

# 1 Synchrony matters more than species richness in plant community stability at a 2 global scale

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93 **Abstract**

94 The stability of ecological communities is critical for the stable provisioning of  
95 ecosystem services, such as food and forage production, carbon sequestration and soil  
96 fertility. Greater biodiversity is expected to enhance stability across years by decreasing  
97 synchrony among species, but the drivers of stability in nature remain poorly resolved.  
98 Our analysis of time-series from 79 data sets across the world showed that stability was  
99 associated more strongly with the degree of synchrony among dominant species than  
100 with species richness. The relatively weak influence of species richness is consistent  
101 with theory predicting that the effect of richness on stability weakens when synchrony is  
102 higher than expected under random fluctuations, which was the case in most  
103 communities. Land management, nutrient addition and climate change treatments, had  
104 relatively weak **and varying** effects on stability, modifying how species richness,  
105 synchrony and stability interact. Our results demonstrate the prevalence of biotic drivers  
106 on ecosystem stability, with the potential for environmental drivers to alter the intricate  
107 relationship among richness, synchrony and stability.

108 **Keywords:** evenness, global change drivers, species richness, stability, synchrony.

109 **Significance**

110 The stability of ecological communities under ongoing climate and land-use change is  
111 fundamental to the sustainable management of natural resources through its effect on  
112 critical ecosystem services. Biodiversity is hypothesized to enhance stability **through**  
113 **compensatory effects (decreased synchrony between species). However, the relative**  
114 **importance and interplay between different** biotic and abiotic drivers of stability  
115 remains controversial. By analyzing long-term data from natural and semi-natural  
116 ecosystems across the globe, we found that the degree of synchrony among dominant  
117 species was the main driver of stability, rather than species richness *per se*. **These biotic**  
118 **effects overrode environmental drivers, which influenced the stability of communities**  
119 **by modulating the effects of richness and synchrony.**

120 Understanding the mechanisms that maintain ecosystem stability (1) is essential for the  
121 stable provisioning of multiple ecosystem functions and services (2, 3). Although  
122 research on community stability has decades of history in ecology (4), with stability  
123 often measured as the inverse coefficient of variation across years of community  
124 abundance or biomass, the main drivers of stability remain elusive (5). Both abiotic and  
125 biotic drivers [e.g., climate, land-use and species diversity (6–8)] are expected to govern  
126 community stability. Among biotic drivers, the hypothesis that increases in species  
127 diversity begets stability in communities and ecosystems [Fig. 1 (2, 9–11)] has  
128 generated ongoing debate (12, 13).

129         The stabilizing effect of biodiversity has been attributed to various mechanisms  
130 (12). Most biodiversity-stability mechanisms at single trophic levels involve some form  
131 of compensatory dynamics, which occur when year-to-year temporal fluctuations in the  
132 abundance of some species are offset by fluctuations of other species (4, 14).  
133 Compensatory dynamics are associated with decreased synchrony among species, with  
134 synchrony defined as the extent to which species population sizes co-vary positively  
135 over time. Decreased synchrony, which is predicted to stabilize communities (Fig. 1a),  
136 can result from species-specific responses to environmental fluctuations (15–17) and  
137 from temporal changes in competitive hierarchies (18), as well as stochastic  
138 fluctuations. Importantly, it is expected that species richness can increase stability (Fig.  
139 1c) by decreasing synchrony (Fig. 1e). This positive effect of richness on stability can  
140 be, in fact, a result of an increased chance that the community will contain species with  
141 differing responses to abiotic drivers or competition, leading to a reduction in synchrony  
142 (12). However, the effect of richness on stability should weaken when synchrony is  
143 higher than expected if species were fluctuating randomly and independently [*SI*  
144 *Appendix*, see Supplementary text S1 for expanded information (19)]. At the same time,

145 other biotic drivers, together with richness and synchrony, have the potential to interact  
146 and buffer the effects of on-going climatic and land-use changes. These additional biotic  
147 drivers include community evenness, which can both increase or decrease synchrony (1)  
148 or the presence of more stable species, **for example**, characterized by more conservative  
149 resource strategies (20). Long-term empirical data from natural communities can help us  
150 reveal the real-world effects of biotic drivers on community stability (6).

151 Here we explore the generality of biodiversity-synchrony-stability relationships,  
152 and their implications in a global change context, across multiple ecosystems and a  
153 wide range of environments. We compiled data from 7788 natural and semi-natural  
154 vegetation plots that had annual measurements spanning at least six years, sourced from  
155 79 data sets distributed across the World (*SI Appendix*, Fig. S1). Most of the data sets  
156 include information about human activities related to global change through the  
157 application of experimental treatments, including fertilization, herbivore exclusion,  
158 grazing, fire and climate manipulations (hereafter environmental treatments).  
159 Biodiversity, synchrony and stability are known to vary in response to climate and land-  
160 use, although knowledge of such responses is limited **by lack of comparative data across**  
161 **major habitats** and geographic extent (8, 13, 21). The compiled data allowed us to  
162 compare the relationships between species richness, synchrony [using the *log V* index,  
163 (21)] and stability against theoretical predictions (summarized in Fig. 1), across  
164 vegetation types, climates, and land-uses.

165

## 166 **Results and Discussion**

### 167 **Interplay between species richness, synchrony and stability**

168 Our results confirmed the general prevalence of negative synchrony-stability  
169 relationships: 71% of the data sets exhibited negative and significant relationships ( $R^2_m$

170 = 0.19, i.e. variance explained by the fixed effects over all individual plots; Fig. 1b). We  
171 found similar results for other synchrony indices (*SI Appendix*, Figs. S2a-c). These  
172 findings support theoretical predictions (Fig. 1a) and previous empirical evidence (2, 6,  
173 11) that lower levels of synchrony in species fluctuations stabilize overall community  
174 abundance, despite the large range of vegetation types, environmental treatments, and  
175 biogeographic regions we considered.

176 Our results highlight a second global pattern consistent with theory (Fig. 1c):  
177 higher species richness was associated with greater community stability ( $R^2_m = 0.06$ ;  
178 Fig. 1d). However, this relationship was not nearly as strong: only 29% of the data sets  
179 showed a positive and significant relationship. The high proportion of non-significant  
180 species richness-stability relationships was unexpected, as species richness is generally  
181 considered one of the strongest drivers of stability (8–10, 22). Nevertheless, in  
182 observational data sets species richness may covary with other factors that influence  
183 inter-annual community variability, potentially masking any direct effect of species  
184 richness (23).

185 Species richness was positively and significantly associated with synchrony  
186 across all studies, and the expected negative relationship predicted by theory was found  
187 in only 8% of our data sets (Fig. 1f). Such low frequencies of negative richness-  
188 synchrony relationships contradict both theoretical predictions (Fig. 1e) and previous  
189 studies. For instance, a recent richness-manipulated experimental study showed a  
190 negative relationship between richness and synchrony (24), although this could be  
191 driven by the low levels of species richness applied in that experiment. We note that in  
192 natural or semi-natural communities, such as those analyzed here, richness often  
193 exceeds the low levels commonly applied in experimental studies that manipulate  
194 richness. Our results showed that while the relationship between synchrony and species

195 richness across data sets depended on the index of synchrony considered (Figs. 1f, *SI*  
196 *Appendix*, S2a-c and see Supplementary Text S1 and S2 for expanded information), in  
197 most cases it was relatively weak. Our results thus provide only partial support for the  
198 hypothesis that more diverse communities are more stable due to the negative effect of  
199 richness on synchrony (6, but see 13, 21). Indeed, we expected to observe a negative  
200 relationship between species richness and synchrony, particularly for those plots and  
201 data sets where the relationship between species richness and stability was strong.

202 To better understand our results, we explored a random fluctuation scenario  
203 which we approximated using null models that disrupt synchrony patterns between co-  
204 occurring species (see methods and *SI Appendix*, Supplementary Text S2). Specifically,  
205 we compared the relationships observed among richness, synchrony and stability  
206 against values expected under random species fluctuations. We also considered  
207 potential mathematical constraints on these relationships (*SI Appendix*, Supplementary  
208 Text S1 and S2). This modelling exercise revealed that the observed relationship  
209 between species richness and stability was weaker than expected under random species  
210 fluctuations (observed relationship  $R^2_m = 0.059$ ; expected relationship  $R^2_m = 0.157$ ).  
211 However, the relationship between synchrony and stability was greater than expected  
212 under the null model (observed relationship  $R^2_m = 0.191$ ; expected relationship  $R^2_m =$   
213  $0.021$ ; *SI Appendix*, Supplementary Text S2), particularly for the index of synchrony we  
214 focused on the main text. **Note, also, that for this index the observed relationship**  
215 **between richness and synchrony was lower than expected by chance (observed**  
216 **relationship  $R^2_m = 0.024$ ; expected relationship  $R^2_m = 0.082$ ; see Methods) and very**  
217 **weak. Most importantly, synchrony between species was higher than expected under the**  
218 random fluctuations scenario, regardless of the index used (based on paired t-test,  $P <$   
219  $0.001$ ;  $t = 6.38$ ; mean observed synchrony =  $-0.02$  and mean expected synchrony = -



220 0.08). These findings show that, in natural ecosystems, synchrony in species  
221 abundances (positive covariances) are more common than random fluctuations or  
222 negative covariances (25), likely because many species-rich communities contain  
223 ecologically similar species, with similar responses to weather (19, 26). When  
224 synchrony is greater than expected under random fluctuations, the effect of richness on  
225 synchrony and stability will be reduced [*SI Appendix*, Supplementary Text S1 (1, 19)].  
226 Our results provide empirical evidence that, for a wide range of ecosystems, species  
227 richness does promote stability, but this effect is not necessarily caused by a direct,  
228 negative effect of richness on synchrony.

229

### 230 **Predictors of Ecosystem Stability**

231 We examined whether synchrony and stability are mediated by different drivers, an  
232 issue that is gaining momentum in a global change context (6, 7, 21). We evaluated the  
233 effect of climate, vegetation type, environmental treatments and biotic attributes  
234 (percentage of woody species, species evenness and richness) on synchrony and  
235 community stability (*SI Appendix*, Table S1). Overall, the combined effect of  
236 environmental treatments reduced both temporal synchrony and stability (Figs. 2a and  
237 2b). While the effect size of the combined treatments was small compared to biotic  
238 factors (*SI Appendix*, Table S1), this mostly reflects opposing effects of different  
239 treatment types (*SI Appendix*, see Supplementary text S3 for expanded information).

240       Using only those data sets with similar treatments and associated control plots  
241 (fertilization, herbivore exclusion, grazing intensification, removal plant species, fire  
242 and manipulative climate-change drivers), we ran separate analyses to disentangle the  
243 effect of the environmental treatments on synchrony and stability. Fertilization and  
244 herbivore exclusion significantly decreased synchrony, whereas intensification of

245 grazing significantly increased synchrony (Fig. 2c). These relationships were partially  
246 unexpected because previous studies have shown that fertilization could promote  
247 synchrony (10) while grazing intensification could decrease it (13). However, in  
248 agreement with our results, Lepš *et al.* (21) demonstrated in a local study that while  
249 nutrient enrichment increases competition among plant species, it also decreases  
250 stability by increasing differences in productivity between favourable and unfavourable  
251 years. This could override the potential compensatory dynamics due to synchrony.  
252 Moreover, herbivore exclusion or a reduction in grazing intensity acted to increase  
253 community stability (Fig. 2d). These results suggest that herbivory affects interspecific  
254 competition, promoting the species best-adapted to grazing, but reducing the year-to-  
255 year stability of the community (21). Overall, these results show that changes in  
256 environmental drivers, associated to global change scenarios, can disrupt the interplay  
257 between diversity, synchrony and stability, even reversing the expected effects of biotic  
258 drivers on stability. Thus the joint consideration of a wide variety of factors provides  
259 novel insights into the relationships underlying synchrony and stability, enhancing the  
260 future prediction of community stability in the face of global changes.

261       It should be noted that nutrient addition and/or grazing pressure could promote  
262 directional changes in species composition, with some species increasing over the years  
263 and others decreasing (27). This could cause a decrease in synchrony values for indices  
264 studied here (28), with the indices not only reflecting year-to-year fluctuations due to  
265 compensatory dynamics but also these long-term trends. More research is certainly  
266 needed in the future to account for the effect of directional trends on the interplay of  
267 biotic and abiotic effects on stability.

268       We found that forest understorey vegetation was more synchronous and less  
269 stable than grasslands, shrublands and savannas (Fig. 2b), similarly to Blüthgen *et al.*

270 (13). We suggest that forest understorey vegetation has weaker compensatory effects  
271 that lead to destabilization. Also, this result could be related to the fact that we excluded  
272 from the analyses the tree layer, i.e. the most stable vegetation layers in these systems.  
273 Alternatively, this vegetation might support a greater proportion of rare species, which  
274 benefit from shared favourable conditions (29) increasing the synchrony of the  
275 community. Finally, communities with a greater proportion of woody species were  
276 more stable. The longer life span of woody species and their structural storage of carbon  
277 and nutrients should buffer them against environmental fluctuations and the fluctuations  
278 of other species, although we note that longer measurement timescales may be required  
279 to accurately capture their dynamics.

280 Finally, we found evidence of a positive evenness-synchrony association (Fig.  
281 2a) and a negative evenness-stability association (Fig. 2b). In other words, low  
282 synchrony is more common in communities with low evenness that are dominated by a  
283 few species. These communities appear to fluctuate less and are **therefore** more stable  
284 (30, 31). This finding suggests two potential ecological mechanisms. First, these few  
285 species could be the best-adapted species and tend to perform **well across years (i.e.**  
286 **have comparatively little fluctuations)**, thus promoting stability. **In some cases, for**  
287 **example, species with slower growth strategies are locally more abundant and stable in**  
288 **time (20)**. Second, a small number of dominant species with different adaptations  
289 (different traits, 21, 32, 33) could lead to decreased synchrony and increased stability at  
290 the community level. If synchrony is a common feature of vegetation [as suggested by  
291 our study and in Houlihan et al. (25)], evenness can have an effect on stability via  
292 synchrony (Fig. 3). Low synchrony among a small number of dominant species could  
293 **thus** represent an important stabilizing effect in ecosystems worldwide.

294

295 **Direct and indirect effects of abiotic and biotic attributes on community stability**

296 To clarify the ensemble of directional effects of abiotic and biotic factors on community  
297 stability, we generated a piecewise structural equation model (Fig. 3). Our model  
298 explained 88% of the variance in community stability, and confirmed that the most  
299 important determinant of stability was the direct negative effect of synchrony.  
300 Analogous results were found when we evaluated either individual habitats or the  
301 control plots among habitats (*SI Appendix*, Figs. S3 and S4) or when other synchrony  
302 indices were used (*SI Appendix*, Figs. S5a and S5b). Further, mean annual temperature  
303 showed a direct, negative effect on stability, as in other studies (6), which was further  
304 reinforced via its indirect effects on evenness, species richness and synchrony (Fig. 3).  
305 Communities in more variable climates, such as Mediterranean environments, should  
306 show large variation in productivity from year to year, increasing synchrony between  
307 species and decreasing stability of the whole community. Again, the positive  
308 associations between species richness-synchrony and evenness-synchrony suggest that  
309 the stabilizing effect of communities originates from lower synchrony among the  
310 dominant species (34) rather than by the number of species *per se* (15, 30), emphasizing  
311 the role of evenness in the distribution of abundance over time.

312 Overall, this study demonstrates the consistent cross-system importance of the  
313 interplay among species richness, synchrony and environmental parameters in the  
314 prediction of community stability. As expected, low synchrony and high species  
315 richness defined the primary stabilizing pattern of communities (9). However, contrary  
316 to expectation, the stabilizing effects of species richness via synchrony were relatively  
317 weak. Yet, despite a prevalence of synchrony between species found in our  
318 communities, richness had a net positive association with stability (direct effect +  
319 indirect effects = 0.23; Fig. 3), implying an important effect of richness unrelated with

320 synchrony. Environmental factors associated with different global change drivers also  
321 directly or indirectly affect stability, and have the potential to reverse the effects of  
322 biodiversity and synchrony on stability, although biotic factors generally had a stronger  
323 effect. Our results suggest that interventions aiming to buffer ecosystems against the  
324 effects of increasing environmental fluctuations should focus on promoting the  
325 maintenance or selection of dominant species with different adaptations or strategies  
326 that will result in low synchrony, rather than by focusing on increasing species richness  
327 *per se*. Further, the evaluation of the direct effects of evenness and environmental  
328 drivers on stability adds new insights on the complex underlying biotic and abiotic  
329 relationships. To consider these different drivers of stability in concert is critical for  
330 defining the potential of communities to remain stable in a global change context.

331

## 332 **Methods**

333 We used data from 79 plant community data sets where permanent or semi-permanent  
334 plots of natural and semi-natural vegetation have been consistently sampled over a  
335 period of 6 to 99 years (*SI Appendix*, Fig. S1 and S6, Table S2 and Supplementary Text  
336 S4). We focused our analyses on vascular plants as the main primary producers  
337 affecting subsequent trophic levels and ecosystem functioning. These data sets have  
338 some differences, such as the method used to quantify *abundance* (*e.g.* aboveground  
339 biomass, visual species cover estimates and species individual frequencies), plot size  
340 (median = 1 m<sup>2</sup>; range = 0.04 to 400 m<sup>2</sup>), vegetation type (grassland, shrubland,  
341 savanna, forest and salt marsh), and number of sampling dates (median = 11.5; range =  
342 6 to 38). The studies encompassed different localities with different species pools and  
343 different types of vegetation responding to different types of treatments. The total

344 number of individual plots was 7788 across the 79 data sets (number of observations ~  
345 190900).

346

### 347 **Climatic data**

348 We collected climatic information related to temperature and precipitation for each of  
349 the 7788 plots using WorldClim ([www.worldclim.org](http://www.worldclim.org)) where location coordinates were  
350 available. Where these were not available, weather data were derived from the study  
351 centroid. We selected four variables: mean annual temperature (°C) and mean annual  
352 precipitation (mm), related to annual trends, and mean annual temperature range and  
353 coefficient of variation of precipitation within years as proxies for annual seasonality  
354 (6). These variables were selected from the 19 available WorldClim climatic variables  
355 because they describe relatively independent climatic features and account for most of  
356 the other climatic relationships observed with our data (see climatic variable correlation  
357 in *SI Appendix*, Table S3).

358

### 359 **Biotic attributes**

360 In each plot, we calculated stability over time as the inverse of the coefficient of  
361 variation (standard deviation/mean) of the year-to-year fluctuations of total *abundance*  
362 of that community. This has been widely used as a reliable estimator of temporal  
363 invariability (35). Standard deviation was based on  $n-1$  degrees of freedom. We only  
364 included data sets using percentage cover as an estimate of community structure if the  
365 summed cover was not constrained.

366 Although we did not measure ecosystem services directly, multiple studies  
367 highlight the importance of a stable vegetation (primary producers) for a stable delivery  
368 of multiple key ecosystem processes. For example, *biomass* or *abundance* are often

369 considered to be ecosystem functions in their own right (e.g. forage production and  
 370 carbon sink), while these can also act as a proxy or driver of other functions, including  
 371 litter quantity, soil organic matter, evapotranspiration or erosion control. Clearly, the  
 372 value of stability depends on its relationship to the provision of specific ecosystem  
 373 services, and temporal invariability does not necessarily imply a positive effect on the  
 374 ecosystem service of interest. Our study aims at identifying ecological drivers of  
 375 stability at a global scale.

376 In each plot, we also calculated various indices that characterize the biotic  
 377 attributes of the community averaged over all annual observations: average species  
 378 richness [average number of species (2, 36)], the average percentage of woody species  
 379 per year, and evenness (using the  $E_{var}$  index) (37).

$$380 \quad E_{var} = 1 - 2/\pi \arctan \left\{ \frac{\sum_{s=1}^S (\ln(x_s) - \sum_{t=1}^S \ln(x_t) / S)^2 / S}{\sum_{t=1}^S \ln(x_t)} \right\} \quad (1)$$

381 where  $S$  is total number of species in the community and  $x_s$  is the abundance of  
 382 the  $s$ -th species. Finally, we calculated synchrony (log-variance ratio index:  $\log V$ ) (21)  
 383 as follows:

$$384 \quad \log V = \ln \left( \frac{\text{var}(\sum_{i=1}^S x_i)}{\sum_{i=1}^S \text{var}(x_i)} \right) \quad (2)$$

385 where  $x_i$  is the vector of abundances of the  $i$ -th species over time. The  $\log V$   
 386 index ranges from  $-\ln(S)$  to  $+\ln(S)$ . For this index, positive values indicate a common  
 387 response of the species (synchrony, formally positive sum of covariances in the  
 388 variance-covariance matrix), while values close to zero indicate a predominance of  
 389 random fluctuations, and negative values indicate negative covariation between species.

390 One theoretical issue of this index is that its upper limit is a function of species richness  
 391 and evenness, questioning its independence from those parameters. Our results,  
 392 however, were not affected by this constraint. It is important to note that the observed  
 393 index value can vary considerably within its theoretical range; in fact the relationship

394 between richness and  $\log V$  index is very weak. The chance of reaching maximum  
395 synchrony decreases with the number of species. To reach maximum synchrony, there  
396 must always be perfect synchrony between all species pairs, no matter how many  
397 species are in the community [i.e. with  $n$  species, the correlation of  $n(n-1)/2$  pairs must  
398 be perfect (i.e. 1) within each pair]. The values of synchrony that would be close to the  
399 maximum 1 were not present in real communities (such as those that are the focus of  
400 this manuscript). Thus, the upper limit of  $\log V$ , which represents the caveat to the use  
401 of this metric, is not invalidating our results.

402 To ensure that our results were not biased by the choice of this index, we  
403 calculated other commonly used indices, specifically the Gross (11), Gross' weighted  
404 (13) and phi (38) synchrony indices. Following Blüthgen *et al.* (13), we weighted the  
405 abundance of species to decrease the influence of rare species that can vary substantially  
406 while having a negligible abundance. Both Gross and Gross' weighted synchrony  
407 indices were positively correlated with  $\log V$  index ( $r = 0.75$  and  $0.86$ , respectively, *SI*  
408 *Appendix*, Table S4) and gave concordant results. The phi synchrony index was also  
409 positively correlated with the  $\log V$  index but negatively with species richness ( $r = 0.48$   
410 and  $0.41$ , respectively, *SI Appendix*, Table S4), an expected output as this index builds  
411 in the decrease in synchrony with increasing species richness expected when species  
412 have independent population dynamics (38). We only present the results of  $\log V$  in the  
413 main text both for clarity and because the models with this index had the lowest AIC  
414 values and explained more variance ( $R^2_m = 0.59$ , *SI Appendix*, Table S1) than those  
415 using the alternate indices. Similarly, this index showed a greater difference between the  
416 observed synchrony-stability relationships and the ones generated by null-models (*SI*  
417 *Appendix*, see Supplementary texts S2 for expanded information).



418 Previous research has identified the relationship between stability and  
419 synchrony, both in biological (12) and mathematical terms (1). However, it has also  
420 been shown that stability is affected by a number of other factors (1, 8, 12, 21, 24).  
421 Given these multiple influences, the relationship between synchrony and stability would  
422 not necessarily be expected to be consistently significant or characterised by a strong  
423 correlation. We assessed this relationship for the different indices in comparison with  
424 null-models that assume random, independent species fluctuations (*SI Appendix*, see  
425 Supplementary texts S1 and S2 for expanded information).

426 We also considered the vegetation type of each plot based on the  
427 characterization of the community by the authors of the study (grassland, shrubland,  
428 savanna, forest and salt marsh). Savanna was characterized as a grassland scattered with  
429 shrubs and/or trees while maintaining an open canopy. For forest plots, we restricted our  
430 analysis to data sets that measured understorey vegetation.

#### 431 **Analysis**

432 **Analysis**

433 Linear models were used to evaluate the relationships between: i) synchrony and species  
434 richness; ii) species richness and stability; and iii) synchrony and stability. In all cases,  
435 richness and stability were ln-transformed to improve their normality. We obtained the  
436 slope and the significance for these relationships individually for each of the 79 data  
437 sets as well as for all the plots together. We used a null model approach to compare the  
438 observed values of stability and synchrony and observed richness-synchrony and  
439 richness-stability relationships to expected values under a random fluctuation scenario.  
440 To do so, we randomized species abundances within a plot across years, by means of  
441 torus randomizations (also referred to as cyclic shifts). This approach preserves the  
442 temporal sequence of values within a species, but changes the starting year. In each  
443 individual plot, the sequence of abundance values of each species was shifted 999 times,

444 using a modification of the ‘cyclic\_shift’ function in the *codyn* package for the R  
445 statistical software (39). This procedure kept the total (i.e. summed) species abundance  
446 constant for each species but varied (and therefore disconnected) the temporal co-  
447 incidence of species abundances within years. Based on the 999 randomizations, we  
448 calculated values of mean expected synchrony and stability. We used a paired t-test to  
449 evaluate the relationship between observed and expected values of synchrony. We then  
450 tested the relationship between observed species richness and (i) observed and expected  
451 synchrony and (ii) observed and expected stability, using linear mixed-effects models  
452 with data set as a random factor. Additionally, we used the same models to test the  
453 relationship between observed synchrony and stability, and expected synchrony and  
454 stability.

455         We performed linear mixed-effects models over all individual plots ( $n = 7788$ )  
456 to assess the effects of the abiotic and biotic variables on synchrony ( $\log V$ ). We  
457 included climatic data, vegetation type, percentage of woody species, evenness, species  
458 richness, number of years each plot was sampled and environmental treatments as  
459 predictors in the model; data set was a random factor. Environmental treatments  
460 constituted a binary variable (0 = control plots *vs* 1 = environmental treatments). The  
461 mean and confidence interval of the parameter estimates of the predictors were used to  
462 model their effects on synchrony values among all the plots of the 79 studies. Mean  
463 annual precipitation, temperature annual range, richness and stability were ln-  
464 transformed to improve their normality. All predictors were centred on their mean and  
465 standardized by their standard deviation. For vegetation type, the parameter estimates  
466 were obtained by fixing grasslands as a reference level for the other habitats. We  
467 analyzed the effects of the biotic and abiotic factors and synchrony values on stability,  
468 using the same approaches previously described. Although plot size was originally

469 included in our model, this variable was not significant ( $\chi^2 < 0.01$ ;  $P = 0.95$ ) so was  
470 removed as predictor. To evaluate the individual effect of each environmental treatment  
471 on synchrony values and stability, treatments were grouped into six categories  
472 (fertilization, herbivore exclusion, grazing intensity, removal, fire and manipulative  
473 climate-change drivers), retaining only data sets where these treatments were applied or  
474 assessed.

475       Finally, we conducted a stepwise selection of a piecewise structural equation  
476 model [SEM (40)] to test direct and indirect pathways of biotic and abiotic factors on  
477 stability. A piecewise SEM is a confirmatory path analysis using a d-step approach (41,  
478 42). This analysis is a flexible framework to incorporate different model structures,  
479 distributions and assumptions. This method is based on an acyclic graph that  
480 summarizes the hypothetical relationships between variables to be tested using the C  
481 statistic (43). We built an initial SEM containing all possible biotic and abiotic  
482 relationships, independent of the vegetation type evaluated. Then, we used the Akaike  
483 information criterion (AIC) to select the minimal and best model (43) based on the  
484 initial SEM, using the stepAIC procedure (40). This process selects the most important  
485 paths and removes the majority of non-significant paths. Standardized path coefficients  
486 were used to measure the direct and indirect effects of predictors (44). We conducted  
487 the SEM analyses across all individual plots ( $n = 7788$ ), for non-treatment plots across  
488 all habitats ( $n = 4013$ ), and for plots of each vegetation type separately (except in salt  
489 marsh). In all the models, data sets were considered as a random factor.

490       All analyses were carried out with R (R Core Team, 2016) (45), using packages  
491 piecewiseSEM (46), lme4 (47), and modified source code in codyn (39).

492

493 **Data Availability** The data that support the findings of this study are available at  
494 Figshare (48).

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514 F.B., T.G, A.V., C.C. and L.G. collected or provided the data used in this analysis. E.V.  
515 and T.G. assembled data. E.V., L.G. and F.B performed the analyses. E.V. wrote the  
516 first draft of the manuscript and all the authors (especially F.B. and L.G.) contributed  
517 substantially to the revisions. The authors declare no competing interest.

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- 632

633 **Figure Legends**

634

635 **Fig. 1.** Relationships between synchrony and stability (a, b), richness and stability (c, d),  
636 and richness and synchrony (e, f). Richness and stability were ln-transformed. Left  
637 panels (a, c, e) are the schematic representation of these relationships following  
638 theoretical predictions (1, 12, 19, 49). Right panels depict these relationships for each  
639 data set (b, d, f;  $n = 79$ ). Red, blue and grey lines respectively represent the statistically  
640 significant positive, negative and non-significant slopes. Black lines show each  
641 relationship based on all plots ( $n = 7788$ ), using a linear mixed-effects model with data  
642 sets as a random factor; these were all statistically significant. The synchrony index was  
643  $\log V(21)$ .

644 **Fig. 2.** Effects of multiple abiotic and biotic drivers on the synchrony values (a, c) and  
645 stability (b, d) of the different communities. We show the averaged parameter estimates  
646 (standardized regression coefficients) of model predictors, the associated 95%  
647 confidence intervals. In panels a and b, all the predictors were evaluated together using  
648 general linear mixed-effect models ( $n = 7788$ ). The colours represent the different  
649 drivers of vegetation type (orange, grassland is the reference level), climatic data (blue),  
650 biotic attributes (green), number of measurements (grey) and global change treatments  
651 (black). The effects of each environmental treatment on synchrony values and stability  
652 (c, d) were evaluated separately and only for the studies where each driver was  
653 measured [fertilization:  $n = 1058$ , DS (number of data sets evaluated) = 17; herbivore  
654 exclusion:  $n = 2284$ , DS = 19; grazing intensity:  $n = 1920$ , DS = 24; removal plant  
655 species:  $n = 518$ , DS = 8; fire:  $n = 974$ , DS = 11; manipulative climate change:  $n = 122$ ,  
656 DS = 5].



657 **Fig. 3.** Piecewise structural equation model showing the direct and indirect effects of  
658 multiple abiotic and biotic drivers on the stability across the 79 data set (Fisher's C  
659 statistic:  $C = 14.96$ ,  $p = 0.134$ ,  $n = 7788$ ). Marginal ( $R^2_m$ ) values showing variance  
660 explained by the fixed effects, and conditional ( $R^2_c$ ) values showing variance explained  
661 by the entire model, are provided for each response variable. Solid lines represent  
662 positive effects, while dashed lines indicate negative effects. Blue and red lines  
663 represent statistically significant effects and grey lines non-significant effects. The  
664 width of each arrow is proportional to the standardized path coefficients (more  
665 information *SI Appendix*, Table S5).