Phytoplankton biodiversity is more important for ecosystem functioning in highly variable thermal environments

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The 21st century has seen an acceleration of anthropogenic climate change and biodiversity loss, with both stressors deemed to affect ecosystem functioning. However, we know little about the interactive effects of both stressors and in particular about the interaction of increased climatic variability and biodiversity loss on ecosystem functioning. This should be remedied because larger climatic variability is one of the main features of climate change. Here, we demonstrated that temperature fluctuations led to changes in the importance of biodiversity for ecosystem functioning. We used microcosm communities of different phytoplankton species richness and exposed them to a constant, mild, and severe temperature-fluctuating environment. Wider temperature fluctuations led to steeper biodiversity–ecosystem functioning slopes, meaning that species loss had a stronger negative effect on ecosystem functioning in more fluctuating environments. For severe temperature fluctuations, the slope increased through time due to a decrease of the productivity of species-poor communities over time. We developed a theoretical competition model to better understand our experimental results and showed that larger differences in thermal tolerances across species led to steeper biodiversity–ecosystem functioning slopes. Species-rich communities maintained their ecosystem functioning with increased fluctuation as they contained species able to resist the thermally fluctuating environments, while this was on average not the case in species-poor communities. Our results highlight the importance of biodiversity for maintaining ecosystem functions and services in the context of increased climatic variability under climate change.

biodiversity–ecosystem functioning | climate change | temperature fluctuation | marine phytoplankton | temperature variability

Climate change and biodiversity loss are two of the most pressing ecological issues of the century (1, 2). Because biodiversity is positively related to ecosystem functioning (3–8), the accelerating species loss is expected to lead to a decrease in ecosystem functioning and ecosystem services (9–13).

Climate change increases both the mean and variance in temperature (1, 14), which can further hamper ecosystem functioning (15–17). Increased temperature variance in particular is expected to pose a greater risk to biodiversity than increased mean (18, 19). However, much less is known about the potential interactive effects of biodiversity loss and climate change on ecosystem functioning (but refer to refs. 20 to 23) and particularly between the potential interactive effects of biodiversity loss and temperature fluctuations. To better understand the potential impacts of increased climatic variation and biodiversity loss on ecosystems, it is thus important to investigate the effect of temperature fluctuations on the biodiversity–ecosystem functioning (BEF) relationship.

Climate change has complex effects on biodiversity and ecosystem functioning. Warmer climates can lead to both a loss (24–29) and an increase in biodiversity (30, 31). At the local scale, the effect of increased temperature on species richness shows mixed trends, with studies finding declines (32–34), increases (30, 35), or no discernible trend (36, 37). The effects of increased thermal variability also remain unclear: positive, negative, or no effects on richness have been reported (16, 38–42). Furthermore, climate change can alter ecosystem functioning, either directly or indirectly through changes in biodiversity (16, 43–47).

In addition to affecting diversity and ecosystem functioning, increased temperature mean and variation can modify the relationship between biodiversity and ecosystem functioning. In bacteria and phytoplankton, warmer temperatures resulted in a steeper slope of the relationship between log ecosystem functioning and log species richness (21, 22, 48). Steeper slopes of the BEF relationship indicate that the effect of biodiversity on ecosystem functioning is stronger in warmer environments: that is, the loss of one species has a more detrimental effect on ecosystem functioning as temperatures increase. Interestingly, a recent study on picophytoplankton showed that the steepness of the biodiversity–ecosystem functioning slope relied on both short-term temperature and community evolutionary history (23). Less is known about the effect of temperature fluctuations on BEF relationships. A study on protozoan–bacteria consumer–resource relationships showed that the slope between diversity and biomass became shallower with increased fluctuations (49); another study on fungal assemblages showed that polycultures decomposed leaves better than monocultures under fluctuating temperatures (50).

Several mechanisms might lead to a change in the relationship between biodiversity and ecosystem functioning with temperature

Significance

The combined acceleration of climate change and biodiversity loss necessitates understanding how ecosystem functions and services will be affected. Most studies focus on the effects of increasing mean temperatures, but climate change will increase temperature fluctuations too. We performed an experiment and developed a model to understand how increased temperature fluctuations affected the importance of biodiversity for ecosystem functioning in phytoplankton communities. Increased temperature fluctuations led to steeper biodiversity–ecosystem functioning slopes, which indicates that biodiversity loss has a stronger negative effect on ecosystem functioning than when conditions are more stable. Our model suggests that steeper slopes are associated with variation in thermal tolerances across species, as species-rich systems contained species able to resist the thermally fluctuating environments.

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fluctuations. We focus on three mechanisms of potential relevance on fluctuating environments: tolerance differences, species interactions, and temporal asynchrony. First, different species within a community have different thermal tolerances, that is, they handle thermal stress differently. When temperature mean or fluctuation increases, these underlying interspecific differences can manifest more strongly. This, in turn, can lead species-rich communities to perform better than species-poor communities due to their containing of species able to resist the stressful conditions, leading to increased slopes of BEF with stress (51). This was the case in marine phytoplankton communities, where differences in species thermal tolerances led to a larger effect of biodiversity on ecosystem functioning in more physiologically stressful, warmer environments (22). Theory suggests that when the environment becomes too stressful and exceeds the thermal tolerances of all species, the slopes of BEF become shallower again (48, 51). In a context of increased temperature fluctuations, one can expect that differences in average tolerances to the varying environmental conditions among species would lead to variation in the relationship of ecosystem functioning with species richness. Thus, we expect that communities with a larger spread in thermal tolerances should have a steeper BEF relationship.

Second, species interactions can change in response to changes in the thermal environment. Strong competition among species can lead to shallower BEF slopes, where adding one species does not increase ecosystem functioning much when species compete for the same resources [i.e., small niche differences (52, 53)]. On the contrary, large niche differences or facilitative interactions can lead to opposite relationships, where adding one species strongly increases overall ecosystem functioning. If increased temperature fluctuations cause a change in competitive interactions, this in turn can lead to a modification of the BEF slope. Models investigating the effect of temperature mean and variation on BEF relationships have suggested that temperature-driven changes in the intensity of competition could indeed play a role in driving the relationship (49).

Third, asynchrony in species temporal dynamics within a community, for instance due to temperature fluctuations, can lead to increased ecosystem productivity and temporal stability through an insurance effect (5, 54). This can lead to a community that is dominated by different species depending on their tolerance to the current environmental conditions (e.g., "warm-adapted" species increasing in abundance and dominating when temperature is hotter, and "cold-adapted" species dominating when temperature is cooler). Such mechanism would lead more diverse communities to perform better in thermally fluctuating environments than species-poor communities. These three mechanisms can co-occur and lead to changes in BEF with temperature fluctuations.

The effects of biodiversity on ecosystem functioning often increases through time (55, 56). Thus, the impact of species loss on functioning is larger as ecosystems assemble. Such temporal effects can arise from a temporal increase in productivity of species-rich communities (e.g., through increases in complementarity through time, for instance when legumes increase nutrient availability for other plant species by fixing atmospheric nitrogen), a decrease in productivity of species-poor communities (e.g., through increases in abundance of antagonistic soil microorganisms in plant communities), or a combination of both (55, 57, 58). Temporal fluctuations could, in turn, interfere with ecosystem temporal dynamics, and it is worth investigating whether this could lead to changes in the biodiversity–ecosystem relationships over time.

Here, we used a proof-of-concept experiment and a theoretical model to understand how increasing temperature fluctuations affected BEF relationships and whether these relationships changed over time. We experimentally manipulated the species richness of phytoplankton communities at a control temperature of 25 °C, a moderate temperature fluctuation treatment of between 22 and 28 °C every other day, and a severe fluctuation treatment of between 19 and 31 °C every other day using a random partitioning experimental design (ref. 59, Fig. 1). We quantified the impact of temperature fluctuations and temporal scale (i.e., after 5 and 15 d) on the relationship between biodiversity and ecosystem production. This experimental design allowed quantifying the impacts of random species loss on ecosystem functioning as well as evaluating the relative contribution of each species to ecosystem production. We used three measures of ecosystem production, either total cell abundance, total biomass, or total chlorophyll *a* content. Such measures have been used in similar experiments (22, 48, 49), and measures of biomass production have been widely used in plants (11). However, it is to note that ecosystem functioning can be also measured as a flux, such as C fixation, O_2 production, or nutrient recycling, that we were unfortunately unable to measure here. Including such fluxes could lead to different expectations of the BEF slope and is beyond the scope of our study. We further explored the relative importance of the three different mechanisms outlined above (tolerance differences, species interactions, and temporal asynchrony) as drivers of our experimental results. We did so by means of our experimental data and a simple theoretical model of species competition. In particular, we tested whether potential changes in BEF slope were linked to a change in species interactions or a greater spread in thermal tolerances and explored the impact of temporal asynchrony in the model, using cell abundance as a measure for ecosystem function.

Results

BEF Relationships across Time and Temperature Fluctuation Regimes. Ecosystem production measured as phytoplankton cell abundance increased linearly with species richness on a log-log scale, corresponding to a power-law dependence on linear scales. The slope of the relationship between biodiversity and ecosystem functioning, which quantifies the effect of the loss of one species on ecosystem functioning, varied with temperature fluctuation treatments and with time, with a triple interaction between richness, temperature fluctuations, and time of sampling (Fig. 2 and Table 1). A contrast analysis showed no statistically significant differences in the slopes of BEF relationships between temperature fluctuation treatments after 5 d (Fig. 2 and *SI Appendix*, Table S1). However, by the end of the experiment (after 15 d), the slope increased for the moderate and extreme temperature fluctuation treatment, leading to steeper BEF slopes for larger temperature fluctuations (Fig. 2 and *SI Appendix*, Table S1). This meant that when thermal fluctuation was large, the loss of a species had a stronger negative effect on total community abundance than in environments that were less variable. At constant temperatures, the exponent of the relationship between cell abundance and species richness at day 15 on a log-log scale was 0.35 ± 0.09, while it was twice this value in the severe fluctuation treatment, at 0.67 ± 0.09 (Fig. 2).

The intercepts of the BEF relationships, which represent the mean ecosystem functioning when species richness was equal to one, also varied among treatments. We found a higher total community abundance in the constant relative to the two fluctuating treatments after 5 d and in the constant and mildly fluctuating relative to the severely fluctuating treatment after 15 d (Figs. 2 and 3 and *SI Appendix*, Table S2). Interestingly, the greater BEF slope compensated almost completely for this negative effect of thermal fluctuations on total community abundance for the richest communities (i.e., those initiated with 12 species), with a slightly lower total community abundance in the severely fluctuating treatment compared to the constant environment after 5 d and no differences after 15 d (Fig. 3 and *SI Appendix*, Table S2). Furthermore, temporal effects at the severe fluctuation treatment were linked to a decrease in total community abundance over time for the low-richness communities, with no change for the high-richness communities (Fig. 3 and *SI Appendix*, Table S3).

When using both total biomass and total chlorophyll *a* as measures of ecosystem production, we found similar results as for

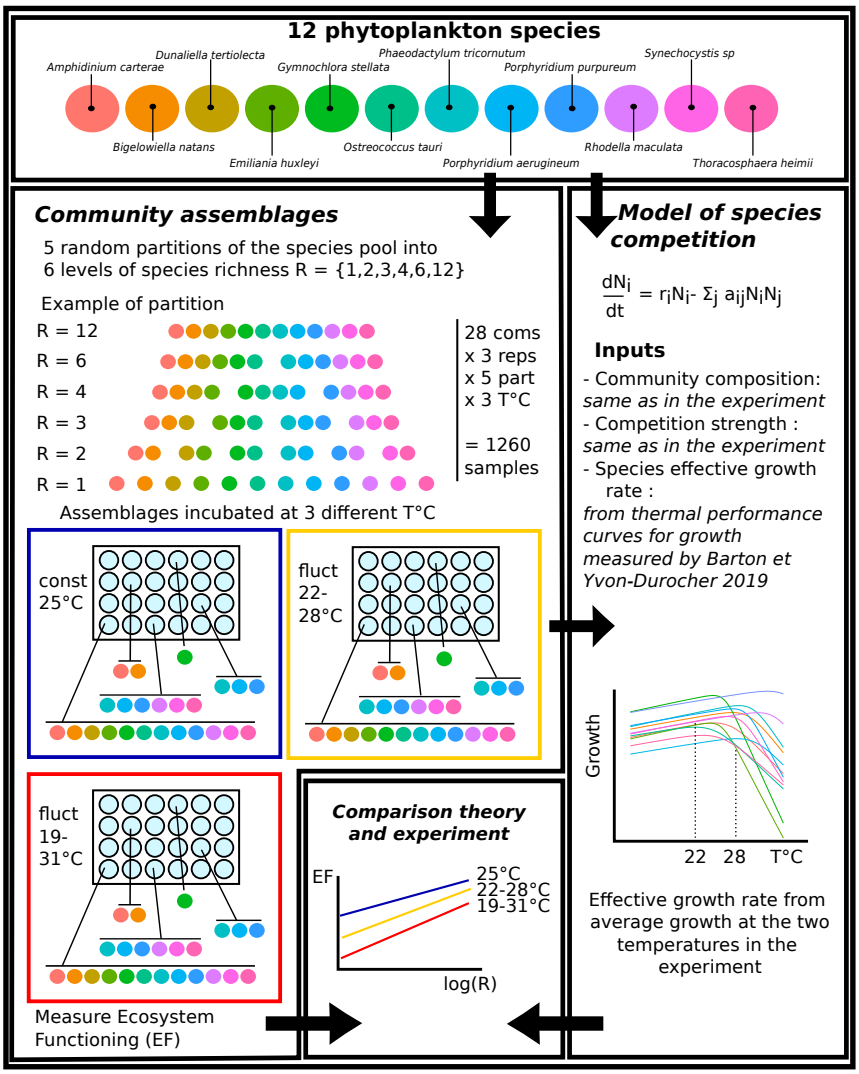

Fig. 1. Flowchart of the experimental design and its comparison with the theoretical model.

abundance, with a triple interaction between time, biodiversity, and temperature fluctuation treatment on ecosystem function (*SI Appendix*, Figs. S1 and S2 and Tables S4–S7). A contrast analysis of the high- and low-richness communities showed that for low-richness communities, the severely fluctuating treatment had lower values of total chlorophyll *a* than the two other treatments at both temporal scales, and this negative effect was compensated for the most diverse communities, with no difference between temperature treatments (*SI Appendix*, Fig. S3 and Table S8). Finally, temporal increases in BEF slope for chlorophyll *a* were linked to a steeper increase in ecosystem functioning with time for the high-richness compared to the low-richness communities (*SI Appendix*, Fig. S3 and Table S9). When using biomass as a measure, we found similar results, with lower values of total biomass across time in the severely fluctuating treatment in the low-richness communities, while this negative effect was compensated after 15 d for the high-richness communities (*SI Appendix*, Fig, S4 and Tables S10 and S11).

Exploration of the Mechanisms. We investigated both theoretically and empirically the mechanisms related to the observed changes in BEF slopes with ecosystem functioning measured as community abundance. We created a simple competition model parametrized with species thermal tolerances (*SI Appendix*, Fig, S5), in which the competition coefficient between species α could vary. We first showed that severely fluctuating temperature treatments led overall to steeper BEF slopes than constant or mild thermal fluctuation treatments (Fig. 4*A*). When we parametrized our model with both the species thermal tolerances and the competition coefficient derived from the experimental data (*SI Appendix*, Fig. S6), the theoretical outcomes fell within the 95% CIs of the experimental slopes (Fig. 4*B* and *SI Appendix*, Fig. S7). Furthermore, comparing the modeled ecosystem functioning values among treatments for the monocultures and the 12-species communities, we found similar patterns as for the experimental data: severe fluctuations leading to lower ecosystem functioning in low-richness communities, an effect nullified in the high-richness communities (*SI Appendix*, Fig. S8).

A first mechanism potentially driving the observed change in the BEF slope is a change in the spread in species thermal tolerances. In our experiment, species differed in their thermal tolerances and showed a wider spread in the distribution of tolerance to thermal fluctuations in the severe fluctuation compared to mild fluctuation and constant temperature treatments (*SI Appendix*, Fig. S5). A theoretical exploration of our model shows that a wider spread in thermal tolerances can lead to steeper BEF slopes (*SI Appendix*, Appendix 1 and Fig. S9). Indeed, when conditions are good, such as at 25 °C, all species are able to perform relatively well, and adding new species will lead to a small increase in

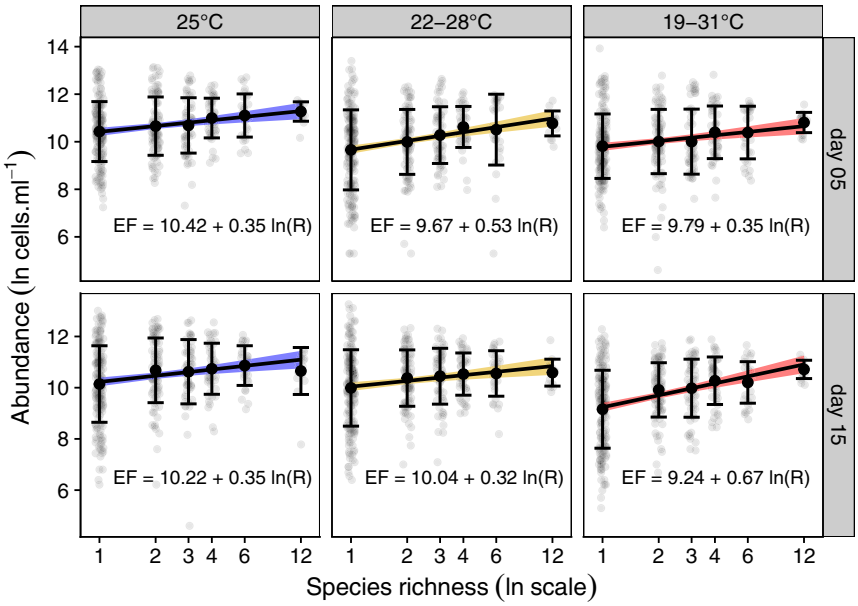

Fig. 2. The relationship between biodiversity and ecosystem functioning depends on the interaction between temperature fluctuation treatment and time. From *Left* to *Right*: constant 25 °C temperature treatment (blue CI), alternating 22 and 28 °C temperature every other day (yellow CI), and alternating 19 and 31 °C temperature every other day (red CI). *Top*: 5 d, and *Bottom*: 15 d of experiment. Gray points represent ecosystem functioning for each of the 1,260 communities (420 per temperature fluctuation treatment) measured as in total cell abundance (ln cells · milliliter^{-1}). Black points and error bars are the mean ± SD for each level of species richness. Lines and CIs correspond to the fitted curves for the most parsimonious linear mixed model (Table 1). The slope of the relationship between biodiversity and ecosystem functioning depends on the interaction between temperature treatment and time (Table 1), with no differences in slopes between treatments after 5 d but an increase in the slope of the extreme fluctuation treatment over time leading to steeper BEF slopes at high levels of temperature fluctuations at the end of the experiment (*SI Appendix*, Table S1).

ecosystem functioning. However, when the conditions become more stressful, such as in the 19 to 31 °C fluctuation treatment, only a handful of species are able to tolerate these new conditions. Thus, increasing the biodiversity leads to a greater chance that the community will contain at least one species able to tolerate the conditions, with a strong increase of ecosystem functioning with biodiversity. We further explored the effect of this spread on the experimental data. If spread is important in driving changes in BEF relationships, we expect that there should be an interactive effect of species richness and spread in thermal tolerances of the species pool on ecosystem functioning. In particular, BEF slopes should be steeper for wider spread of thermal tolerances in the species pool, and species with a greater thermal tolerance would contribute more to ecosystem functioning. Our experimental results agree with both expectations: we found that the relative spread in effective growth rate within the species pool interacted with species richness to drive ecosystem function measured as total abundance (value for the interaction: $F_{1,1256} = 9.1$, $P = 0.003$, $R^2 = 0.12$). Alternative measures of spread, such as the coefficient of variation of thermal tolerances, gave the same significant interaction ($F_{1,1256} = 9.4$, $P = 0.002$, $R^2 = 0.12$). Furthermore, the species that had the highest effective growth rate [i.e., average of growth rate at the two extreme temperatures of the treatment from a thermal tolerance curve (60) (*SI Appendix*, Fig. S5)] had the largest contribution to ecosystem functioning measured as total abundance, as shown by the positive relationship between species coefficient [a measure of contribution to ecosystem functioning (59), where positive and negative values indicate an above- and below-average contribution to ecosystem functioning, respectively, *SI Appendix*, Fig. S10] and thermal tolerance (Fig. 5*A*). Furthermore, we found the same

Table 1. Comparison of linear mixed models estimating the effect of temperature fluctuations, species richness, and time on ecosystem production

Step	Model	n par	χ^2	df	*P* value	R^2m	R^2c	AIC	ΔAIC	AIC weight
0	Intercept+(1|id)	3				0.00	0.52	8,292	213	0.000
1	T+(1|id)	5	77.7	2	1.3e-17	0.05	0.52	8,218	140	0.000
2	T+D+(1|id)	6	6.8	1	9.1e-03	0.05	0.52	8,213	135	0.000
3	T+D+ln(R)+(1|id)	7	88.3	1	5.5e-21	0.10	0.52	8,127	48	0.000
4	T+D+T*ln(R)+(1|id)	9	2.1	2	3.4e-01	0.10	0.52	8,129	50	0.000
5	T+D+T*ln(R)+D*ln(R)+(1|id)	10	0.5	1	4.7e-01	0.10	0.52	8,130	52	0.000
6	T+D+T*ln(R)+D*ln(R)+D*T+(1|id)	12	42.8	2	5.2e-10	0.10	0.54	8,092	13	0.001
7	T+D+T*ln(R)+D*ln(R)+D*T+D*T*ln(R)+(1|id)	14	17.0	2	2.0e-04	0.11	0.54	8,078	0	0.999

The linear mixed models describe the effect of temperature fluctuations (T, as a factor), species richness (ln(R)), time (D, days since the start of the experiment, as a factor), and their interaction, plus a random effect of sample identity on ecosystem functioning. At each step, terms are added to the linear model, and we compare the two models through a likelihood ratio test. Marginal and conditional R^2 and AIC are calculated for each model, as well as ΔAIC from the model with lowest AIC and AIC weights. Lower AIC values indicate an improved model. Analyses revealed that the model with lowest AIC included the interaction between temperature fluctuations, time, and species richness. Reference *SI Appendix*, Table S1 for a post hoc, multiple comparisons analysis on the slope of the BEF relationship by temperature fluctuation treatment and time. n par, number of parameters; df, degrees of freedom.

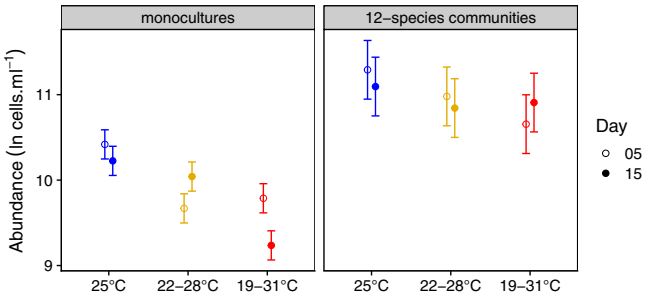

Fig. 3. Comparing ecosystem functioning for the monocultures and 12-species communities across the different temperature fluctuation treatments. Values of ecosystem functioning (abundance in ln cells · milliliter^{-1}) for the monocultures and 12-species communities in the three temperature fluctuation treatments and the two times. Values and 95% CIs are derived from a contrast analysis of the model represented in Fig. 2 (*SI Appendix*, Table S2). Increased temperature fluctuations lead to lower ecosystem functioning in the low-richness communities, while this detrimental effect is compensated for the 12-species-rich communities (*SI Appendix*, Table S2). Furthermore, increased temperature fluctuations lead to decreased ecosystem functioning over time in the low-richness communities (*SI Appendix*, Table S3), with no effect in the species-rich communities.

relationship between modeled species coefficient and thermal tolerance (Fig. 5*B*) and a correlation between experimental and theoretically derived species coefficients (Fig. 5*C*). It is interesting to note that our results might be driven by the choice of species, as the larger spread of thermal tolerances in the 19 to 31 °C fluctuating treatment is largely due to the high tolerance of *Ostreococcus tauri* (*SI Appendix*, Fig. S5). Redoing model simulations without this species yielded a strong decrease in the difference in BEF slope between treatments, although the slope was still steeper in the severely fluctuating treatment (*SI Appendix*, Fig. S11). Part of the effect of biodiversity on ecosystem functioning is due to idiosyncratic effects of the species composition, as shown by the effect of species identity (Fig. 5). Results might vary quantitatively with different species pools, but the slope of the BEF relationship should be steeper in severely fluctuating treatments as the chance to find a species that is highly tolerant to thermal stress should increase with species richness.

A second mechanism that could drive the BEF slopes is a change in the strength of interspecific competition. Indeed, our theoretical model showed that the BEF slope can change with the strength of interspecific competition, with a gradual decrease of the slope with increasing competition coefficient α (Fig. 4*A* and *SI Appendix*, Appendix 1). We thus used the experimental data at day 15 to test whether potential changes in competitive interactions might have driven the observed results. If the change in BEF slope with temperature fluctuation treatment was linked to competitive interactions, we expected to observe a difference in interaction strength between species depending on the temperature fluctuation treatment, and we expected that the average interaction strength measured in each temperature treatment would interact with biodiversity to drive ecosystem function. This was not the case in our experiment, as interaction strength did not differ between treatments (ANOVA $F_{1,159} = 2.22$, $P = 0.11$, *SI Appendix*, Fig. S6), and there was no interaction between richness and mean interaction strength on ecosystem functioning (value for the interaction $F_{1,1256} = 0.82$, $P = 0.36$). It is interesting to note that our model did not need a change in interaction strength to explain our experimental results, as using the average competition coefficient α estimated in the experiment (*SI Appendix*, Fig. S6) was enough for the model predictions to fall within the 95% CIs of the experimental slopes (Fig. 4*B* and *SI Appendix*, Fig. S7).

Finally, a third mechanism is the insurance effect, whereby species fluctuate asynchronously depending on the environmental conditions. Our experimental data did not allow to test this mechanism, as getting full time-series data on all communities was too challenging logistically; however, our model allowed an exploration of this mechanism. Following this hypothesis, we should expect that species' abundance should fluctuate asynchronously with temperature fluctuation depending on species' thermal tolerance and that such asynchronous fluctuations should lead to higher ecosystem functioning with higher diversity. However, our model did not show such effect, as the few most abundant species, driving ecosystem functioning, were all fluctuating in synchrony with temperature fluctuations, preventing the insurance effect from operating (*SI Appendix*, Fig. S12).

Discussion

Temperature variability affected the relationship between biodiversity and ecosystem functioning. We demonstrated that larger temperature fluctuations led to a steeper relationship between phytoplankton biodiversity and production over time. We used a simple theoretical competition model to help in understanding the mechanisms driving differences in the BEF relationship across environments with distinct thermal fluctuations. It is to note that our theoretical model does not allow us to accept or reject a specific mechanism but to explore the relative contribution of different mechanisms to the experimental results. We found that a likely mechanism might be the spread of species' thermal tolerances (i.e., interspecific variation in thermal tolerances). The reason is twofold. First, the contribution of species to community functioning in our experiment was linked to their thermal traits. Second, BEF relationships in both the experiment and the model were linked to the spread of species' thermal tolerances. However, we did not find any indication of a change in competitive interactions with temperature fluctuation in our experiment and no effect of experimentally measured competition strength on the BEF slope, suggesting that this mechanism was not at play here, although our study did not allow us to test this mechanism more rigorously. Similarly, we did not find support for asynchronous fluctuations among species as a mechanism explaining our results.

Ecosystem functioning increased with species richness through a linear relationship on log-log scale. The intercept of this relationship indicates ecosystem production at low levels (one species) of richness. The steepness of the slope elucidates the importance of biodiversity for ecosystem functioning. We found that temperature

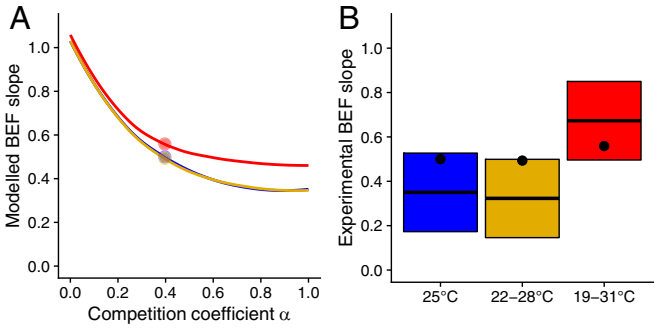

Fig. 4. Comparison of the modeled and experimental results regarding the slope of the BEF relationship. (*A*) Modeled BEF slope depending on the temperature (blue: constant 25 °C treatment; yellow: fluctuating 22 to 28 °C treatment; and red: fluctuating 19 to 31 °C treatment) and on the competition coefficient α (*SI Appendix*, Fig. S6). The dots correspond to the competition coefficient estimated in our experiment (*SI Appendix*, Fig. S7). (*B*) Experimental BEF slopes at day 15 in the three temperature treatments compared to the modeled slopes. Boxplots correspond to effect sizes and 95% CI and dots to the modeled BEF slopes for α equal to the observed 0.40 value (*SI Appendix*, Fig. S6).

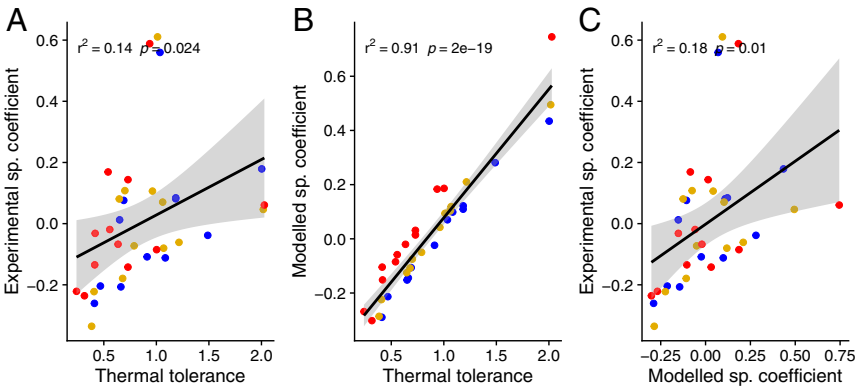

Fig. 5. Species contribution to ecosystem functioning depends on their thermal tolerance. (*A*) Relationship between species contribution to ecosystem functioning (species coefficient, *SI Appendix*, Fig. S10) measured in the experiment and thermal tolerance measured as the mean growth over the three temperature fluctuation treatments from thermal tolerance curves (effective growth rate, *SI Appendix*, Fig. S5). (*B*) Relationship between species contribution to ecosystem functioning derived from the theoretical data and thermal tolerance. (*C*) Relationship between species contribution to ecosystem functioning in the experiment and contribution to ecosystem functioning derived from the model results. Blue: constant 25 °C treatment; yellow: fluctuating 22 to 28 °C treatment; red: fluctuating 19 to 31 °C treatment. $n = 36$ (12 species per temperature treatment).

fluctuations decreased ecosystem production in species-poor communities. This was due to nonlinear averaging of thermal tolerances. Indeed, because phytoplankton species were in the concave part of their thermal tolerance curve, the time-averaged tolerance in fluctuating conditions was lower than the tolerance at a constant average temperature (61, 62). Furthermore, the BEF slope was steeper over longer timescales in the moderate and severe thermal fluctuation treatment. This indicates that for the same decrease in species richness, ecosystem production decreased more in severely fluctuating environments. Interestingly, the magnitude of the change in slope was quite important, with a 91% increase in slope between the constant and severe fluctuations treatments, higher than the 53% increase in slope with a 6 °C temperature increase in ref. 48, and the 44% increase in slope with a 5 °C temperature increase in ref. 22. Future meta-analysis should aim at understanding which environmental drivers linked to climate change (e.g., changes in temperature mean, variance, or frequency of extreme climatic events) have the stronger impact on the BEF slope. In addition, ecosystem functioning for the communities of maximum diversity did not change across temperature treatments over time, suggesting that a greater diversity (12 species relative to 1) was able to compensate for the negative impact of larger environmental fluctuations.

We further found that the slope of the BEF relationship changed through time. This agrees with studies on plant communities that found that the impact of biodiversity on ecosystem functioning increases through time (55, 56, 58, 63–67). This temporal increase of the BEF slope could arise from an increase in the productivity of the high-richness communities over time (55), a decrease in the productivity of the low-richness communities (57), or different rates of increase or decrease over time in the high- and low-richness communities (58). In our experiment, the temporal increase in slope depended on the temperature fluctuation treatment and on the measure for ecosystem production considered: while it was present for the moderate and severe fluctuating treatment when using abundance as a measure, it was present only for the severe fluctuation treatment when using biomass and for both constant and severe fluctuating treatments using chlorophyll *a* as a measure. Furthermore, the reason for the increase in slope also depended on the metric used: for abundance, it was due to a decrease in the production of the 1-species communities, with no temporal effect in the 12-species communities. For biomass, there was a decrease in the production in 1-species communities in the stable and severely fluctuating treatment, but in 12-species communities, ecosystem function actually increased with time in the two fluctuating treatments. Finally, for chlorophyll *a* it was due to an increase in production over time for all treatments at both richness levels but a steeper increase in the production of the 12-species communities. The dependency of the temporal effect on the ecosystem metric considered is in line with other studies, showing that changes at either low- or high-richness communities can drive the slope depending on the ecosystem function considered (58). Our study focused on abundance/biomass production as a measure of ecosystem functioning, however further studies should aim at understanding whether other ecosystem functions, such as such as C fixation, O_2 production, or nutrient recycling, would also lead to steeper BEF slopes with increased fluctuations. More interestingly, the effect of time varied with temperature fluctuation treatments, with a lower abundance over time in the low-richness communities in the severe fluctuating treatment but no effect in the constant temperature treatment. It is to note that our experiment was of short temporal duration (15 d). However, given the fast reproductive rate of phytoplankton (around 0.9 generations per day on average), it encompassed a larger number of generations than most of the experiments on terrestrial plants reviewed in ref. 55, where the median experiment length was 730 d, or ∼2 generations of perennial plant species. Overall, our results show that as in grassland communities (66), increases in slopes seem to be due to both increases in production at high richness and decreases in production at low richness, and further show that the reason behind the strengthening of the biodiversity–ecosystem relationship over time might depend on the environmental context and specifically on the temperature fluctuation level.

We investigated theoretically the variation in the BEF slope with temperature fluctuations. Using a simple Lotka–Volterra competition model at steady state, we found that the strength of the BEF slope depended on two fundamental parameters: the spread of species' thermal tolerances in the species pool, and competition strength. Parameterizing the model with thermal tolerance curves for growth measured for these species by Barton and Yvon-Durocher (60), and with a competition coefficient directly estimated from the experiment, we obtained BEF slopes similar to those in our experiment. The steeper slopes characteristic of the severe fluctuation treatment were linked to the variability in the thermal tolerance of the species composing the communities. Indeed, species that had higher thermal tolerances in fluctuating conditions were also the ones that contributed the most to ecosystem functioning. Furthermore, the spread in thermal tolerances in the species pool interacted with biodiversity to drive ecosystem functioning in our experiment. Thus, as suggested by our theoretical model, species pools with a larger spread of thermal traits

were better able to cope with the increasing temperature fluctuations, leading to greater BEF slopes.

Although our model shows that competition strength can potentially be a major factor in determining the strength of the BEF relationship, with weaker competition leading to steeper BEF slopes, our experimental results suggest that this mechanism was not an important driver here. Indeed, we found no effect of temperature fluctuations on competition strength in the experiment and no interaction between competition strength and biodiversity on ecosystem functioning. Furthermore, using the average value of competition strength across treatments we accurately predicted the experimental BEF slope, suggesting that a change in competitive interactions was not needed to explain our results. Importantly, our model assumes that interaction structure between species is symmetric, while this might not be the case in the experiment. Indeed, some species might be better competitors regardless of their thermal tolerance, and thermal tolerance could further affect competitive abilities (68). Our experimental communities showed some variation in relative interaction intensity (RII) including some facilitative interactions (*SI Appendix*, Fig. S6), which might contribute to some unexplained variation in the BEF slope. Thus, we cannot fully reject the hypothesis that variation in species interaction strength might affect the BEF slope, although the spread in thermal tolerances seems to be the strongest driver.

Interestingly, while the temporal insurance hypothesis posits that the slope of the BEF relationship should be steeper in temporally variable environments due to different species dominating the community dynamics through time (5), our theoretical model suggests that such a mechanism might not be an important driver here, although we did not have experimental results to support this hypothesis. Indeed, the most abundant species fluctuated in synchrony with each other in response to the environmental conditions, with no sign of asynchrony that could lead to greater ecosystem function overall. In our model, the species that had the larger average growth rate over the two temperature conditions dominated the community all the time, and such time-averaged growth rate was linked to greater contribution to community functioning in the experimental results.

The purpose of our model was to explore the mechanisms operating in the experiment. To do so, we made a number of simplifications. In particular, the model assumes equilibrium in which nutrient renewal is constant, while nutrients in our experiment are only added at the beginning. Relaxing this assumption, we found that the model results depend on the rate of nutrient depletion (*SI Appendix*, Appendix 1 and Fig. S13). We show that communities reach a quasi equilibrium that coincides with the Lotka–Volterra equilibrium and remain in this state for a time that depends on the rate of nutrient uptake, until a sharp decrease in abundances when nutrients are completely exhausted in the environment. In our experiment, it is likely that species were at stationary growth phase and thus carrying capacity by day 15 (*SI Appendix*, Fig. S14), and thus the simple Lotka–Volterra equilibrium might be a good approximation of the reality.

Our experimental results contrast with those of Parain et al. (49) on protozoan–bacteria consumer–resource communities. The authors found a decrease in the BEF slope value with increased mean and variation of temperature. Using a similar competition model to the one developed here, they found that the mechanism behind their results was a temperature-induced increase in consumer attack rates, which translated into higher effective competitive interactions among consumers. Baert et al. (51) showed theoretically and empirically that the slope of the BEF had a hump-shaped relationship with environmental stress. In their study, the BEF slope increased from low to medium values of environmental stress due to the increased probability that more diverse communities contain a stress-tolerant species. However, when stress levels were high, the BEF relationship collapsed into a horizontal line as stress was sufficiently high to inhibit the growth of all species. This effect was confounded by changes in species interactions that are more idiosyncratic and might depend on species identities, making predictions more difficult. In our system, thermal fluctuations can be considered an environmental stress, as evidenced by the strongly decreased effective growth rate in almost all species in the severe fluctuation treatment (*SI Appendix*, Fig. S5). However, our extreme (i.e., 19 to 31 °C) fluctuation treatment was not sufficiently high to inhibit the growth of all species, explaining the steeper slope with increasing temperature fluctuation. Overall, temperature fluctuations can lead to drastically different responses of the BEF relationship depending on whether it leads to a change in species interactions or is driven by differences in thermal tolerances. A better understanding of the conditions in which increased temperature variability leads to one, the other, or a mix of both is needed in order to predict ecosystem responses in the face of climate change and biodiversity loss. Simple competitive models such as ours, Parain et al. (49), or Baert et al. (51) can help understanding whether and when species traits affect BEF relationships.

Conclusion

The combination of rapid climate change and human-driven biodiversity loss makes understanding how changing climatic conditions and biodiversity levels will affect ecosystem functioning an imperative. Our proof-of-concept study showed both experimentally and theoretically that due to variation in phytoplankton species' thermal tolerances, thermal fluctuations affected the slope of the relationship between biodiversity and ecosystem functioning. When climatic conditions fluctuate strongly, the slope of the relationship is steeper, suggesting that biodiversity loss has a stronger negative effect on ecosystem functioning than when the environment is more stable. This is particularly true over longer timescales, as the slope of the relationship becomes steeper over time in the severe fluctuation treatment. Changes in BEF slope were primarily linked to differences and variability in thermal tolerances. Although, theoretically, modifications in competitive interactions can also play a role, we found no support for this mechanism and neither for the effect of asynchronous populations fluctuations. Because climate change entails both changes in the mean and variance in temperature and because increased temperatures have also been found to increase the slope of the BEF relationship, we should now understand the potential for interactive effects between mean and temperature fluctuations. Further studies should also aim at scaling-up our results to more complex communities and ecosystems (69), taking into account trophic diversity as well as more realistic mesocosm and natural settings increasing the spatial and temporal scale.

Materials and Methods

Species and Culture Conditions. We used 12 species of marine phytoplankton for the experiment: *Amphidinium carterae*, *Bigelowiella natans*, *Dunaliella tertiolecta*, *Emiliania huxleyi*, *Gymnochlora stellata*, *O. tauri*, *Porphyridium aerugineum*, *Porphyridium purpureum*, *Phaeodactylum tricornutum*, *Rhodella maculata*, *Synechocystis* sp., and *Thoracosphaera heimii*. These species encompass most of the biogeochemically and ecologically important groups (Chlorophytes, Coccolithophores, Cyanobacteria, Diatoms, Dinoflagellates, Rhodophytes, and Prasinophytes; *SI Appendix*, Table S12). Strains of each species were sourced from an experiment run at Exeter University (United Kingdom) by Barton and Yvon-Durocher (60), in which the authors studied thermal tolerance curves for growth of culture collection strains of 18 marine phytoplankton species including these 12 species. Stocks of each of the strains were transferred from Exeter University to the Station d'Ecologie Théorique et Expérimentale (Moulis, France). Species were cultured on Keller's K + Si medium in a Panasonic MLR-352 incubator at 20 °C on a 12:12 light–dark cycle with a light intensity of 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and kept under nutrient replete, exponential growth conditions by transferring 1 mL of each culture into new medium every week for ∼3 mo before the experiment.

BEF Experiment. We created artificial communities using the random partition design described by Bell et al. (59) to study how the relationship between biodiversity and ecosystem functioning varied with temperature fluctuations.

We randomly combined species into communities with different species richness levels from 1, 2, 3, 4, 6, and 12 species. At each species richness level, we constructed the community assemblages by sampling all of the 12 species without replacement (Fig. 1), allowing each species to be represented an equal number of times (22). We repeated the sampling five times to form five independent partitions of the species pool so that the number of assemblages for each richness level (R) was $5 \times 12/R$. We then replicated each assemblage three times. We subjected all replicated communities to three temperature fluctuation treatments, constant 25 °C, fluctuating between 22 and 28 °C and fluctuating between 19 and 31 °C, which led us to get a total of $3 \times 3 \times 5 \times (12 + 6 + 4 + 3 + 2 + 1) = 1{,}260$ communities for the whole experiment.

We used 54 24-well plates (18 plates per temperature) filled with 2 mL K+Si medium to create the experimental communities. We inoculated each well with 1,200 cells.mL^{-1} of each community (i.e., 100 cells · mL^{-1} per species for 12-species communities, 200 cells · mL^{-1} per species for 6-species communities, 300 cells · mL^{-1} per species for 4-species communities, 400 cells · mL^{-1} per species for 3-species communities, 600 cells · mL^{-1} per species for 2-species communities, and 1,200 cells · mL^{-1} per species for monocultures). We randomized the position of the communities within the plates.

To minimize evaporation and contamination within the wells while allowing gas exchange, we covered plates with AeraSeal breathable membrane. We then grew the communities in three Panasonic incubators on a 12:12 light–dark cycle at either constant 25 °C temperature, fluctuation every other day between 22 and 28 °C, or fluctuation every other day between 19 and 31 °C. To refill water loss due to evaporation, we added 0.4 mL distilled water every 2 to 3 d to each well. After 5 and 15 d of experiment, we sampled 100 μL from each community onto a 96-well plate. We chose these two time points based on the data collected by Barton and Yvon-Durocher (60), whose growth curves collected at temperatures close to our experimental temperatures showed that species were likely in their exponential phase of growth at day 5, while they should reach stationary phase of growth by day 15 (*SI Appendix*, Fig, S14). Samples were preserved with 10 μL of 1% sorbitol solution as a cryoprotectant, incubated 1 h in the dark, and then frozen at −80 °C until further analysis. Plates were defrosted, and we determined total cell density in each sample by flow cytometry (BD FACSCanto II high throughput sampler). Plates were run on the flow cytometer on 0.5 μL · s^{-1} flow rate, with three times 50 μL mixing and a cleaning of 400 μL between each sample to avoid contamination of measurements between samples.

Data Analyses. We extracted flow cytometry standard files from the flow cytometer into R version 3.5.3 (70) using the Bioconductor package FlowCore to get cell counts and the associated cytometric properties (forward scatter [FSC, a proxy of size], side scatter [SSC], and far red fluorescence [PerCP.Cy5, a proxy of chlorophyll *a* content]). We first filtered the data to remove noise by removing every data point where $\log_{10}$(PerCP.Cy5) < 1.5, $\log_{10}$(FSC) < 3.3, and $\log_{10}$(SSC) < 1.5, which were below minimum values observed for live cells of these species. We then used the calibration curves described in *SI Appendix*, Appendix 2 to estimate cell chlorophyll *a* content in pg · cell^{-1} from PerCP.Cy5 values and cell biomass in pgC · cell^{-1} from FSC values.

We calculated community abundance as the total number of cells per mL and total biomass and chlorophyll *a* content as the sum of biomass or chlorophyll *a* across all cells scaled to numbers per mL. Because the theoretical model we present focuses on growth rate and abundance, we present the cell abundance data in the main text and use this metric as a measure of ecosystem functioning. However, similar results are found with the total chlorophyll *a* content and total biomass, presented in *SI Appendix*.

We used linear mixed models with lme4 package to understand how the relationship between BEF varied with time and temperature fluctuation treatments. We first fitted a linear mixed model of log abundance against the temperature fluctuation treatments as a factor as well as a random effect of sample identity to account for nonindependence between time points, and we added sequentially day of sampling (as a factor, day 5 or day 15), log-transformed species richness, and the two-way and three-way interactions between the three factors. We compared models of increasing complexity with Akaike Information Criterion (AIC). The best model included the triple interaction between time, temperature fluctuation treatment, and log species richness. We used post hoc contrasts to assess whether the BEF slope differed between each pairwise combination of temperature fluctuation treatment levels for a given date with emtrends function from emmeans package adjusting *P* values with Tukey method. We also tested whether the BEF slope differed between the two dates for each temperature fluctuation treatment level with the same methods.

In a second step, we aimed to understand whether ecosystem function depended on species thermal tolerances, measured for growth by Barton and Yvon-Durocher (60)'s experiment. Tolerance was calculated as either the growth rate at 25 °C for the constant treatment or the average of the growth rates at 22 and 28 °C (respectively, 19 and 31 °C, hereafter named effective growth rate) for the fluctuating treatments (*SI Appendix*, Fig. S5). Using the average of the two temperatures is reasonable because the change in the temperature in the incubators is very fast (from 19 °C to 31 °C and conversely in <20 min). We first measured the spread in thermal tolerances in the species pool for each temperature fluctuation level as the difference between the maximum and the minimum effective growth rate scaled by maximum effective growth rate. We then assessed whether such spread affected the BEF relationship by modeling ecosystem functioning at day 15 as a function of the interaction between spread in thermal tolerance and log richness in a linear model. To test whether the results were congruent with different measures of spread, we redid the analysis using the coefficient of variation of species thermal tolerance. Second, we assessed whether each species' contribution to ecosystem functioning was linked to their thermal tolerance. We used the residuals from the best supported model of the first step (Table 1) to fit a linear mixed model of community composition, with 12 variables representing each species' presence–absence status and their interaction with temperature as a factor, as well as sample identity as a random effect. This method provides species coefficients that allow understanding the effect of each species on ecosystem functioning relative to an average species (59). Species with a positive coefficient contribute to ecosystem functioning above the average species, while negative coefficients show a below-average contribution. We used a linear model to link these species coefficients to each species' thermal tolerance.

We also aimed at evaluating interspecific competition strength in the experiment. To do so, we used a random forest classification algorithm to discriminate cells from each species in each two-species community and calculate relative abundance at day 15 and thus to calculate abundance of each species within the two-species communities (*SI Appendix*, Appendix 3). We then calculated pairwise species interactions by the RII (71) from the ratio of the difference and sum of abundance of the species in monoculture B_o and the abundance of the species in polyculture B_w, $RII = \frac{B_w - B_o}{B_w + B_o}$. Note that because total initial abundance was kept constant across diversity levels (as usual in BEF experiments), we can only use RII at day 15. We first tested whether RII varied with temperature fluctuation treatment with an ANOVA. We then tested whether RII affected the BEF relationship by modeling ecosystem functioning as a function of the interaction between log richness and average RII in each temperature fluctuation treatment.

Theoretical Model.

Model definition. We constructed a model to generate predictions and test mechanisms for the BEF slope at different levels of thermal fluctuation. The model is based on the competitive Lotka–Volterra equations, which describe the dynamics of species abundance N_i, where species index i runs over S species:

$$\frac{dN_i}{dt} = r_i N_i - \sum_j a_{ij} N_i N_j.$$

The model parameters are r_i, the intrinsic growth rate of species i, and a_{ij} is the competition strength of species j on species i. To keep the model parameterizable, we assumed symmetric competition: that is, all intraspecific competition strengths are equal, $a_{ii} = a_0$ for all i, and all interspecific competition strengths are equal, $a_{ij} = a_1$ for all i and j with $i \neq j$. Environmental conditions affects intrinsic growth rates r_i and potentially also interaction strengths a_0 and a_1. Despite its simplicity, this model has been shown to provide insights in the effects of a changing environment on the BEF relationship (49, 51).

Model analysis. We investigated how the slope of the relationship between log species richness and log community abundance depends on the model parameters (*SI Appendix*, Appendix 1). Our model focuses on community abundance at steady state, which we considered to correspond to the day 15 conditions in the experiments, as single-species growth curves show that species are at stationary growth phase and thus carrying capacity by day 15 (*SI Appendix*, Fig. S14). Furthermore, it is to note that although in principle steady state of communities and ecosystems can differ strongly from steady state of the one-species population dynamics, in our model these different steady states are reached at similar times. We found that at steady state, the BEF slope is determined by only two model features: 1) the spread of intrinsic growth rates between species, and 2) the ratio of inter- to intraspecific competition strength, $\alpha = a_1 / a_0$. Moreover, this result remains approximately valid for the treatments with thermal fluctuations. It suffices to replace the model parameters r_i, a_0, and a_1 by their average over the two

temperatures of the fluctuation treatment. Note that we focus our theoretical analysis on production at steady state as it does not depend on initial biomass conditions (*SI Appendix*, Appendix 1) and is hence more easy to verify than the prediction for the transient regime, which is affected by both the model parameters and the initial conditions.

The key parameters of our model are instances of the two broad categories of coexistence mechanisms (52, 53, 72). In analogy with coexistence theory, we denote the spread of intrinsic growth rates, either at a fixed temperature for the constant treatment or averaged over two temperatures for the fluctuation treatments, "tolerance differences." The ratio of inter- to intraspecific competition strength α, sometimes called the competition coefficient, determines "niche differences," which are small for $\alpha \sim 1$ and large for $\alpha \sim 0$.

The model predicted the following dependencies of the BEF slope on the two key model parameters (*SI Appendix*, Fig. S9). If all species have approximately the same growth rate (weak tolerance differences), then the BEF slope decreases gradually from one at $\alpha = 0$ (nonoverlapping niches, no interspecific competition) to zero at $\alpha = 1$ (no niche differences, interspecific competition equal to intraspecific competition). In the case of strong tolerance differences, the BEF slope decreases more slowly from one at $\alpha = 0$ toward a lower value at $\alpha = 1$.

Model parameterization. To obtain a prediction for the BEF slope that can be compared to the experimental results, we estimated first the two key model parameters. We determined the intrinsic growth rates using the thermal tolerance curves measured by ref. 60. For the constant treatment (25 °C), we set the intrinsic growth rates r_i equal to the tolerance measured at this temperature. For the variable treatments (22 to 28 °C and 19 to 31 °C), we took the average of the tolerances measured at the two temperatures of the fluctuation regime (*SI Appendix*, Fig. S5). Note that under the model assumptions only relative values of species tolerance matter for the BEF slope (*SI Appendix*, Appendix 1).

We estimated the ratio of inter- to intraspecific competition using RIIs (71) (*SI Appendix*, Fig. S6). We computed the steady-state solution of the model for the same two-species communities that were used to determine the empirical distribution of RIIs. We repeated this computation for a range of values of the competition coefficient α. These results allowed us to establish a relationship between α and the average RII, dependent on the empirically estimated intrinsic growth rates. By evaluating this relationship at the average of the empirical RII distribution, we obtained our estimate of the competition coefficient α. We then plugged in the estimates for the intrinsic growth rates and the competition coefficient α in the theoretical model. We used the same random partitioning design as in the experiment to obtain 88 community compositions separated into six richness levels (R = 1, 2, 3, 4, 6, and 12 species). By regressing steady-state community abundance against initial species richness on a log-log scale, we obtained our prediction for the BEF slope. Importantly, the data used to generate the theoretical prediction were largely independent from the data used to construct the empirical BEF relationship. The effective growth rates were from ref. 60, and the competition coefficient was estimated from the individual species abundances in the two-species polycultures, while only the total community abundance matters for the BEF relationship.

Data Availability. Data and code are available on Zenodo at https://doi.org/10.5281/zenodo.5078310 (73).

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