on stability, but indirectly

343     influenced stability mainly via the effects on overall synchrony (Figure S5b). Overall, our analysis

344     of a taxonomically diverse set of communities from freshwater and terrestrial systems confirms

345     the importance of richness for stability, and additionally provides novel insight into the effects of

346     different types of synchrony on stability (McCann 2000; Xu *et al.* 2021).

347     Overall synchrony and tail-dependent synchrony revealed different insights about the stability of

348     ecological communities. First, not only do our results confirm that richness is an important driver

349     of stability in terrestrial communities, but they also reveal that over a broad gradient of richness

350     measures of overall synchrony explained little variation in the stability of freshwater and terrestrial

351     communities (Figure 3a). When tail-dependent synchrony is not considered, we overestimate the

352     stability of terrestrial and freshwater communities (Figure 3a). Furthermore, these overestimates

353     of stability increase with increasing species richness (Figure 3a). Second, our analysis recovers the

354     expected negative relationship between stability and overall synchrony for freshwater

355     communities (Figure 3b, right panel) and between stability and tail-dependent synchrony for

356     terrestrial communities (Figure 3b, left panel). In terrestrial systems, our analysis reveals that

357     stability is strongly dependent on tail-dependent synchrony rather than overall synchrony. This

358     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

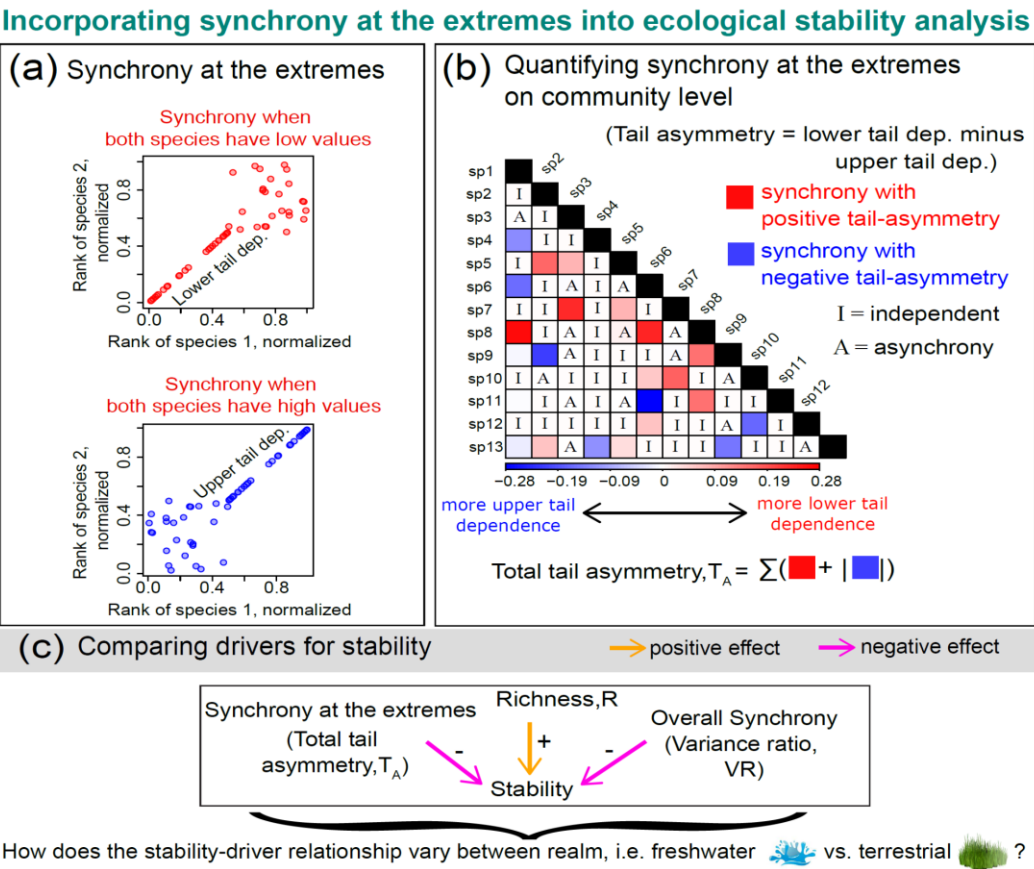379  community dynamics given ongoing global environmental change.

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

381 decades (Fischer *et al.* 2021), therefore, species will likely find themselves either at the edge or

382 beyond their physiological tolerance limit (Khaliq *et al.* 2014; Buckley & Huey 2016). Such

383 threshold-like biological responses of populations are often observed in response to environmental

384 fluctuations in general (Brown & Brown 1998; Bragazza 2008), and to extreme climatic events in

385 particular (Ummenhofer & Meehl 2017). In such scenarios, measures of tail-dependent synchrony

386 will help elucidate the influence of extreme environmental events on community dynamics and

387 gauge the severity of community responses to extreme events. As a result, continuing to focus on

388 overall synchrony may underestimate both the interspecific diversity of population responses to

389 environmental change and the susceptibility of communities to ongoing disturbances (Walter *et*

390 *al.* 2022) .

391 In sum, considering both overall synchrony and tail-dependent synchrony will help disentangle

392 relationships between species richness, environmental change, and community stability as they

393 provide complementary yet critical information for conservation planning (Maxwell *et al.* 2019).

394 Overall synchrony can be used to assess the susceptibility of an entire community to environmental

395 change, while tail-dependent synchrony focuses on the impact of those species that either benefit

396 (become simultaneously abundant) or suffer (become simultaneously scarce) in response to such

397 environmental change. Until now, it has not been appreciated that tail-dependent synchrony can

398 have strong impacts on the stability of higher levels of biological organization – i.e., the

399 community. Given concerns about ecosystems being pushed beyond their capacity to sustain

400 humanity (Wang-Erlandsson *et al.* 2022), it is essential to integrate our understanding of the

401 importance of tail-dependent synchrony for community stability into wise decision making for

402 both ecosystem conservation and restoration.

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412     **Competing interests:** The authors declare that they have no competing interests.

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**Figures**



Incorporating synchrony at the extremes into ecological stability analysis

**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.

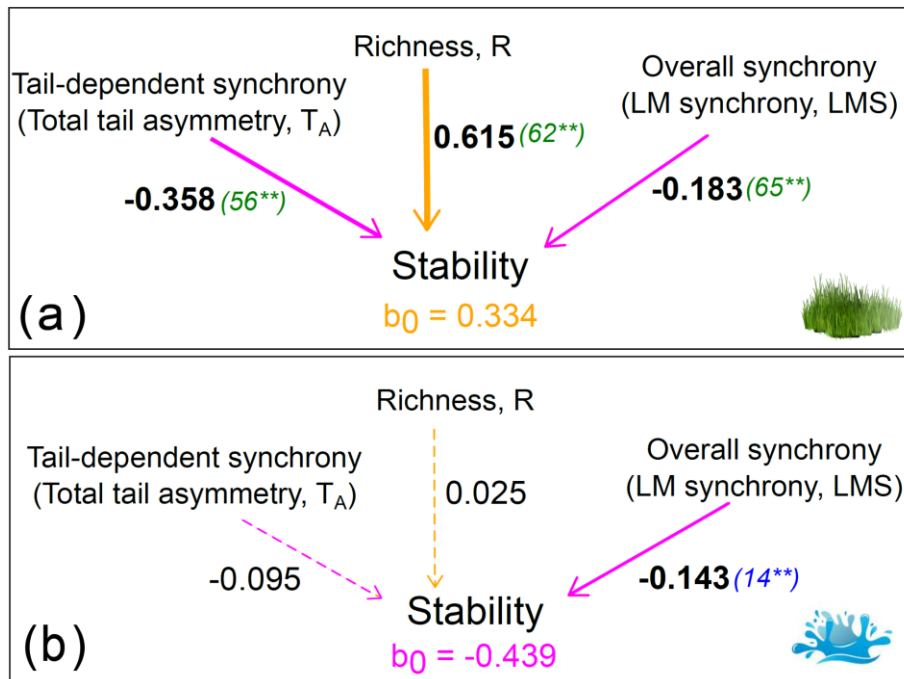**Drivers of stability vary across realms**

**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 = $T_A$)
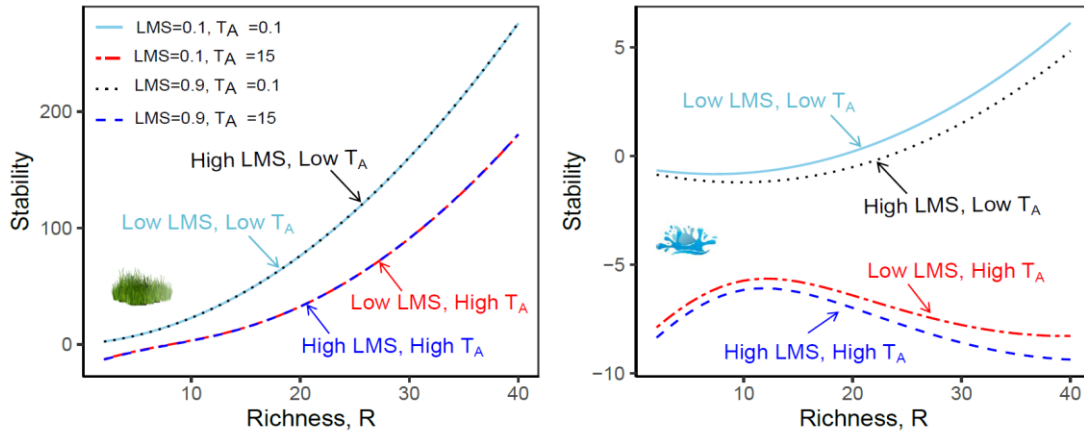
**(b) The negative impacts of tail-dependent synchrony (terrestrial) and overall synchrony (freshwater) on stability**

Scenarios with varying richness (= R)

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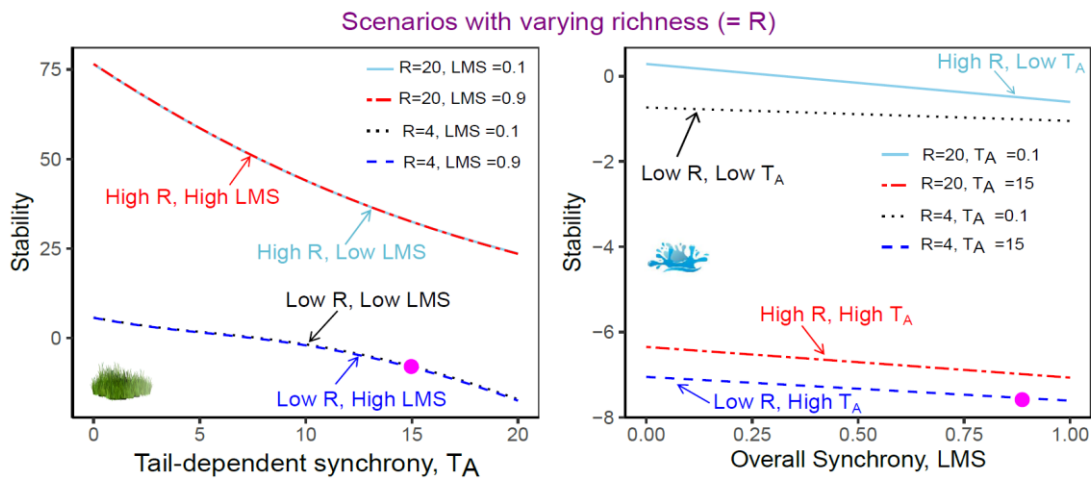
**Figure 3:** Tail-dependent synchrony matters for estimating richness effects on stability (a) and uncovering the effects of synchrony on stability (b). We show here the conditional plots with the posterior estimates from the hierarchical Bayesian model (as shown in Figure 2) conditioning on any two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

457    synchrony, terrestrial stability would be overestimated and freshwater stability would be

458    underestimated. (b) For the terrestrial realm, stability shows a nonlinear decrease with increasing

459    tail-dependent synchrony. The effect of richness was also stronger for terrestrial stability. For the

460    freshwater community, stability decreases with increasing overall synchrony, but the changes due

461    to changes in richness or tail-dependent synchrony are much smaller compared to the terrestrial

462    realm (compare the y-axes). For the species-poor community (R=4), the destabilizing effect of tail-

463    dependent synchrony is so strong that the terrestrial community becomes less stable (-8.21) than

464    the freshwater one (-7.55) beyond a certain threshold (compare the pink dots from both panels,

465    note different y-axes ranges).

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