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# 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 ecosystem  
95 services, such as food and forage production, carbon sequestration and soil fertility.  
96 Greater biodiversity is expected to enhance stability across years by decreasing synchrony  
97 among species, but the drivers of stability in nature remain poorly resolved. Our analysis  
98 of time-series from 79 data sets across the world showed that stability was associated  
99 more strongly with the degree of synchrony among dominant species than with species  
100 richness. The relatively weak influence of species richness is consistent with theory  
101 predicting that the effect of richness on stability weakens when synchrony is higher than  
102 expected under random fluctuations, which was the case in most communities. Land  
103 management, nutrient addition and climate change treatments, had relatively weak and  
104 varying effects on stability, modifying how species richness, synchrony and stability  
105 interact. Our results demonstrate the prevalence of biotic drivers on ecosystem stability,  
106 with the potential for environmental drivers to alter the intricate relationship among  
107 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 remains  
115 controversial. By analyzing long-term data from natural and semi-natural ecosystems  
116 across the globe, we found that the degree of synchrony among dominant species was the  
117 main driver of stability, rather than species richness *per se*. These biotic effects overrode  
118 environmental drivers, which influenced the stability of communities by modulating the  
119 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 often  
123 measured as the inverse coefficient of variation across years of community abundance or  
124 biomass, the main drivers of stability remain elusive (5). Both abiotic and biotic drivers  
125 [e.g., climate, land-use and species diversity (6–8)] are expected to govern community  
126 stability. Among biotic drivers, the hypothesis that increases in species diversity begets  
127 stability in communities and ecosystems [Fig. 1 (2, 9–11)] has generated ongoing debate  
128 (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 over  
135 time. Decreased synchrony, which is predicted to stabilize communities (Fig. 1a), can  
136 result from species-specific responses to environmental fluctuations (15–17) and from  
137 temporal changes in competitive hierarchies (18), as well as stochastic fluctuations.  
138 Importantly, it is expected that species richness can increase stability (Fig. 1c) by  
139 decreasing synchrony (Fig. 1e). This positive effect of richness on stability can be, in fact,  
140 a result of an increased chance that the community will contain species with differing  
141 responses to abiotic drivers or competition, leading to a reduction in synchrony (12).  
142 However, the effect of richness on stability should weaken when synchrony is higher than  
143 expected if species were fluctuating randomly and independently [*SI Appendix*, see  
144 Supplementary text S1 for expanded information (19)]. At the same time, other biotic

145 drivers, together with richness and synchrony, have the potential to interact and buffer  
146 the effects of on-going climatic and land-use changes. These additional biotic drivers  
147 include community evenness, which can both increase or decrease synchrony (1) or the  
148 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 wide  
153 range of environments. We compiled data from 7788 natural and semi-natural vegetation  
154 plots that had annual measurements spanning at least six years, sourced from 79 data sets  
155 distributed across the World (*SI Appendix*, Fig. S1). Most of the data sets include  
156 information about human activities related to global change through the application of  
157 experimental treatments, including fertilization, herbivore exclusion, grazing, fire and  
158 climate manipulations (hereafter environmental treatments). Biodiversity, synchrony and  
159 stability are known to vary in response to climate and land-use, although knowledge of  
160 such responses is limited by lack of comparative data across major habitats and  
161 geographic extent (8, 13, 21). The compiled data allowed us to compare the relationships  
162 between species richness, synchrony [using the *log V* index, (21)] and stability against  
163 theoretical predictions (summarized in Fig. 1), across vegetation types, climates, and  
164 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 ( $R^2_m = 0.06$ ; Fig.  
178 1d). However, this relationship was not nearly as strong: only 29% of the data sets showed  
179 a positive and significant relationship. The high proportion of non-significant species  
180 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 inter-  
183 annual community variability, potentially masking any direct effect of species richness  
184 (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-synchrony  
188 relationships contradict both theoretical predictions (Fig. 1e) and previous studies. For  
189 instance, a recent richness-manipulated experimental study showed a negative  
190 relationship between richness and synchrony (24), although this could be driven by the  
191 low levels of species richness applied in that experiment. We note that in natural or semi-  
192 natural communities, such as those analyzed here, richness often exceeds the low levels  
193 commonly applied in experimental studies that manipulate richness. Our results showed  
194 that while the relationship between synchrony and species richness across data sets

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

202 To better understand our results, we explored a random fluctuation scenario which  
203 we approximated using null models that disrupt synchrony patterns between co-occurring  
204 species (see methods and *SI Appendix*, Supplementary Text S2). Specifically, we  
205 compared the relationships observed among richness, synchrony and stability against  
206 values expected under random species fluctuations. We also considered potential  
207 mathematical constraints on these relationships (*SI Appendix*, Supplementary Text S1 and  
208 S2). This modelling exercise revealed that the observed relationship between species  
209 richness and stability was weaker than expected under random species fluctuations  
210 (observed relationship  $R^2_m = 0.059$ ; expected relationship  $R^2_m = 0.157$ ). However, the  
211 relationship between synchrony and stability was greater than expected under the null  
212 model (observed relationship  $R^2_m = 0.191$ ; expected relationship  $R^2_m = 0.021$ ; *SI*  
213 *Appendix*, Supplementary Text S2), particularly for the index of synchrony we focused  
214 on the main text. Note, also, that for this index the observed relationship between richness  
215 and synchrony was lower than expected by chance (observed relationship  $R^2_m = 0.024$ ;  
216 expected relationship  $R^2_m = 0.082$ ; see Methods) and very weak. Most importantly,  
217 synchrony between species was higher than expected under the random fluctuations  
218 scenario, regardless of the index used (based on paired t-test,  $P < 0.001$ ;  $t = 6.38$ ; mean  
219 observed synchrony = -0.02 and mean expected synchrony = -0.08). These findings show

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

228

### 229 **Predictors of Ecosystem Stability**

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

239       Using only those data sets with similar treatments and associated control plots  
240 (fertilization, herbivore exclusion, grazing intensification, removal plant species, fire and  
241 manipulative climate-change drivers), we ran separate analyses to disentangle the effect  
242 of the environmental treatments on synchrony and stability. Fertilization and herbivore  
243 exclusion significantly decreased synchrony, whereas intensification of grazing  
244 significantly increased synchrony (Fig. 2c). These relationships were partially unexpected

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

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

267         We found that forest understorey vegetation was more synchronous and less stable  
268 than grasslands, shrublands and savannas (Fig. 2b), similarly to Blüthgen *et al.* (13). We  
269 suggest that forest understorey vegetation has weaker compensatory effects that lead to

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

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

293

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

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

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

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

330

## 331 **Methods**

332 We used data from 79 plant community data sets where permanent or semi-permanent  
333 plots of natural and semi-natural vegetation have been consistently sampled over a period  
334 of 6 to 99 years (*SI Appendix*, Fig. S1 and S6, Table S2 and Supplementary Text S4). We  
335 focused our analyses on vascular plants as the main primary producers affecting  
336 subsequent trophic levels and ecosystem functioning. These data sets have some  
337 differences, such as the method used to quantify *abundance* (*e.g.* aboveground biomass,  
338 visual species cover estimates and species individual frequencies), plot size (median = 1  
339 m<sup>2</sup>; range = 0.04 to 400 m<sup>2</sup>), vegetation type (grassland, shrubland, savanna, forest and  
340 salt marsh), and number of sampling dates (median = 11.5; range = 6 to 38). The studies  
341 encompassed different localities with different species pools and different types of  
342 vegetation responding to different types of treatments. The total number of individual  
343 plots was 7788 across the 79 data sets (number of observations ~ 190900).

344

345 **Climatic data**

346 We collected climatic information related to temperature and precipitation for each of the  
347 7788 plots using WorldClim (www.worldclim.org) where location coordinates were  
348 available. Where these were not available, weather data were derived from the study  
349 centroid. We selected four variables: mean annual temperature (°C) and mean annual  
350 precipitation (mm), related to annual trends, and mean annual temperature range and  
351 coefficient of variation of precipitation within years as proxies for annual seasonality (6).  
352 These variables were selected from the 19 available WorldClim climatic variables  
353 because they describe relatively independent climatic features and account for most of  
354 the other climatic relationships observed with our data (see climatic variable correlation  
355 in *SI Appendix*, Table S3).

356

357 **Biotic attributes**

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

364 Although we did not measure ecosystem services directly, multiple studies  
365 highlight the importance of a stable vegetation (primary producers) for a stable delivery  
366 of multiple key ecosystem processes. For example, *biomass* or *abundance* are often  
367 considered to be ecosystem functions in their own right (e.g. forage production and carbon  
368 sink), while these can also act as a proxy or driver of other functions, including litter  
369 quantity, soil organic matter, evapotranspiration or erosion control. Clearly, the value of

370 stability depends on its relationship to the provision of specific ecosystem services, and  
371 temporal invariability does not necessarily imply a positive effect on the ecosystem  
372 service of interest. Our study aims at identifying ecological drivers of stability at a global  
373 scale.

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

$$378 \quad E_{var} = 1 - 2/\pi \arctan \left\{ \frac{\sum_{s=1}^S (\ln(x_s) - \sum_{t=1}^S \ln(x_t) / S)^2 / S}{\sum_{i=1}^S \ln(x_i)} \right\} \quad (1)$$

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

$$382 \quad \log V = \ln \left( \frac{\text{var}(\sum_{i=1}^S x_i)}{\sum_{i=1}^S \text{var}(x_i)} \right) \quad (2)$$

383 where  $x_i$  is the vector of abundances of the  $i$ -th species over time. The  $\log V$  index  
384 ranges from  $-\ln(S)$  to  $+\ln(S)$ . For this index, positive values indicate a common response of  
385 the species (synchrony, formally positive sum of covariances in the variance-covariance  
386 matrix), while values close to zero indicate a predominance of random fluctuations, and  
387 negative values indicate negative covariation between species. One theoretical issue of  
388 this index is that its upper limit is a function of species richness and evenness, questioning  
389 its independence from those parameters. Our results, however, were not affected by this  
390 constraint. It is important to note that the observed index value can vary considerably  
391 within its theoretical range; in fact the relationship between richness and  $\log V$  index is  
392 very weak. The chance of reaching maximum synchrony decreases with the number of  
393 species. To reach maximum synchrony, there must always be perfect synchrony between  
394 all species pairs, no matter how many species are in the community [i.e. with  $n$  species,

395 the correlation of  $n(n-1)/2$  pairs must be perfect (i.e. 1) within each pair]. The values of  
396 synchrony that would be close to the maximum 1 were not present in real communities  
397 (such as those that are the focus of this manuscript). Thus, the upper limit of  $\log V$ , which  
398 represents the caveat to the use of this metric, is not invalidating our results.

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

415 Previous research has identified the relationship between stability and synchrony,  
416 both in biological (12) and mathematical terms (1). However, it has also been shown that  
417 stability is affected by a number of other factors (1, 8, 12, 21, 24). Given these multiple  
418 influences, the relationship between synchrony and stability would not necessarily be  
419 expected to be consistently significant or characterised by a strong correlation. We

420 assessed this relationship for the different indices in comparison with null-models that  
421 assume random, independent species fluctuations (*SI Appendix*, see Supplementary texts  
422 S1 and S2 for expanded information).

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

## 428 **Analysis**

430 Linear models were used to evaluate the relationships between: i) synchrony and species  
431 richness; ii) species richness and stability; and iii) synchrony and stability. In all cases,  
432 richness and stability were ln-transformed to improve their normality. We obtained the  
433 slope and the significance for these relationships individually for each of the 79 data sets  
434 as well as for all the plots together. We used a null model approach to compare the  
435 observed values of stability and synchrony and observed richness-synchrony and  
436 richness-stability relationships to expected values under a random fluctuation scenario.  
437 To do so, we randomized species abundances within a plot across years, by means of  
438 torus randomizations (also referred to as cyclic shifts). This approach preserves the  
439 temporal sequence of values within a species, but changes the starting year. In each  
440 individual plot, the sequence of abundance values of each species was shifted 999 times,  
441 using a modification of the 'cyclic\_shift' function in the *codyn* package for the R  
442 statistical software (39). This procedure kept the total (i.e. summed) species abundance  
443 constant for each species but varied (and therefore disconnected) the temporal co-  
444 incidence of species abundances within years. Based on the 999 randomizations, we  
445 calculated values of mean expected synchrony and stability. We used a paired t-test to

446 evaluate the relationship between observed and expected values of synchrony. We then  
447 tested the relationship between observed species richness and (i) observed and expected  
448 synchrony and (ii) observed and expected stability, using linear mixed-effects models  
449 with data set as a random factor. Additionally, we used the same models to test the  
450 relationship between observed synchrony and stability, and expected synchrony and  
451 stability.

452         We performed linear mixed-effects models over all individual plots ( $n = 7788$ ) to  
453 assess the effects of the abiotic and biotic variables on synchrony ( $\log V$ ). We included  
454 climatic data, vegetation type, percentage of woody species, evenness, species richness,  
455 number of years each plot was sampled and environmental treatments as predictors in the  
456 model; data set was a random factor. Environmental treatments constituted a binary  
457 variable (0 = control plots vs 1 = environmental treatments). The mean and confidence  
458 interval of the parameter estimates of the predictors were used to model their effects on  
459 synchrony values among all the plots of the 79 studies. Mean annual precipitation,  
460 temperature annual range, richness and stability were ln-transformed to improve their  
461 normality. All predictors were centred on their mean and standardized by their standard  
462 deviation. For vegetation type, the parameter estimates were obtained by fixing  
463 grasslands as a reference level for the other habitats. We analyzed the effects of the biotic  
464 and abiotic factors and synchrony values on stability, using the same approaches  
465 previously described. Although plot size was originally included in our model, this  
466 variable was not significant ( $\chi^2 < 0.01$ ;  $P = 0.95$ ) so was removed as predictor. To evaluate  
467 the individual effect of each environmental treatment on synchrony values and stability,  
468 treatments were grouped into six categories (fertilization, herbivore exclusion, grazing  
469 intensity, removal, fire and manipulative climate-change drivers), retaining only data sets  
470 where these treatments were applied or assessed.

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

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

488

489 **Data Availability** The data that support the findings of this study are available at Figshare  
490 (48).

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511 F.B performed the analyses. E.V. wrote the first draft of the manuscript and all the authors  
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628

629 **Figure Legends**

630

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

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

651 **Fig. 3.** Piecewise structural equation model showing the direct and indirect effects of  
652 multiple abiotic and biotic drivers on the stability across the 79 data set (Fisher's C  
653 statistic:  $C = 14.96$ ,  $p = 0.134$ ,  $n = 7788$ ). Marginal ( $R^2_m$ ) values showing variance

654 explained by the fixed effects, and conditional ( $R^2_c$ ) values showing variance explained  
655 by the entire model, are provided for each response variable. Solid lines represent positive  
656 effects, while dashed lines indicate negative effects. Blue and red lines represent  
657 statistically significant effects and grey lines non-significant effects. The width of each  
658 arrow is proportional to the standardized path coefficients (more information *SI Appendix*,  
659 Table S5).