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

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Abstract

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

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

Results and Discussion

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^2m

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 ($R^2m = 0.06$;

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

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

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

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

Predictors of Ecosystem Stability

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

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

grazing significantly increased synchrony (Fig. 2c). These relationships were partially

unexpected because previous studies have shown that fertilization could promote

synchrony (10) while grazing intensification could decrease it (13). However, in

agreement with our results, Lepš *et al.* (21) demonstrated in a local study that while

nutrient enrichment increases competition among plant species, it also decreases

stability by increasing differences in productivity between favourable and unfavourable

years. This could override the potential compensatory dynamics due to synchrony.

Moreover, herbivore exclusion or a reduction in grazing intensity acted to increase

community stability (Fig. 2d). These results suggest that herbivory affects interspecific

competition, promoting the species best-adapted to grazing, but reducing the year-to-

year stability of the community (21). Overall, these results show that changes in

environmental drivers, associated to global change scenarios, can disrupt the interplay

between diversity, synchrony and stability, even reversing the expected effects of biotic

drivers on stability. Thus the joint consideration of a wide variety of factors provides

novel insights into the relationships underlying synchrony and stability, enhancing the

future prediction of community stability in the face of global changes.

It should be noted that nutrient addition and/or grazing pressure could promote

directional changes in species composition, with some species increasing over the years

and others decreasing (27). This could cause a decrease in synchrony values for indices

studied here (28), with the indices not only reflecting year-to-year fluctuations due to

compensatory dynamics but also these long-term trends. More research is certainly

needed in the future to account for the effect of directional trends on the interplay of

biotic and abiotic effects on stability.

We found that forest understorey vegetation was more synchronous and less

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 Houlahan 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

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

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

Overall, this study demonstrates the consistent cross-system importance of the interplay among species richness, synchrony and environmental parameters in the prediction of community stability. As expected, low synchrony and high species richness defined the primary stabilizing pattern of communities (9). However, contrary to expectation, the stabilizing effects of species richness via synchrony were relatively weak. Yet, despite a prevalence of synchrony between species found in our communities, richness had a net positive association with stability (direct effect + 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

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^2; range $= 0.04$ to 400 m^2), 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

Climatic data

348   We collected climatic information related to temperature and precipitation for each of

349   the 7788 plots using WorldClim (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 (ºC) 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

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 $$Evar = 1 - 2/\pi \arctan\left\{\sum_{s=1}^{S}(\ln(x_s) - \sum_{t=1}^{S} ln(x_t)/S)^2/S\right\} \qquad (1)$$

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 $$log V = \ln\left(\frac{var(\Sigma_{i=1}^{S} x_i)}{\Sigma_{i=1}^{S} var(x_i)}\right) \qquad (2)$$

385 where x_i is the vector of abundances of the *i-th* species over time. The *log V*

386 index ranges from -Inf 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

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

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

We performed linear mixed-effects models over all individual plots (n = 7788) to assess the effects of the abiotic and biotic variables on synchrony (*log V*). We included climatic data, vegetation type, percentage of woody species, evenness, species richness, number of years each plot was sampled and environmental treatments as predictors in the model; data set was a random factor. Environmental treatments constituted a binary variable (0 = control plots *vs* 1 = environmental treatments). The mean and confidence interval of the parameter estimates of the predictors were used to model their effects on synchrony values among all the plots of the 79 studies. Mean annual precipitation, temperature annual range, richness and stability were ln-transformed to improve their normality. All predictors were centred on their mean and standardized by their standard deviation. For vegetation type, the parameter estimates were obtained by fixing grasslands as a reference level for the other habitats. We analyzed the effects of the biotic and abiotic factors and synchrony values on stability, 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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632

Figure Legends

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

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

660   explained by the fixed effects, and conditional (R^2c) 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
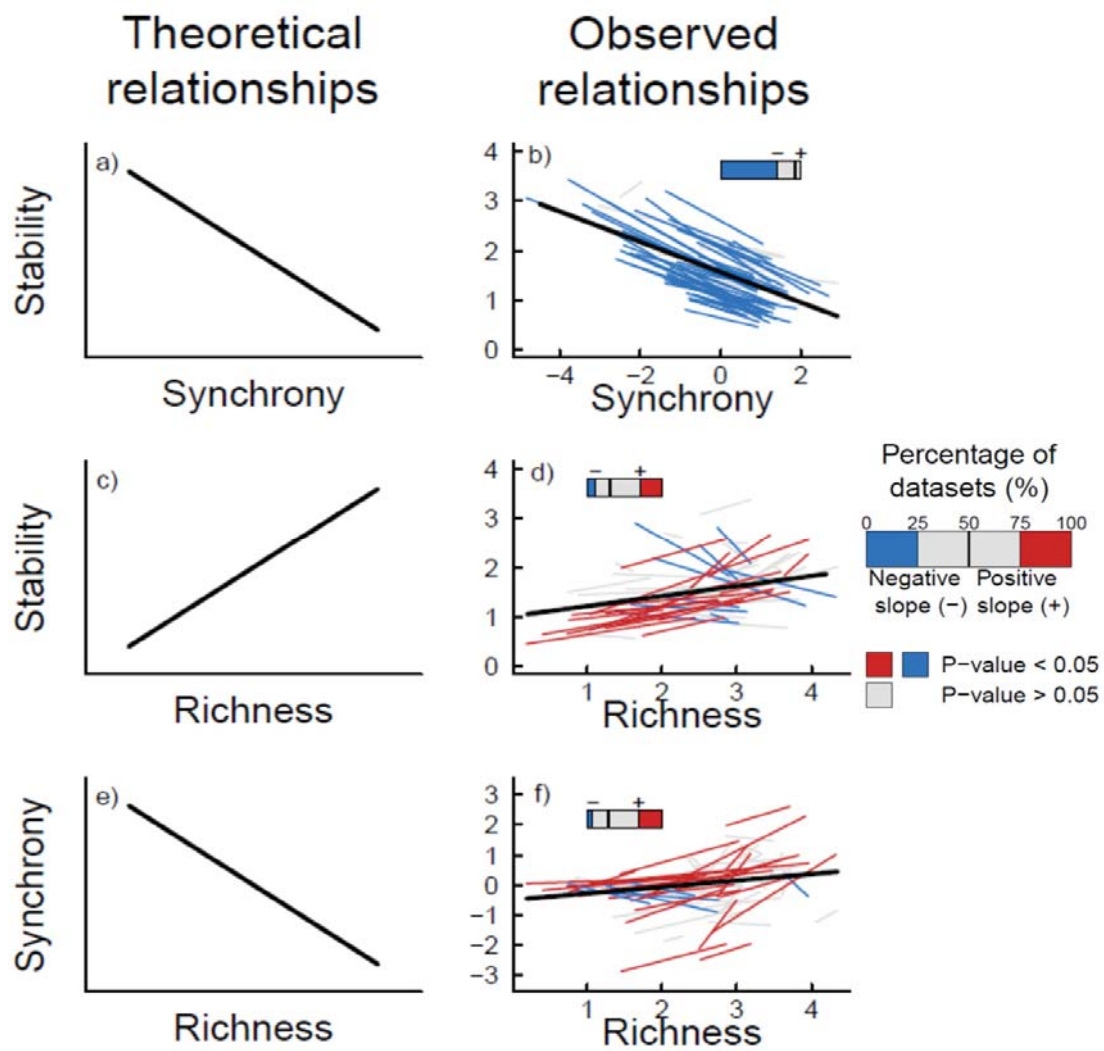
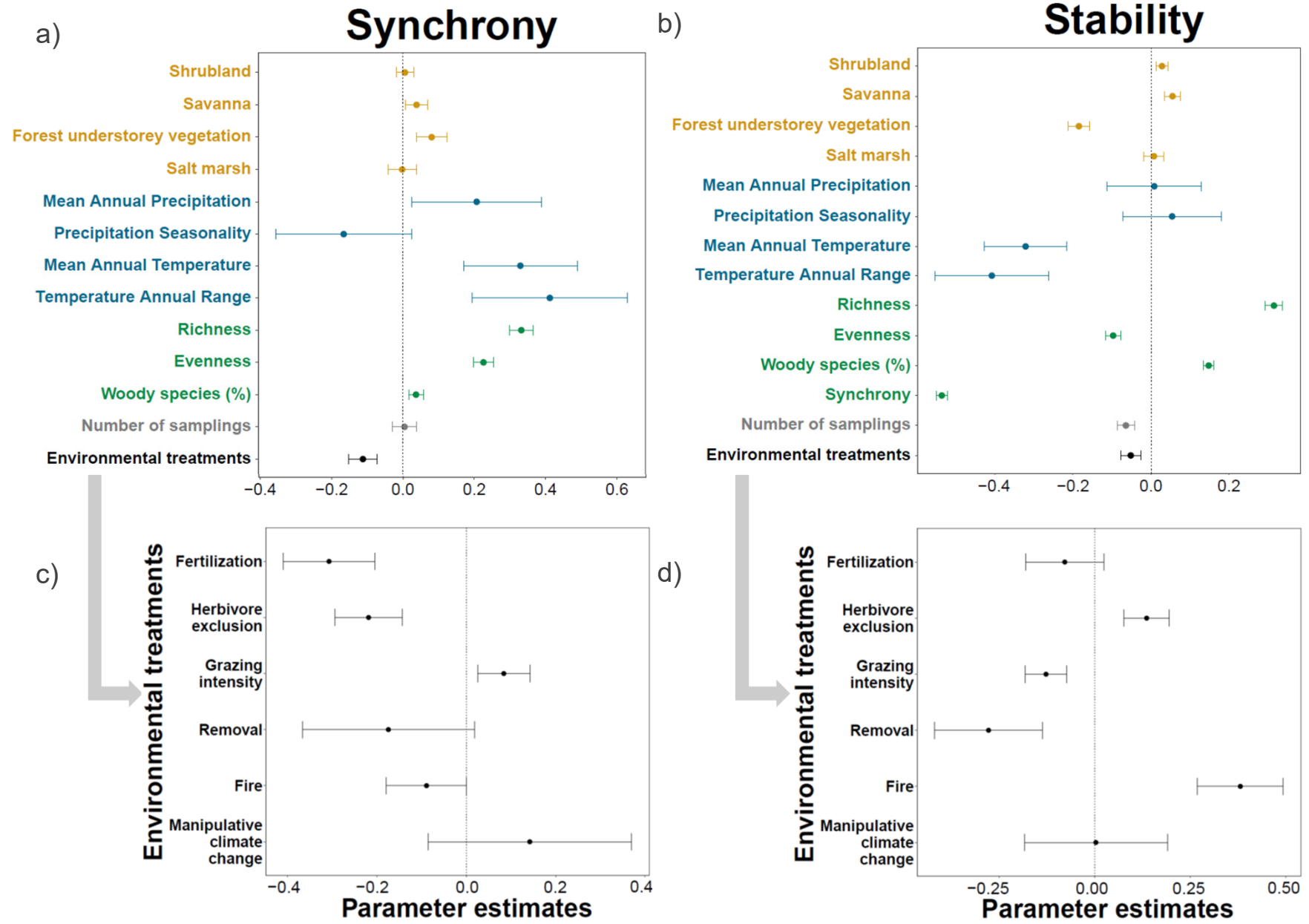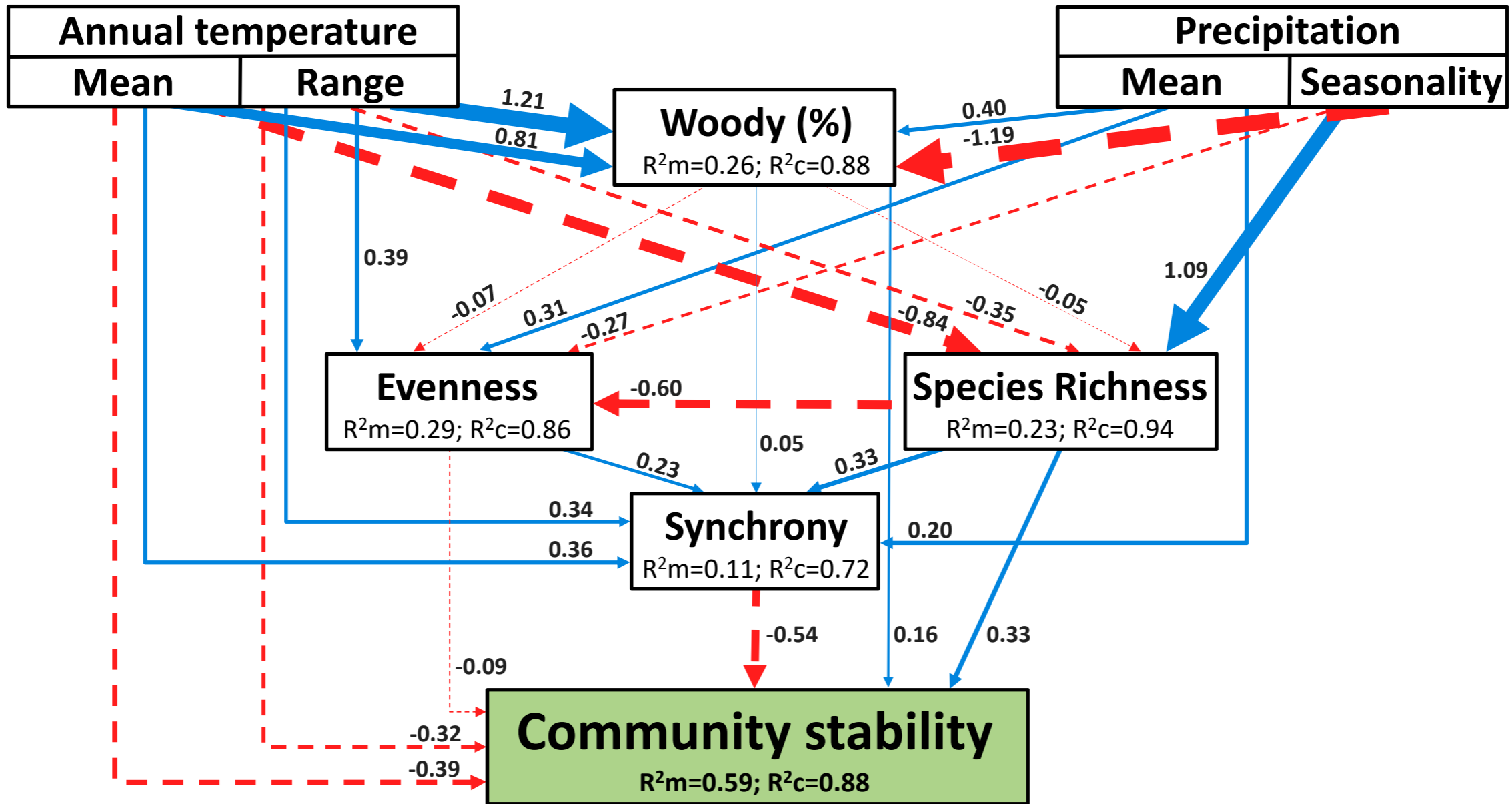665   information *SI Appendix,* Table S5).

Fig. 1.

Fig. 2.

Fig. 3.