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

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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 datasets 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.

evenness | climate change drivers | species richness | stability | synchrony

Understanding the mechanisms that maintain ecosystem stability (1) is essential for the stable provisioning of multiple ecosystem functions and services (2, 3). Although research on

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Significance

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

community stability has decades of history in ecology (4), with stability often measured as the inverse coefficient of variation across years of community abundance or biomass, the main drivers of stability remain elusive (5). Both abiotic and biotic drivers [e.g., climate, land use, and species diversity (6–8)] are expected to govern community stability. Among biotic drivers, the hypothesis that increases in species diversity beget stability in communities and ecosystems (Fig. 1) (2, 9–11) has generated ongoing debate (12, 13).

The stabilizing effect of biodiversity has been attributed to various mechanisms (12). Most biodiversity–stability mechanisms at single trophic levels involve some form of compensatory dynamics, which occur when year-to-year temporal fluctuations in the abundance of some species are offset by fluctuations of other species (4, 17). Compensatory dynamics are associated with decreased synchrony among species, with synchrony defined as the extent to which species population sizes covary positively over time. Decreased synchrony, which is predicted to stabilize communities (Fig. 1*A*), can result from species-specific responses to environmental fluctuations (18–20) and from temporal changes in competitive hierarchies (21), as well as stochastic fluctuations. Importantly, it is expected that species richness can increase stability (Fig. 1*C*) by decreasing synchrony (Fig. 1*E*). This positive effect of richness on stability can be, in fact, a result of an increased chance that the community will contain species with differing responses to abiotic drivers or competition, leading to a reduction in synchrony (12). However, the effect of richness on stability should weaken when synchrony is higher than expected if species were fluctuating randomly and independently (*SI Appendix*, Supplementary Text S1 has expanded information) (14). At the same time, other biotic drivers, together with richness and synchrony, have the potential to interact and buffer the effects of ongoing climatic and land-use changes. These additional biotic drivers include community evenness, which can both increase or decrease synchrony (1), or the presence of more stable species that are characterized by more conservative resource strategies (22). Long-term empirical data from natural communities can help us reveal the real-world effects of biotic drivers on community stability (6).

Here, we explore the generality of biodiversity–synchrony–stability relationships, and their implications in a global change context, across multiple ecosystems and a wide range of environments. We compiled data from 7,788 natural and seminatural vegetation plots that had annual measurements spanning at least 6 y, sourced from 79 datasets distributed across the world (*SI Appendix*, Fig. S1). Most of the datasets include information about human activities related to global change through the application of experimental treatments, including fertilization, herbivore exclusion, grazing, fire, and climate manipulations (hereafter environmental treatments). Biodiversity, synchrony, and stability are known to vary in response to climate and land use, although knowledge of such responses is limited by lack of comparative data across major habitats and geographic extent (8, 13, 16). The compiled data allowed us to compare the relationships between species richness, synchrony [using the log*V* index (16)], and stability against theoretical predictions (summarized in Fig. 1) across vegetation types, climates, and land uses.

Results and Discussion

Interplay between Species Richness, Synchrony, and Stability. Our results confirmed the general prevalence of negative synchrony–stability relationships: 71% of the datasets exhibited negative and significant relationships (R^2m = 0.19; i.e., variance explained by the fixed effects over all individual plots) (Fig. 1*B*). We found similar results for other synchrony indices (*SI Appendix*, Fig. S2). These findings support theoretical predictions (Fig. 1*A*) and previous empirical evidence (2, 6, 11) that lower levels of synchrony in species fluctuations stabilize overall community abundance, despite the large range of vegetation types, environmental treatments, and biogeographic regions we considered.

Our results highlight a second global pattern consistent with theory (Fig. 1*C*): higher species richness was associated with greater community stability (R^2m = 0.06) (Fig. 1*D*). However, this relationship was not nearly as strong: only 29% of the datasets showed a positive and significant relationship. The high proportion of nonsignificant species richness–stability relationships was unexpected, as species richness is generally considered one of the strongest drivers of stability (8–10, 23). Nevertheless, in observational datasets species richness may covary with other

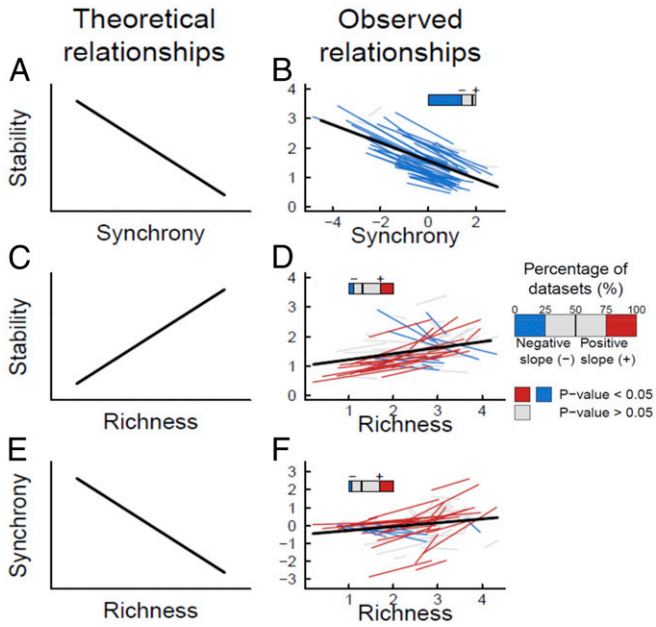

Fig. 1. Relationships between synchrony and stability (*A* and *B*), richness and stability (*C* and *D*), and richness and synchrony (*E* and *F*). Richness and stability were ln transformed. *A*, *C*, and *E* are the schematic representations of these relationships following theoretical predictions (1, 12, 14, 15). *B*, *D*, and *F* depict these relationships for each dataset (n = 79). Red, blue, and gray lines represent the statistically significant positive, negative, and nonsignificant slopes, respectively. Black lines show each relationship based on all plots (n = 7,788) using a linear mixed effects model with datasets as a random factor; these were all statistically significant. The synchrony index was log*V* (16).

factors that influence interannual community variability, potentially masking any direct effect of species richness (24).

Species richness was positively and significantly associated with synchrony across all studies, and the expected negative relationship predicted by theory was found in only 8% of our datasets (Fig. 1*F*). Such low frequencies of negative richness–synchrony relationships contradict both theoretical predictions (Fig. 1*E*) and previous studies. For instance, a recent richness-manipulated experimental study showed a negative relationship between richness and synchrony (25), although this could be driven by the low levels of species richness applied in that experiment. We note that in natural or seminatural communities, such as those analyzed here, richness often exceeds the low levels commonly applied in experimental studies that manipulate richness. Our results showed that while the relationship between synchrony and species richness across datasets depended on the index of synchrony considered (Fig. 1*F* and *SI Appendix*, Fig. S2; *SI Appendix*, Supplementary Texts S1 and S2 have 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, 13, 16). Indeed, we expected to observe a negative relationship between species richness and synchrony, particularly for those plots and datasets 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 (*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 Texts S1 and S2). This modeling 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 in the 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) (*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) is more common than random fluctuations or negative covariances (26), likely because many species-rich communities contain ecologically similar species, with similar responses to weather (14, 27). 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, 14). 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, 16). 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 (Fig. 2 *A* and *B*). While the effect size of the combined treatments was small compared with biotic factors (*SI Appendix*, Table S1), this mostly reflects opposing effects of different treatment types (*SI Appendix*, Supplementary Text S3 has expanded information).

Using only those datasets 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. 2*C*). 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. (16) demonstrated in a local study that while nutrient enrichment increases competition among plant species, it also decreases stability by increasing differences in productivity between favorable and unfavorable 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. 2*D*). 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 (16). Overall, these results show that changes in environmental drivers, associated with 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 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 (28). This could cause a decrease in synchrony values for indices studied here (29), with the indices reflecting not only 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 understory vegetation was more synchronous and less stable than grasslands, shrublands, and savannas (Fig. 2*B*), similarly to Blüthgen et al. (13). We suggest that forest understory vegetation has weaker compensatory effects that lead to destabilization. Also, this result could be related to the fact that we excluded from the analyses the tree layer (i.e., the most stable vegetation layers in these systems). Alternatively, this vegetation might support a greater proportion of rare species, which benefit from shared favorable conditions (30) increasing the synchrony of the community. Finally, communities with a greater proportion of woody species were more stable. The longer life span of woody species and their structural storage of carbon and nutrients should buffer them against environmental fluctuations and the fluctuations of other species, although we note that longer measurement timescales may be required to accurately capture their dynamics.

Finally, we found evidence of a positive evenness–synchrony association (Fig. 2*A*) and a negative evenness–stability association (Fig. 2*B*). In other words, low synchrony is more common in communities with low evenness that are dominated by a few species. These communities appear to fluctuate less and are therefore more stable (31, 32). This finding suggests two potential ecological mechanisms. First, these few species could be the best-adapted species and tend to perform well across years (i.e., have comparatively little fluctuations), thus promoting stability. In some

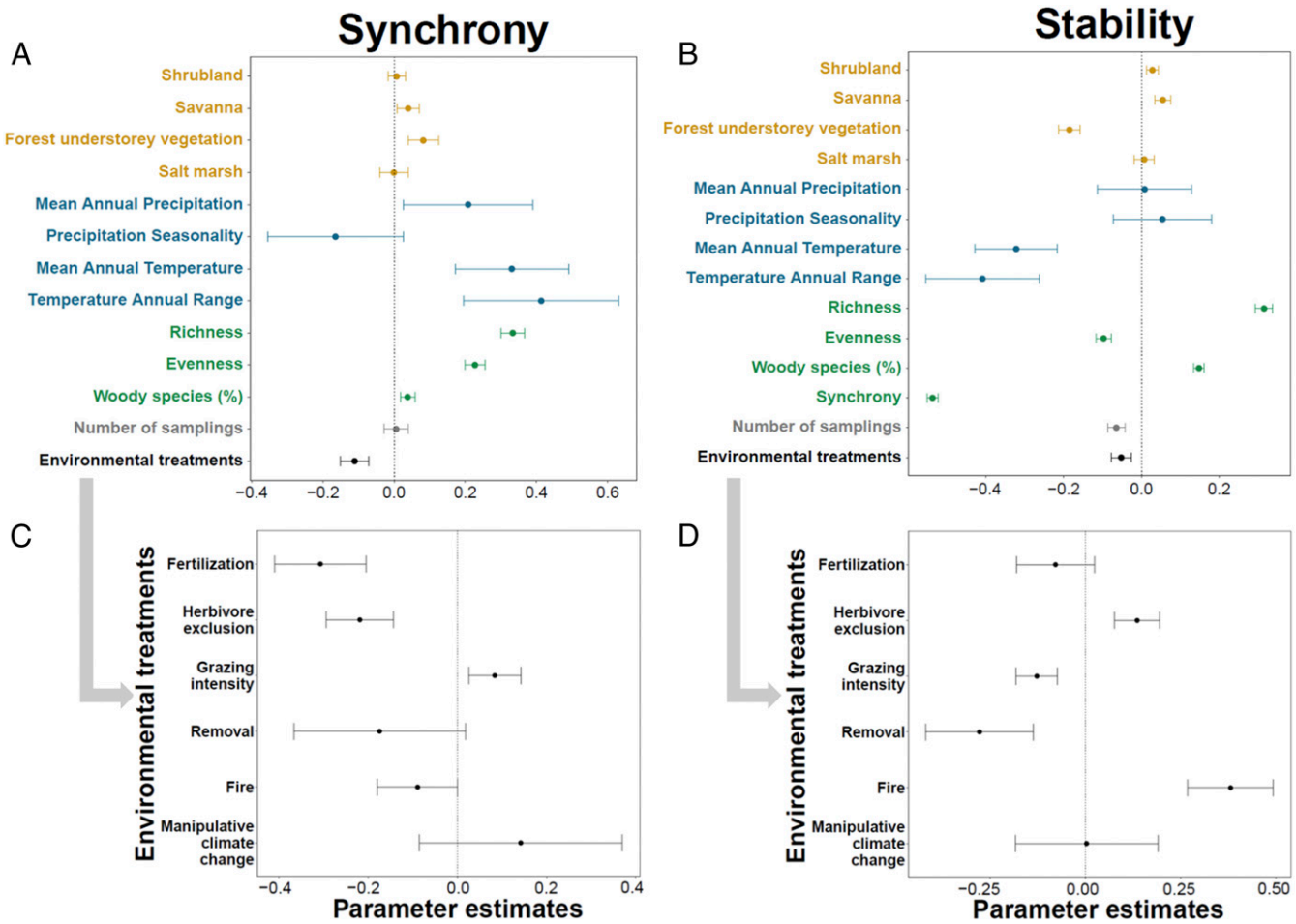

Fig. 2. Effects of multiple abiotic and biotic drivers on the synchrony values (*A* and *C*) and stability (*B* and *D*) of the different communities. We show the averaged parameter estimates (standardized regression coefficients) of model predictors and the associated 95% CIs. In *A* and *B*, all of the predictors were evaluated together using general linear mixed effect models (n = 7,788). The colors represent the different drivers of vegetation type: grassland is the reference level (orange), climatic data (blue), biotic attributes (green), number of measurements (gray), and global change treatments (black). The effects of each environmental treatment on synchrony values and stability (*C* and *D*) were evaluated separately and only for the studies where each driver was measured (fertilization: n = 1,058, ND [number of datasets evaluated] = 17; herbivore exclusion: n = 2,284, ND = 19; grazing intensity: n = 1,920, ND = 24; removal plant species: n = 518, ND = 8; fire: n = 974, ND = 11; manipulative climate change: n = 122, ND = 5).

cases, for example, species with slower growth strategies are locally more abundant and stable in time (22). Second, a small number of dominant species with different adaptations (different traits) (16, 33, 34) could lead to decreased synchrony and increased stability at the community level. If synchrony is a common feature of vegetation [as suggested by our study and in Houlahan et al. (26)], evenness can have an effect on stability via synchrony (Fig. 3). Low synchrony among a small number of dominant species could thus represent an important stabilizing effect in ecosystems worldwide.

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*, Fig. S5 *A* and *B*). 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 (35) rather than by the number of species per se (18, 31), 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

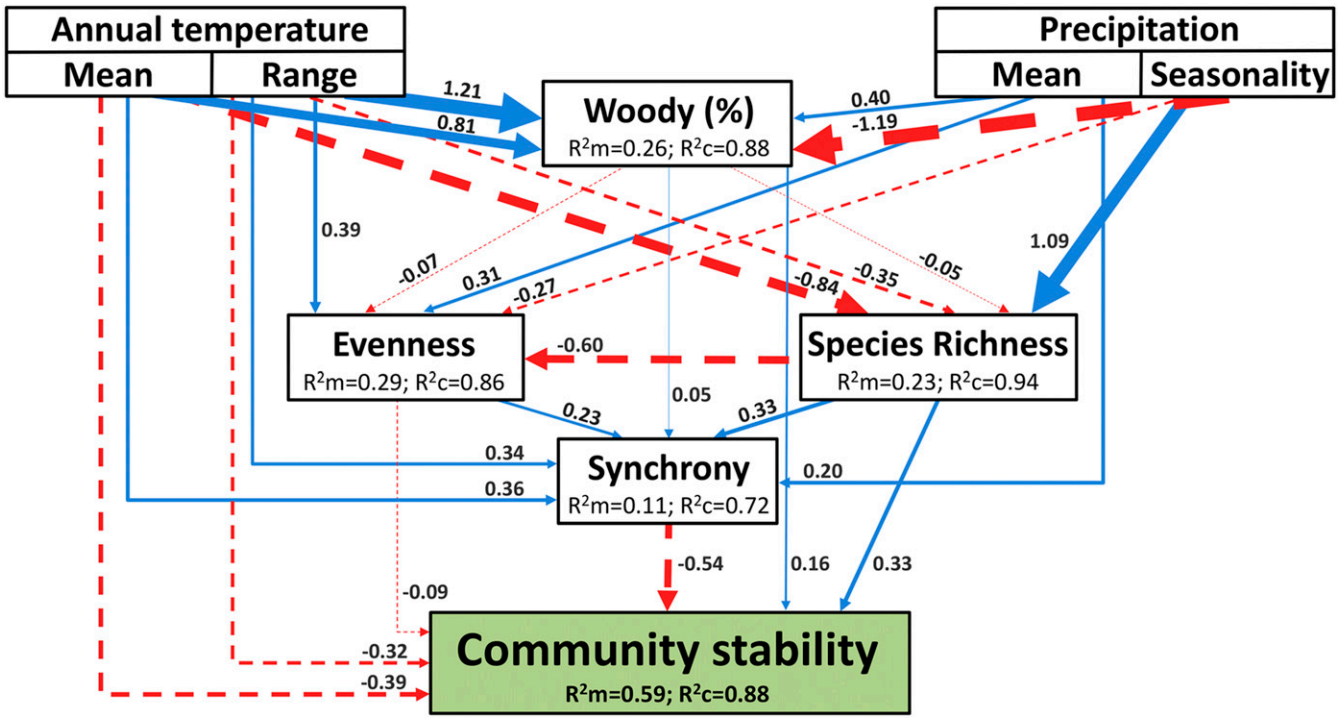

Fig. 3. Piecewise structural equation model showing the direct and indirect effects of multiple abiotic and biotic drivers on the stability across the 79 datasets (Fisher's *C* statistic: $C = 14.96$, $P = 0.134$, $n = 7{,}788$). Marginal (R^2m) values showing variance explained by the fixed effects and conditional (R^2c) values showing variance explained by the entire model are provided for each response variable. Solid lines represent positive effects, while dashed lines indicate negative effects. Blue and red lines represent statistically significant effects, and gray lines represent nonsignificant effects. The width of each arrow is proportional to the standardized path coefficients (more information is *SI Appendix*, Table S5).

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

Methods

We used data from 79 plant community datasets where permanent or semipermanent plots of natural and seminatural vegetation have been consistently sampled over a period of 6 to 99 y (*SI Appendix*, Figs. S1 and S6, Supplementary Text S4, and Table S2). We focused our analyses on vascular plants as the main primary producers affecting subsequent trophic levels and ecosystem functioning. These datasets have some differences, such as the method used to quantify abundance (e.g., aboveground biomass, visual species cover estimates, and species individual frequencies), plot size (median = 1 m^2; range = 0.04 to 400 m^2), vegetation type (grassland, shrubland, savanna, forest, and salt marsh), and number of sampling dates (median = 11.5; range = 6 to 38). The studies encompassed different localities with different species pools and different types of vegetation responding to different types of treatments. The total number of individual plots was 7,788 across the 79 datasets (number of observations ~ 190,900).

Climatic Data. We collected climatic information related to temperature and precipitation for each of the 7,788 plots using WorldClim (https://www.worldclim.org/) where location coordinates were available. Where these were not available, weather data were derived from the study centroid. Among available variables, we retained four: mean annual temperature (degrees Celsius) and mean annual precipitation (millimeters), related to annual trends, and mean annual temperature range and coefficient of variation of precipitation within years as proxies for annual seasonality (6). These variables were selected from the 19 available WorldClim climatic variables because they describe relatively independent climatic features and account for most of the other climatic relationships observed with our data (climatic variable correlation is in *SI Appendix*, Table S3).

Biotic Attributes. In each plot, we calculated stability over time as the inverse of the coefficient of variation (SD/mean) of the year-to-year fluctuations of total abundance of that community. This has been widely used as a reliable estimator of temporal invariability (36). SD was based on $n - 1$ degrees of freedom. We only included datasets using percentage cover as an estimate of community structure if the summed cover was not constrained.

Although we did not measure ecosystem services directly, multiple studies highlight the importance of a stable vegetation (primary producers) for a stable delivery of multiple key ecosystem processes. For example, biomass and abundance are often considered to be ecosystem functions in their own right (e.g., forage production and carbon sink), while these can also act as a proxy or driver of other functions, including litter quantity, soil organic matter, evapotranspiration, or erosion control. Clearly, the value of stability depends on its relationship to the provision of specific ecosystem services, and temporal invariability does not necessarily imply a positive effect on the ecosystem service of interest. Our study aims at identifying ecological drivers of stability at a global scale.

In each plot, we also calculated various indices that characterize the biotic attributes of the community averaged over all annual observations: average species richness [average number of species (2, 37)], the average percentage of woody species per year, and evenness (using the *Evar* index) (38):

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

where S is total number of species in the community and x_s is the abundance

of the sth species. Finally, we calculated synchrony (log-variance ratio index: log$V$) (16) as follows:

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

where x_i is the vector of abundances of the ith species over time. The log$V$ index ranges from −Inf to +ln(S). For this index, positive values indicate a common response of the species (synchrony, formally positive sum of covariances in the variance–covariance matrix), while values close to zero indicate a predominance of random fluctuations, and negative values indicate negative covariation between species. One theoretical issue of this index is that its upper limit is a function of species richness and evenness, questioning its independence from those parameters. Our results, however, were not affected by this constraint. It is important to note that the observed index value can vary considerably within its theoretical range; in fact, the relationship between richness and log$V$ index is very weak. The chance of reaching maximum synchrony decreases with the number of species. To reach maximum synchrony, there must always be perfect synchrony between all species pairs, no matter how many species are in the community [i.e., with n species, the correlation of n (n − 1)/2 pairs must be perfect (i.e. 1) within each pair]. The values of synchrony that would be close to the maximum one were not present in real communities (such as those that are the focus of this manuscript). Thus, the upper limit of log$V$, which represents the caveat to the use of this metric, is not invalidating our results.

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 (39) 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 (39). We only present the results of log$V$ in the text both for clarity and because the models with this index had the lowest Akaike information criterion (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*, Supplementary Text S2 has expanded information).

Previous research has identified the relationship between stability and synchrony, both in biological (12) and mathematical terms (1). However, it has also been shown that stability is affected by a number of other factors (1, 8, 12, 16, 25). Given these multiple influences, the relationship between synchrony and stability would not necessarily be expected to be consistently significant or characterized by a strong correlation. We assessed this relationship for the different indices in comparison with null models that assume random, independent species fluctuations (*SI Appendix*, Supplementary Texts S1 and S2 have expanded information).

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

Analysis. Linear models were used to evaluate the relationships between 1) synchrony and species richness, 2) species richness and stability, and 3) synchrony and stability. In all cases, richness and stability were ln transformed to improve their normality. We obtained the slope and the significance for these relationships individually for each of the 79 datasets as well as for all of the plots together. We used a null model approach to compare the observed values of stability and synchrony and observed richness–synchrony and richness–stability relationships to expected values under a random fluctuation scenario. To do so, we randomized species abundances within a plot across years, by means of torus randomizations (also referred to as cyclic shifts). This approach preserves the temporal sequence of values within a species but changes the starting year. In each 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 (40). This procedure kept the total (i.e., summed) species abundance constant for each species but varied (and therefore, disconnected) the temporal coincidence 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, 1) observed and expected synchrony, and 2) observed and expected stability, using linear mixed effects models with dataset 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 = 7,788) 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; dataset was a random factor. Environmental treatments constituted a binary variable (0 = control plots vs. 1 = environmental treatments). The mean and CI of the parameter estimates of the predictors were used to model their effects on synchrony values among all of 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 centered on their mean and standardized by their SD. 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 included in our model, this variable was not significant ($\chi^2 < 0.01$; $P = 0.95$) and so, was removed as predictor. To evaluate the individual effect of each environmental treatment on synchrony values and stability, treatments were grouped into six categories (fertilization, herbivore exclusion, grazing intensity, removal, fire, and manipulative climate change drivers), retaining only datasets where these treatments were applied or assessed.

Finally, we conducted a stepwise selection of a piecewise structural equation model (41) to test direct and indirect pathways of biotic and abiotic factors on stability. A piecewise structural equation model is a confirmatory path analysis using a d-step approach (42, 43). This analysis is a flexible framework to incorporate different model structures, distributions, and assumptions. This method is based on an acyclic graph that summarizes the hypothetical relationships between variables to be tested using the C statistic (44). We built an initial structural equation model containing all possible biotic and abiotic relationships, independent of the vegetation type evaluated. Then, we used the AIC to select the minimal and best model (44) based on the initial structural equation model, using the step AIC procedure (41). This process selects the most important paths and removes the majority of nonsignificant paths. Standardized path coefficients were used to measure the direct and indirect effects of predictors (45). We conducted the structural equation model analyses across all individual plots (n = 7,788), for nontreatment plots across all habitats (n = 4,013), and for plots of each vegetation type separately (except in salt marsh). In all of the models, datasets were considered as a random factor.

All analyses were carried out with R (R Core Team) (46) using packages piecewiseSEM (47), lme4 (48), and modified source code in codyn (40).

Data Availability. The data that support the findings of this study are available in a txt format at Figshare (49) (https://doi.org/10.6084/m9.figshare.7886582.v1).

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