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## Biodiversity increases and decreases ecosystem stability

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**Abstract:** Losses and gains in species diversity affect ecological stability<sup>1,2,3,4,5,6,7</sup> and the sustainability of ecosystem functions and services<sup>8,9,10,11,12,13</sup>. Experiments and models have revealed positive, negative and no effects of diversity on individual components of stability, such as temporal variability, resistance and resilience<sup>2,3,6,11,12,14</sup>. How these stability components covary remains poorly understood<sup>15</sup>. Similarly, the effects of diversity on overall ecosystem stability<sup>16</sup>, which is conceptually akin to ecosystem multifunctionality<sup>17,18</sup>, remain unknown. Here we studied communities of aquatic ciliates to understand how temporal variability, resistance and overall ecosystem stability responded to diversity (that is, species richness) in a large experiment involving 690 micro-ecosystems sampled 19 times over 40 days, resulting in 12,939 samplings. Species richness increased temporal stability but decreased resistance to warming. Thus, two stability components covaried negatively along the diversity gradient. Previous biodiversity manipulation studies rarely reported such negative covariation despite general predictions of the negative effects of diversity on individual stability components<sup>3</sup>. Integrating our findings with the ecosystem multifunctionality concept revealed hump- and U-shaped effects of diversity on overall ecosystem stability. That is, biodiversity can increase overall ecosystem stability when biodiversity is low, and decrease it when biodiversity is high, or the opposite with a U-shaped relationship. The effects of diversity on ecosystem multifunctionality would also be hump- or U-shaped if diversity had positive effects on some functions and negative effects on others. Linking the ecosystem multifunctionality concept and ecosystem stability can transform the perceived effects of diversity on ecological stability and may help to translate this science into policy-relevant information.

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# 1 Biodiversity increases and decreases 2 ecosystem stability

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45 **Losses and gains in species diversity affect ecological stability<sup>1–7</sup> and the sustainability**  
46 **of ecosystem functions and services<sup>8–13</sup>. Experiments and models reveal positive,**  
47 **negative, and no effects of diversity on individual components of stability such as**  
48 **temporal variability, resistance, and resilience<sup>2,3,6,11,12,14</sup>. How these stability components**  
49 **covary is poorly appreciated<sup>15</sup>, as are diversity effects on overall ecosystem stability<sup>16</sup>,**  
50 **conceptually akin to ecosystem multifunctionality<sup>17,18</sup>. We observed how temporal**  
51 **variability, resistance, and overall ecosystem stability responded to diversity (i.e. species**  
52 **richness) in a large experiment involving 690 micro-ecosystems sampled 19 times over**  
53 **40 days, resulting in 12939 samplings. Species richness increased temporal stability but**  
54 **decreased resistance to warming. Thus, two stability components negatively covaried**  
55 **along the diversity gradient. Previous biodiversity manipulation studies rarely reported**  
56 **such negative covariation despite general predictions of negative effects of diversity on**  
57 **individual stability components<sup>3</sup>. Integrating our findings with the ecosystem**  
58 **multifunctionality concept revealed hump- and U-shaped effects of diversity on overall**  
59 **ecosystem stability. That is, biodiversity can increase overall ecosystem stability when**  
60 **biodiversity is low, and decrease it when biodiversity is high, or the opposite with a U-**  
61 **shaped relationship. Effects of diversity on ecosystem multifunctionality would also be**  
62 **hump- or U-shaped if diversity has positive effects on some functions and negative**  
63 **effects on others. Linking the ecosystem multifunctionality concept and ecosystem**  
64 **stability can transform perceived effects of diversity on ecological stability and may**  
65 **assist translation of this science into policy-relevant information.**

66  
67 Ecological stability consists of numerous components including temporal variability,  
68 resistance to environmental change, and rate of recovery from disturbance<sup>1,2,16</sup>. Effects of  
69 species losses and gains on these components are of considerable interest, not least due to  
70 potential effects on ecosystem functioning and hence the sustainable delivery of ecosystem  
71 services<sup>1–13</sup>. A growing number of experimental studies reveal stabilising effects of diversity  
72 on individual stability components. In particular, higher diversity often, but not always,  
73 reduces temporal variability of biomass production<sup>13</sup>. Positive effects of diversity on  
74 resistance are common, though neutral and negative effects on resistance and resilience also  
75 occur<sup>9,13,19,20</sup>. While assessment of individual stability components is essential, a more  
76 integrative approach to ecological stability could lead to clearer conceptual understanding<sup>15</sup>  
77 and might improve policy guidance concerning ecological stability<sup>16</sup>.

78 Analogous to ecosystem multifunctionality<sup>17,18</sup>, a more integrative approach considers  
79 variation in multiple stability components, and the often-ignored covariation among stability  
80 components. The nature of this covariation is of paramount importance, as it defines whether  
81 diversity has consistent effects on multiple stability components, or whether some stability  
82 components increase with diversity while others decrease. Surprisingly, the nature,  
83 prevalence, and implications of negative covariation between stability components along  
84 diversity gradients are almost completely overlooked, including the ensuing possibility for  
85 non-monotonic effects of diversity on overall ecosystem stability.

86 We first describe new experimental findings of how biodiversity affects the intrinsic  
87 stability of ecosystems and their resistance to warming. Temperature is a highly relevant  
88 disturbance due to its importance for biological processes and its great variability through  
89 space and time. However, our findings equally apply to and have implications for other  
90 environmental changes that could result in opposing effects on stability components such as  
91 flooding<sup>12</sup> or chemical stress<sup>21</sup>. We then review other evidence for negative covariation in  
92 effects of diversity on stability and potential mechanisms. Finally, we analyse overall  
93 ecosystem stability, a concept that embraces the covariation between stability components  
94 and their weighting, and show the plausibility of previously overlooked non-monotonic  
95 (hump- and U-shaped) effects of diversity on overall ecosystem stability.

96 We performed a factorial manipulation of the diversity and composition of competing  
97 species (1 to 6 species, 53 unique community compositions) and temperature (six constant  
98 levels, modelled as a linear predictor) in microbial communities of bacterial consumers, and  
99 recorded community biomass dynamics over time. For each replicate we then calculated two  
100 stability components: resistance ( $= [\text{total biomass at } T^{\circ}\text{C} - \text{total biomass at } 15^{\circ}\text{C}] / [T^{\circ}\text{C} -$   
101  $15^{\circ}\text{C}]$  where  $T$  is the temperature of the replicate) and the temporal stability of biomass  
102 (inverse of coefficient of variation of community biomass). While these stability indices are  
103 widely used by empiricists, they should not be mistaken for mathematical definitions such as  
104 asymptotic resilience, which are more precise but also more restrictive<sup>22</sup>.

105 Increased species richness caused greater temporal stability of total biomass (figure 1-  
106 a1) (linear mixed model of log inverse CV: richness effect size 0.33 with a standard error of  
107 0.065) at all temperatures (extended data figure 1). Total biomass increased during the first  
108 week of the experiment and then declined over the next five weeks and total biomass was  
109 higher in more species-rich communities (figure 1-b, 1-c2, extended data table 1) (effect size  
110 for log richness 0.05 [units of mg/mL/log(species richness) unit] with 0.0096 standard error).

111 In contrast, increased species richness decreased resistance of total biomass to  
112 warming (figure 1-a2) (negative effect of log richness in a linear model, effect size of -0.006  
113 [ $\text{mg}/^{\circ}\text{C}/\log(\text{species richness})$  unit] with a standard error of 0.0018). Richness negatively  
114 affected resistance measured on both absolute and relative scales (extended data figure 2).  
115 This effect was corroborated in analyses of total biomass by a negative interaction term  
116 between temperature and richness, which persisted through the experiment except during the  
117 first days (figure 1-c3) ( $\log(\text{richness}) \times \text{temperature}$  interaction of -0.0053 [units of  
118  $\text{mg}/\text{mL}/^{\circ}\text{C}/\log(\text{species richness})$  unit] with standard error of 0.00051) despite large variation  
119 in dynamics of total biomass (figure 1-b). This negative interaction reflects a stronger  
120 negative effect of temperature on total biomass (i.e. lower resistance) in richer communities  
121 (i.e. a richness-dependent response of total biomass to temperature).

122 Hence, temporal stability and resistance were negatively correlated across the species  
123 richness gradient (figure 1-d, RMA analysis with slope = -0.009, 95% CI = -0.0178 to -  
124 0.0051). Niche complementarity, statistical averaging, low overall response diversity, and  
125 possibly lower response diversity in more diverse communities were likely causes of the  
126 opposite effects of richness on temporal stability (extended data figure 3). The two stability  
127 components were, however, positively correlated within any single level of species richness  
128 (figure 1-d, extended data table 2). That is, composition variation without changes in species  
129 richness resulted in positively covarying temporal stability and resistance.

130  
131 Next, we examined studies (including our own) measuring multiple stability  
132 components across diversity gradients based on a review by Donohue et al. (2016)<sup>16</sup> (figure  
133 2, extended data table 3 & 4). Seven of 30 comparisons show positive covariance, twenty  
134 show no covariance, and three showed negative covariance. Our study for the first time  
135 identifies negative covariation between resistance and temporal variability caused by intrinsic  
136 dynamics only. Although infrequently reported, negative covariation is disproportionately  
137 important because it complicates conclusions about and practical implications of effects of  
138 diversity on stability. Furthermore, these studies may be unrepresentative of the true  
139 prevalence of negative covariation, due to it being overlooked, publication bias towards  
140 positive diversity-stability relationships<sup>3</sup> or if the scale of analysis masks such covariation,  
141 e.g. within richness versus across richness.

142 A general mechanistic understanding of why different studies find different  
143 correlations would be a major step forward. Of the 30 pairs of stability components, only  
144 seven were accompanied by quantitative analyses of mechanism for both diversity-stability  
145 relationships (extended data table 4). Response diversity was implicated in five of these  
146 seven. Indeed, response diversity has been identified as an important driver of the resilience  
147 of ecological systems<sup>23,24</sup>, and correlation among effect (i.e. high biomass production) and

148 response (e.g. response to an environmental driver) traits, at least in the absence of strong  
149 interspecific interactions, might predict covariance among stability components<sup>23</sup>. None of  
150 the studies involved manipulation of mechanism.

151  
152 Negative covariation also raises the potential for non-monotonic effects of diversity  
153 on overall ecosystem stability. Ecosystem multifunctionality is the simultaneous  
154 consideration of several ecosystem functions. Similarly, overall ecosystem stability considers  
155 multiple stability components simultaneously<sup>16</sup> (see extended data figure 4 for clarification of  
156 terms and concepts). We first calculated overall ecosystem stability as the sum of  
157 standardised individual ecosystem stability components<sup>25</sup>. For the results of our experiment,  
158 in which one stability component increases linearly with diversity, and another decreases  
159 linearly (figure 1-a1,2), overall ecosystem stability is invariant with species richness since the  
160 two standardized components perfectly balance each other.

161 We further explored the implications of the negative covariation among stability  
162 components. Existing methods for calculating ecosystem multifunctionality include a  
163 mathematical function for converting values of each ecosystem function into a common  
164 currency. Following others<sup>26</sup>, we assumed a logistic shape conversion function, and  
165 converted observed stability components into the common currency, with parameter values  
166 chosen to ensure that the range of the data includes the lower and upper asymptote. Here we  
167 present the influence of the value of the intercept (parameter  $Q$ ) of the conversion function  
168 (figure 3a), which is similar to varying the threshold value when calculating ecosystem  
169 multifunctionality with the threshold approach<sup>27</sup>.

170 The opposing stability-diversity relationships from our experiment, coupled with  
171 logistic conversion functions produced a hump-shaped relationship between overall  
172 ecosystem stability and diversity at low values of  $Q$ , a flat relationship at intermediate values,  
173 and a U-shaped relationship at higher values (figure 3b,c). Effects of richness on overall  
174 ecosystem stability were weaker at the replicate level than the richness level (figure 3b) in  
175 part due to relatively large variability among the replicates within richness levels and also  
176 due to positive covariance of temporal stability and resistance within diversity levels (figure  
177 1d).

178 Finding hump- and U-shaped diversity-stability relationships fundamentally alters the  
179 importance of biodiversity, from it being unimportant (variation in biodiversity has no  
180 consequence), to being state dependent. The hump-shaped and U-shaped relationships  
181 occurred because measured stability components (e.g. resistance) cross the threshold of the  
182 conversion function at different levels of species richness (see link to interactive figure in  
183 Methods). Thus, negatively covarying stability components and non-linear conversion  
184 functions can produce a non-monotonic effect of diversity on overall ecosystem stability.  
185 Furthermore, we expect the same to apply to ecosystem multifunctionality when individual  
186 ecosystem functions negatively covary along a diversity gradient.

187  
188 The chosen mathematical conversion function and its parameter values are therefore  
189 important. Ecosystem multifunctionality-diversity relationships can be negative, neutral or  
190 positive depending on the chosen threshold value<sup>27</sup>. Similarly, different weightings of  
191 ecosystem functions can alter which species and interactions are considered important for  
192 multifunctionality<sup>26</sup>. Other types and parameterisations of conversion functions might  
193 conceivably result in other diversity-stability relationships. For instance, weighting one  
194 ecosystem function (or stability component) highly, would lead to a multifunctionality /  
195 overall ecosystem stability measure that is essentially univariate. We view the choice and  
196 parameterization of conversion functions as an opportunity to tailor estimates of ecosystem  
197 multifunctionality and overall ecosystem stability to their policy and decision making  
198 applications<sup>16,26,28,29</sup>. These conversion functions and estimates of overall ecosystem stability  
199 can then transform the perceived importance of biodiversity change for the sustainable

200 delivery of multiple ecosystem services and may assist in translating the results of scientific  
201 studies into actionable information.

202

## 203 Methods section

204 **Experimental methods**

205 The experiment was conceived and designed to research biodiversity-ecosystem  
206 relationships, with a focus on questions on environmental gradients and effects on temporal  
207 changes / stability, including the one addressed in this article. We factorially manipulated  
208 temperature (15, 17, 19, 21, 23 and 25 °C) and species richness (1 to 6 species of  
209 bacterivorous ciliates: *Colpidium striatum*, *Dexiostoma campylum*, *Loxocephalus* sp.,  
210 *Paramecium caudatum*, *Spirostomum teres*, and *Tetrahymena thermophila*) in 690  
211 microcosms (250 mL Duran bottles). There were two incubators at each temperature.  
212 Manipulating temperature with a replicated gradient is recommended to harness the power of  
213 a regression design, while still allowing us to test for a nonlinear temperature effect<sup>30</sup>. During  
214 prior testing the temperature of liquid in similar microcosms varied around the set-point  
215 temperature by 0.1 °C. Long-term ciliate cultures were kept at 15 °C, and warming usually  
216 decreases their carrying capacities but increases growth rates<sup>31</sup>. For *Colpidium*, temperatures  
217 above 20 °C represent a stress that decreases population growth rate, whereas the other  
218 species are still within their tolerated thermal range.

219 To start the experiment, ciliates were grown to their respective carrying capacities at  
220 20°C in bottles containing 1L of bacterized medium. Throughout the experiment, medium  
221 consisted of protist pellets (Carolina Biological Supplies, Burlington, NC, USA) at a  
222 concentration of 0.055g L<sup>-1</sup> of Chalkley's medium in which the bacterium *Serratia fonticola*  
223 was grown as the resource for all ciliate consumers. Two autoclaved wheat seeds were added  
224 to each bottle for slow nutrient release<sup>32</sup>.

225 Monocultures (species richness = 1) were initiated at a density of 3 individuals mL<sup>-1</sup>  
226 in a total of 100mL medium. Multispecies communities (containing 2 to 6 species) were  
227 initiated with a total of 40 mL ciliate culture topped up with 60 mL fresh medium (100 mL  
228 culture in total). The 40mL cultures were assembled by adding a fixed fraction (i.e. 20 mL for  
229 2 species, 13.33 mL for three species etc.) of each species at their specific carrying capacity,  
230 adopting a substitutive design. Since the number of possible species compositions exceeded  
231 the number of feasible experimental units, we used all possible compositions only for the  
232 monocultures, two and six species communities. For all other levels, species compositions  
233 were selected randomly from the set of all possible compositions such that all species  
234 occurred the same number of times, resulting in a total of 53 different compositions. Each  
235 level of species richness and composition was replicated at least twice, including an  
236 additional replicate for the two and three species level, and 3 additional replicates for the six  
237 species community resulting in 115 experimental units per temperature.

238 We sampled each experimental unit every day for the first 7 days, then 3 times per  
239 week for the following 50 days and a final sampling 7 days later, resulting in time series of  
240 27 time points over a 57-days period. We used video sampling techniques to count and  
241 measure individual ciliates in all communities<sup>33</sup>. For sampling, microcosms were taken out of  
242 the incubator, gently stirred to homogenize the culture and a sample was pipetted into a  
243 counting chamber. The counting chamber was covered with a lid and a 5s long video was  
244 taken under the microscope. The videos were subsequently processed with the R package  
245 BEMOVI<sup>34</sup>.

246 We derived community biomass by summing the biovolume of all individuals of a  
247 given species in a given community and multiplying biovolume with a constant density equal  
248 to water (i.e. 1g/cm<sup>3</sup>). For each community, this resulted in a time series of community  
249 biomass. To avoid analysing monoculture time series whilst starting at a low fraction of the  
250 carrying capacity (3 individuals mL<sup>-1</sup>), compared to our multi-species culture species which  
251 started between 7 and 20 % carrying capacity (depending on richness), we aligned the

monoculture time series such that they started at the day where they crossed 20% of their expected carrying capacity. Results regarding the effect of richness on temporal stability are qualitatively robust to exclusion of monoculture data (extended data figure 1c).

The temporal stability of each replicate community was calculated as the inverse of the coefficient of temporal variation in community biomass (mean community biomass / standard deviation of community biomass). Resistance was measured for each replicate as the absolute difference between total biomass in the replicate and the mean total biomass at 15°C, divided by the temperature difference, with dimensions of milligrams (per ml) per degree Celsius. Resistance values close to 0 indicate high resistance, whereas negative values indicate lower resistance. We also quantified relative resistance as the difference between total biomass in the replicate and the mean total biomass at 15°C divided by the mean total biomass at 15°C (i.e. the loss proportional to the mean biomass at 15°C).

We did not quantify resilience since in a constant environment temporal variability is in principle closely related to resilience<sup>35</sup>. To understand potential drivers and mechanisms, we investigated the role of statistical averaging and species asynchrony. Statistical averaging is assessed by the scaling relationship between the species mean biomass and species variance in biomass<sup>36</sup>. Synchrony was assessed by a metric introduced by Gross et al. (2014)<sup>37</sup> which calculates the average correlation between the biomass of each species and the total biomass of all other species in the group. We used the R package codyn<sup>38</sup> to calculate asynchrony.

## Analyses

Analysis of total biomass used linear mixed effects models<sup>39</sup> (LMMs), with temperature (linear, centred), species richness (log-linear), and their interaction as fixed effects (extended data table 1a). Microcosm identity nested in composition was included as random factor to account for the repeated measurements. Heterogeneity of residuals was accounted for by estimating a composition-specific variance. AIC comparison consistently identified a model with linear temperature effect, as opposed to when temperature was a factor, as most parsimonious (delta AIC of model with nonlinear temperature term was greater than 2 in all comparisons). A simpler analysis of the temporal average of total biomass of each individual microcosm to test the effect of richness, temperature, and their interaction, including a random effect for species composition, yielded quantitatively and qualitatively similar results (see extended data table 1b). Figure 1c shows the estimated effects of LMMs fitted separately for each day with temperature (linear, centred), species richness (log-linear), and their interaction as fixed effects and composition as a random effect. Analyses of temporal stability and resistance did not contain repeated measures and hence only accounted for variation in composition with a random effect. We used the R package nlme for all linear mixed effects models<sup>40</sup>. To calculate associations between resistance and temporal stability among and within richness levels, we calculated reduced major axis regressions (RMA) using the R package lmodel2<sup>41</sup> as both variables potentially contain measurement error. Significance of RMA slopes deviating from zero was assessed by one-tailed permutation tests. All analyses were done in R - the statistical computing environment<sup>42</sup>.

## Review of empirical studies

Based on the review by Donohue et al. (2016)<sup>16</sup> we obtained a set of studies of resilience, resistance, and temporal variability of ecosystem functions in response to direct or indirect experimental manipulations of diversity. Direct manipulations were defined as changing diversity by adding different sets of species to an experimental plot, jar, or other unit, whereas indirect manipulations induced variation in diversity via the experimental treatment, such as fertilization. We only included studies that performed experimental manipulations. To analyse whether specific mechanisms lead to covariation, we noted the type of mechanism proposed for each of the individual diversity-stability components (extended data table 4). Furthermore, we assessed whether a quantitative or verbal argument was provided (or the

mechanisms were not addressed at all) and synthesized the available evidence by vote counting.

### Calculating overall ecosystem stability

An interactive web page

([https://frankpennekamp.shinyapps.io/Overall\\_ecosystem\\_stability\\_demo/](https://frankpennekamp.shinyapps.io/Overall_ecosystem_stability_demo/)) describes the calculation of ecosystem multifunctionality (also known as overall ecosystem functioning) or overall ecosystem stability and illustrates the following. The calculation requires that values of an ecosystem function (e.g. biomass production) or of a stability component (e.g. resistance to temperature) be converted into a common currency. The threshold approach uses a step mathematical function<sup>43</sup>; the averaging approach uses a linear mathematical function (and both equalise relative contributions of different ecosystem functions / stability components)<sup>25</sup>; a principal component approach uses a specific linear mathematical function for each ecosystem function or stability component<sup>44</sup>; and Slade et al. (2017)<sup>26</sup> propose step-like mathematical functions with more or less gradual changes from the lower to higher value. The generalised logistic function (also known as the Richard's function) is flexible enough to give a wide range of shapes of conversion function. If x is the measured variable, and Y is the converted variable, the generalised logistic function is:

$$Y = A + \frac{K - A}{(C + Qe^{-Bx})^{1/v}}$$

A is the lower asymptote.

K is the upper asymptote.

B is the gradient.

v affects the symmetry, and also the value of y(0).

Q affects the value of y(0), i.e. it shifts the function horizontally.

C is typically set to 1.

x is a variable, here the value of the measured ecosystem function or stability component.

Overall ecosystem stability is then the sum of the standardised and converted stability components  $OES = f(z(res)) + f(z(ts))$ , where res is the measured resistance, ts is the measured temporal stability, the function z() subtracts the mean and divides by the standard deviation, and f() is the generalised logistic function. The parameters of f() were A = -1, K = 1, B = 5, v = 1, C = 1 and Q was varied from  $10^{-2}$  to  $10^2$ . These values were chosen to produce converted stability measures that span the range A to K and to have a relatively threshold-like change from A to K.

Standardisation prior to summation results in overall ecosystem stability with mean of zero, emphasising that the units of valuation here are arbitrary (though generally need not be). Standardisation also implies equal weights for different stability components; weighting of functions needs to be further considered and may be specified according to the specific use cases<sup>45</sup>. Differential weightings, if desired and justified, can be incorporated into the conversions functions. Suggestions regarding the choice of conversion functions for managed systems can be found in Slade et al. 2017<sup>26</sup> and Manning et al. 2018<sup>28</sup>.

Unimodal relationships can result from negative covariation among two stability components. How does consideration of more than two components affect the unimodal pattern? While the unimodal relationship is the most pronounced when equal numbers of positive and negative relationships are considered, a unimodal relationship will persist as long as there is at least one opposing stability component (see extended data figure 5).

350 **Code availability**  
351 Code to reproduce the analyses and figures is accessible on Github  
352 [https://github.com/pennekampster/Code\\_and\\_data\\_OverallEcosystemStability](https://github.com/pennekampster/Code_and_data_OverallEcosystemStability)  
353 (DOI: 10.5281/zenodo.1345557).  
354  
355 **Data availability**  
356 The experimental data that support the findings of this study are available in Github  
357 ([https://github.com/pennekampster/Code\\_and\\_data\\_OverallEcosystemStability](https://github.com/pennekampster/Code_and_data_OverallEcosystemStability)) with the  
358 identifier (DOI: 10.5281/zenodo.1345557). Source data for figures 1-3 are provided with  
359 the paper.

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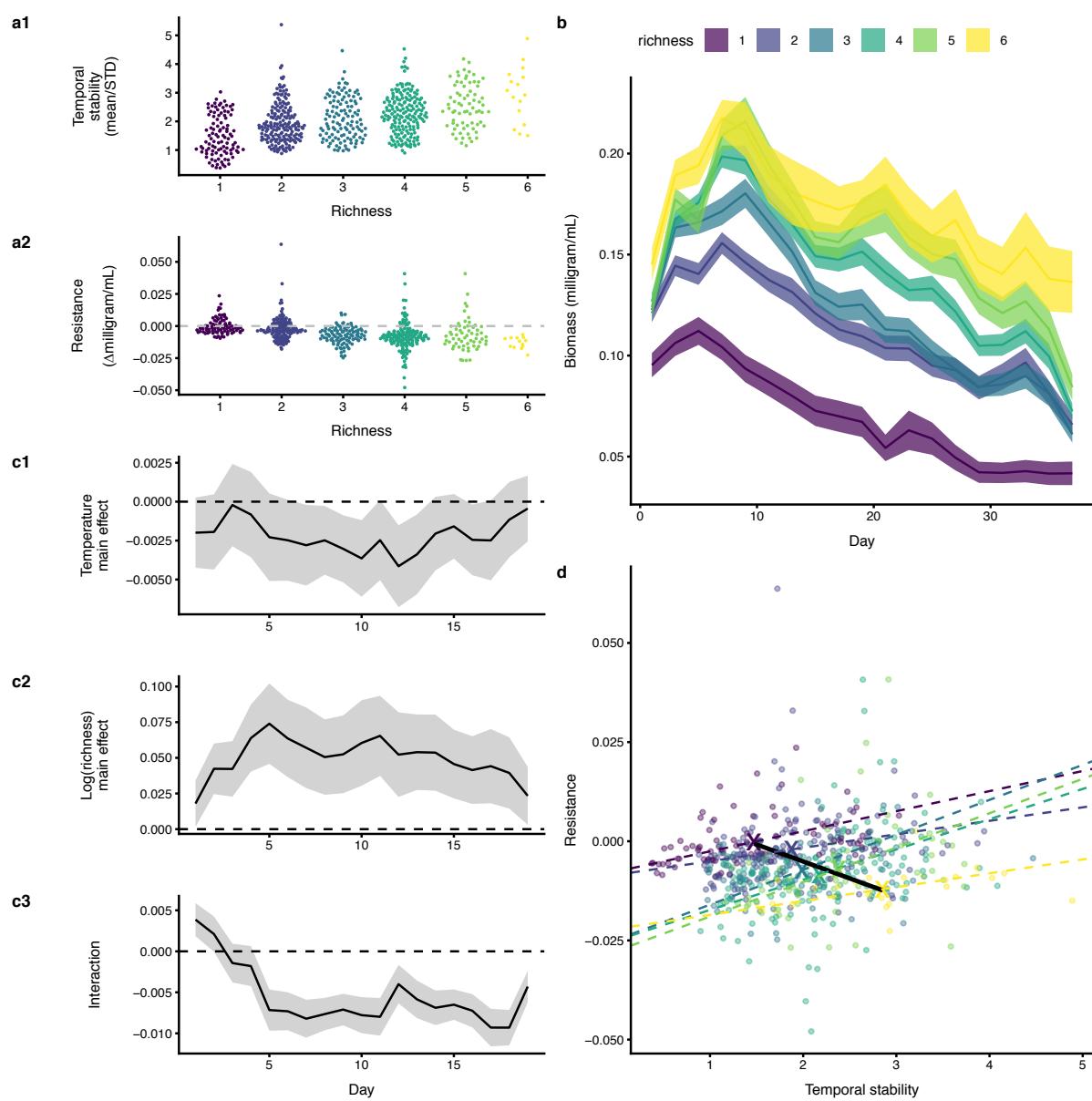
456  
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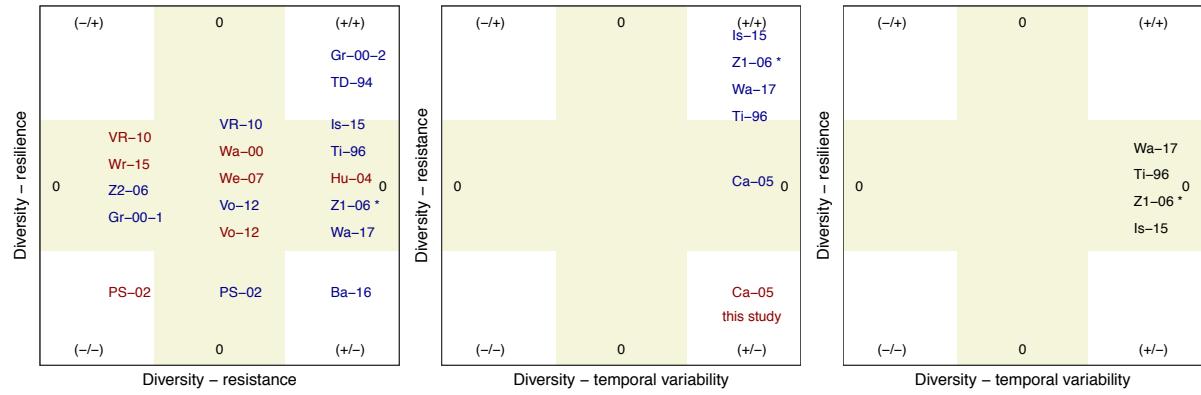
464 **Author Contributions:**

465 Conceived study: OP, FP, FA  
466 Designed experiment: OP, FP, MS, EAF, FA, GMP, TMM, MP  
467 Led experiment: FP  
468 Performed experiment: all, except JG, AT  
469 Prepared data: FP, OP, JG

470 Analysed data: FP, OP, MP, AT, MS  
471 Wrote the first draft: FP, OP  
472 Contributed to revisions of the manuscript: all  
473  
474 **Competing interests:** The authors declare no competing interests.  
475  
476 **Correspondence and requests for materials** should be addressed to F.P. or O.P.  
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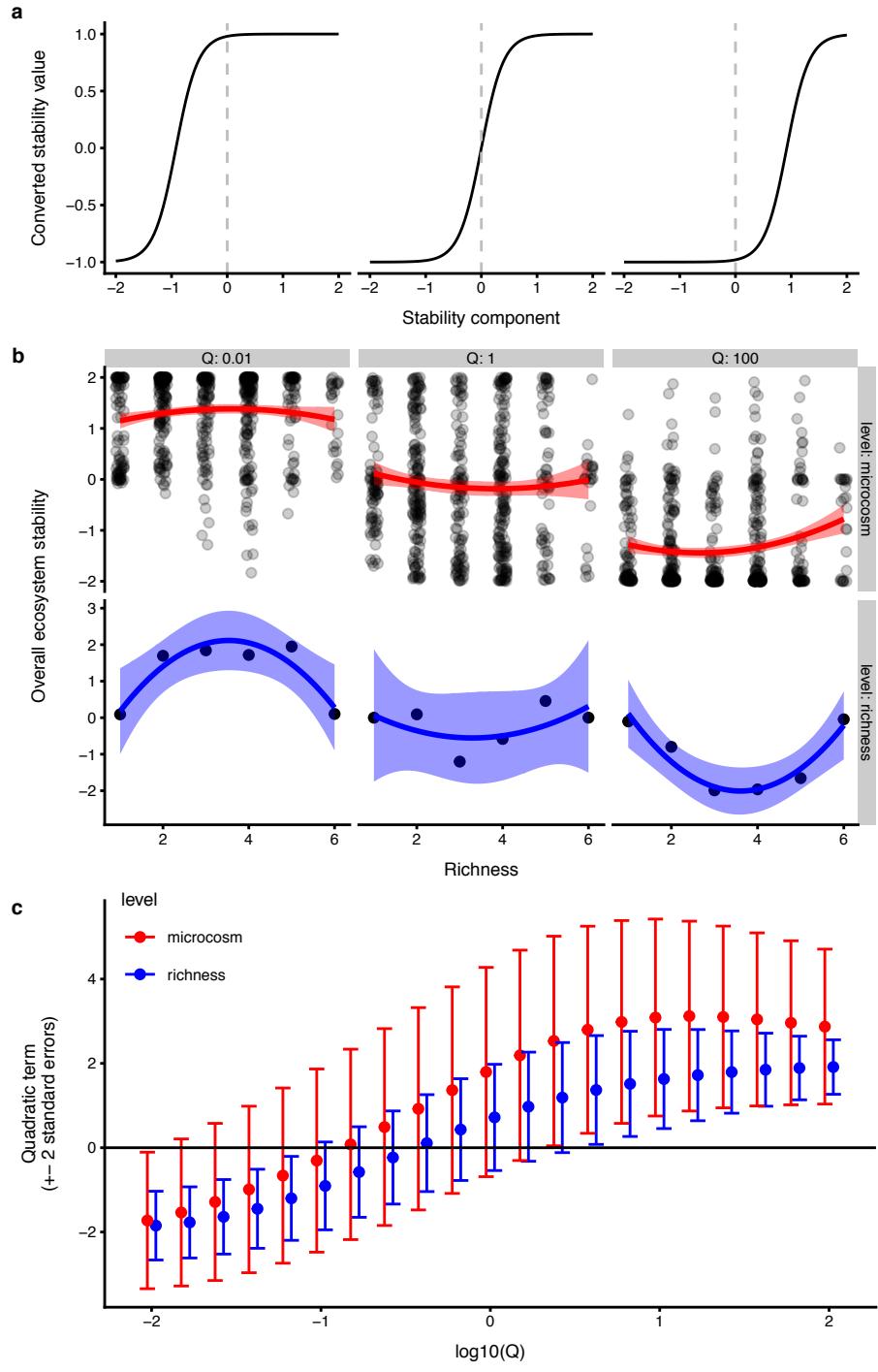
**Figures**

**Figure 1: Biomass and stability in experimental microbial communities.** Richness increased temporal stability (a1, n=681 independent microcosms), but decreased resistance (a2, n = 567 independent microcosms). Average ( $\pm 1$  standard error of the mean) biomass for each diversity level (b, n = 12939 microcosm x day combinations). Temporal dynamics of effect sizes (and 95% confidence intervals) of a linear mixed effects model of total biomass showed on average a negative effect of temperature (c1), a positive effect of diversity (c2), and a more negative effect of temperature at higher richness (persistent negative interaction term, c3) (n = 681 independent microcosms per day). Resistance and temporal stability (n = 567 independent microcosms) covaried negatively across richness (d, solid line through centroid of each richness level, n = 6 independent richness levels) but positively within richness levels (dashed lines).



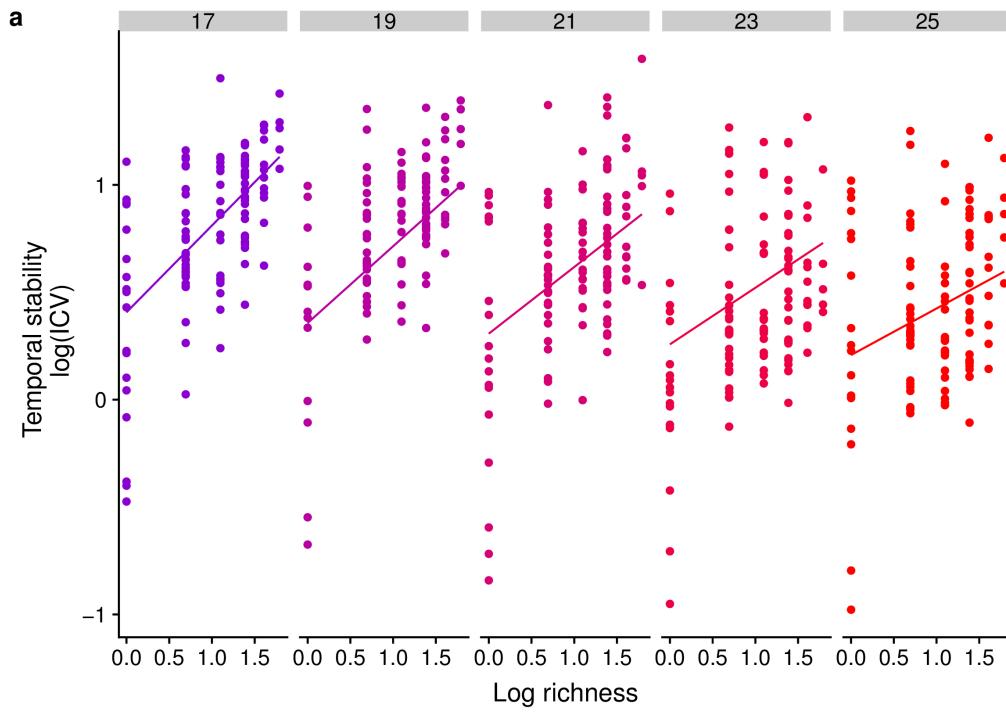
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**Figure 2: Positive, negative and neutral relationships among resistance, resilience and temporal variability in empirical studies with diversity manipulation.** 30 bivariate relationships were reported by 17 independent studies (in addition to this study). Detailed information about individual studies (e.g. code VR-09) is provided in extended data table 3 & 4. Beige regions indicate no covariation. Relative positions within regions are arbitrary and do not indicate relative strengths of relationships. Different colours indicate the effect of diversity on absolute (red) or relative resistance (blue), whereas temporal stability and resilience are shown in black.



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**Figure 3: Hump- and U-shaped diversity-stability relationships.** The intercept of the generalised logistic to convert measured stability components into a common currency varies with parameter  $Q$  (a). The non-aggregated ( $n = 567$  independent microcosms) or aggregated ( $n = 6$  richness levels) data exhibits hump- to flat- to U-shaped diversity-stability relationships as  $Q$  varies. Lines show the fit of a quadratic model and the 95% confidence interval (bands). (b). The variation from hump-shaped to U-shaped relationship depends smoothly on  $Q$ , i.e. the position of the threshold (quantified by the quadratic term of a regression with mean (dot) and 95% confidence intervals (bars)) (c).

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512**Extended data figures:****b**

	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.3320	0.1897	0.4744	0.07250	626	4.58	0.000006
Richness	0.3335	0.2038	0.4631	0.06459	51	5.16	0.000004
Temperature	-0.0249	-0.0360	-0.0137	0.00569	626	-4.37	0.000015
Rich. x temp.	-0.0234	-0.0334	-0.0134	0.00508	626	-4.61	0.000005

CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

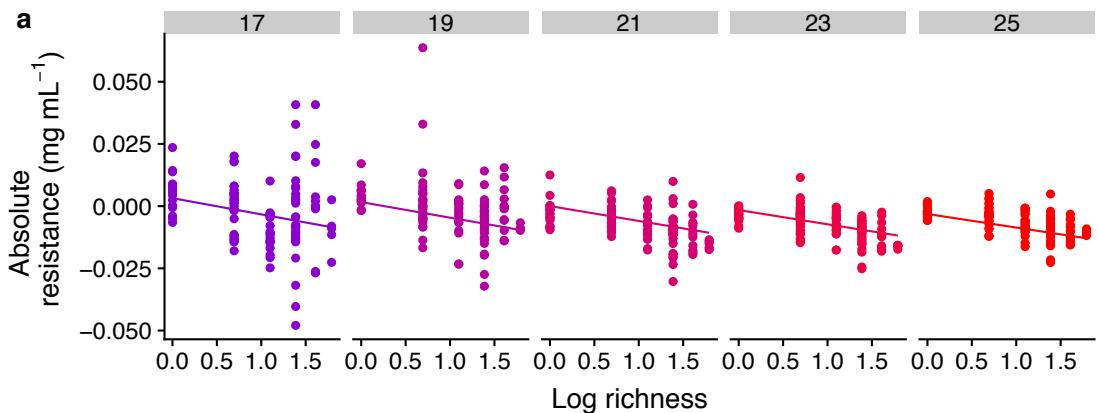
**c**

	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.3937	0.2163	0.57118	0.09032	531	4.36	0.000016
Richness	0.2842	0.1319	0.43648	0.07562	45	3.76	0.000491
Temperature	-0.0317	-0.0506	-0.01272	0.00965	531	-3.28	0.001095
Rich. x temp.	-0.0181	-0.0337	-0.00247	0.00794	531	-2.28	0.023283

CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

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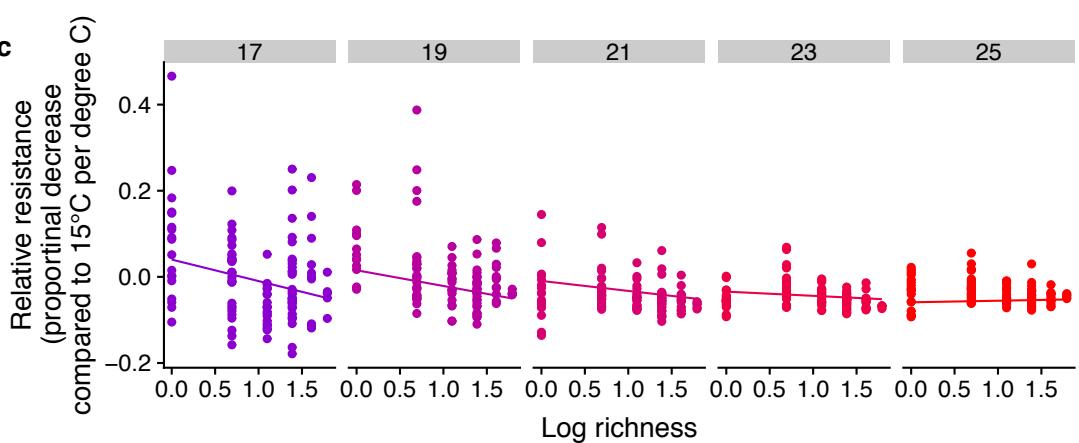
**Extended data figure 1:** Richness increased temporal stability across temperatures. a) The stabilizing effect of richness was present across all temperatures, although temperature has a negative effect on mean stability. b) Result table for linear, mixed effects model of log richness, temperature and their interaction on temporal stability supporting the stabilizing effects of richness and the negative effect of temperature on temporal stability ( $n = 681$  independent microcosms). c) Result table for the same analysis as b) but without the monocultures. Results are qualitatively the same, indicating that the relationship between richness and temporal stability is not only driven by the monocultures ( $n = 580$  independent microcosms).



**b**

	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.000812	-0.003137	0.004760	0.002010	512	0.404	0.686407
Richness	-0.006115	-0.009710	-0.002520	0.001791	51	-3.415	0.001258
Temperature	-0.000796	-0.001215	-0.000376	0.000214	512	-3.726	0.000216
Rich. x temp.	0.000133	-0.000241	0.000507	0.000190	512	0.697	0.486295

**c**

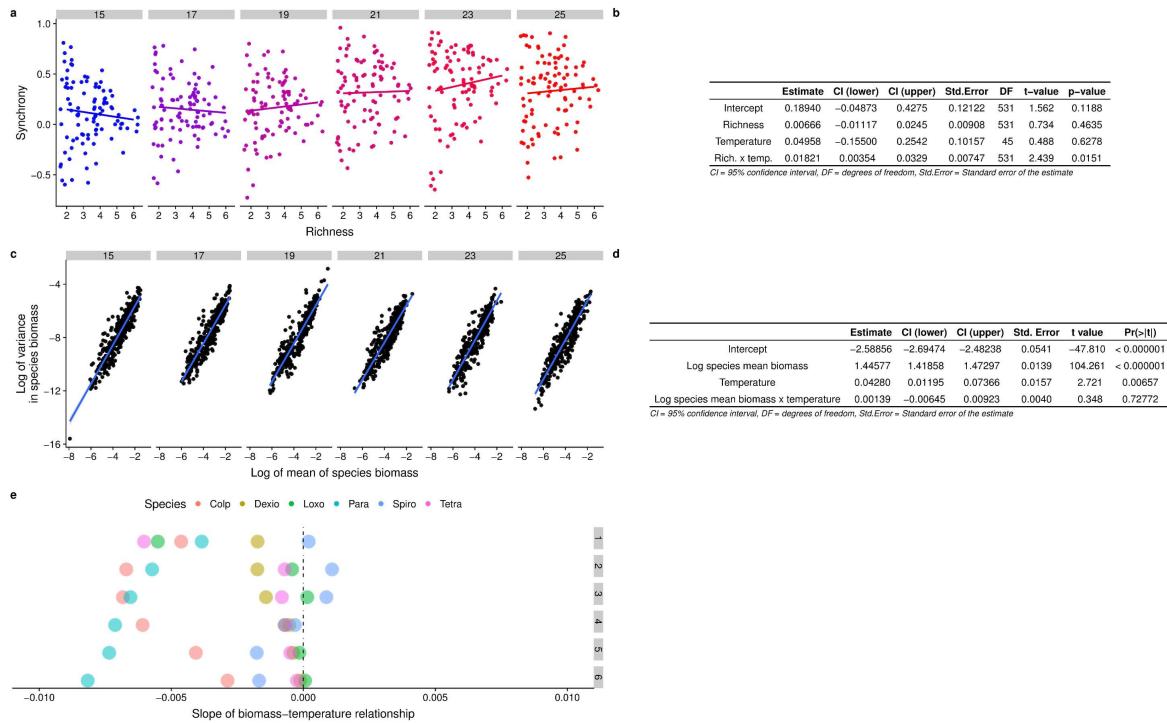


**d**

	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.00284	-0.02027	0.02595	0.01176	512	0.241	0.80951
Richness	-0.02980	-0.05085	-0.00875	0.01048	51	-2.842	0.00643
Temperature	-0.01241	-0.01544	-0.00937	0.00155	512	-8.023	< 0.000001
Rich. x temp.	0.00670	0.00399	0.00941	0.00138	512	4.858	0.000002

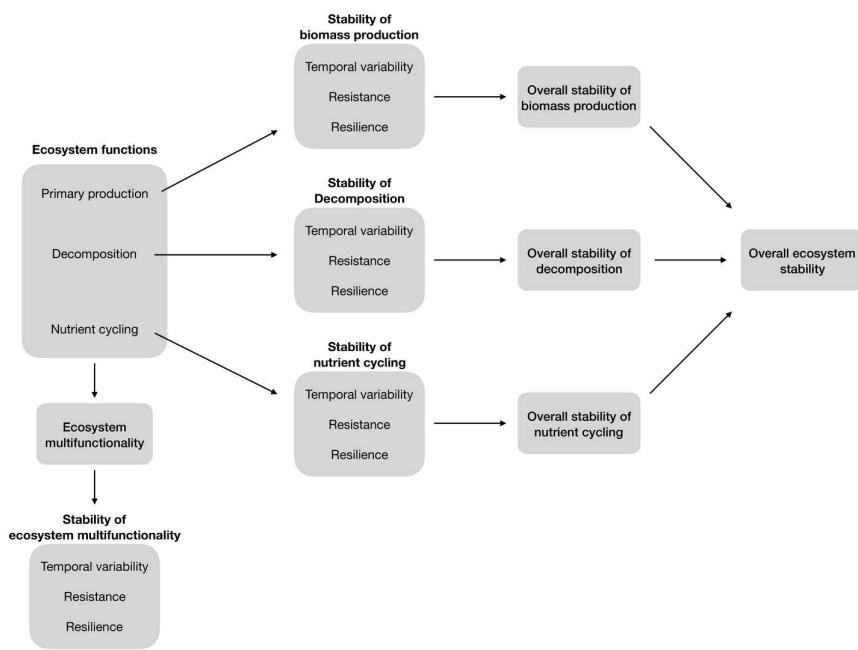
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**Extended data figure 2:** The effect of richness on absolute and proportional resistance. a, c) Richness decreased resistance, regardless whether its measured on the absolute or proportional scale. b, d) Result tables of linear, mixed effects model of richness, temperature and their interaction on absolute and proportional richness ( $n = 567$  independent microcosms).



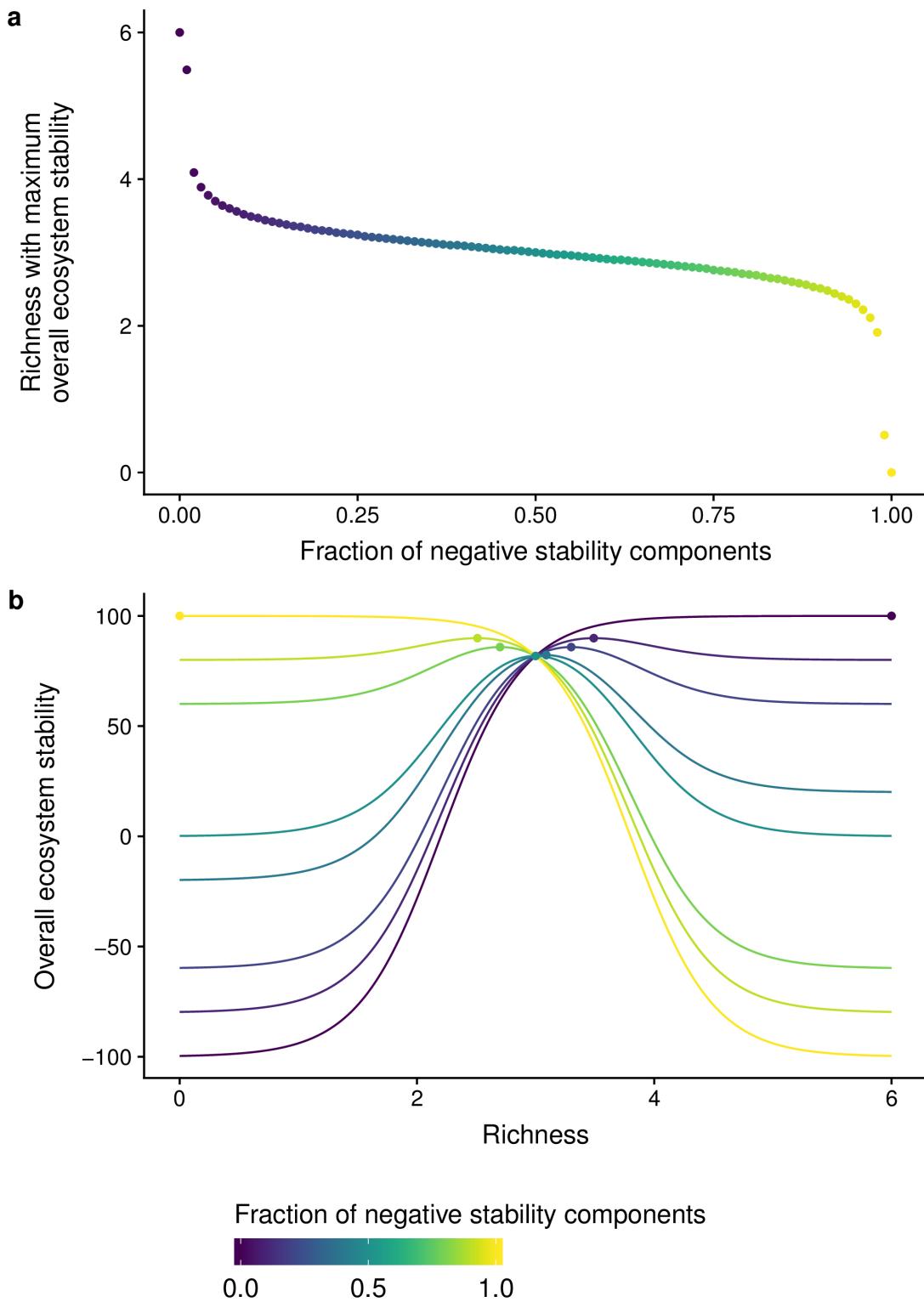
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**Extended data figure 3:** Niche complementarity and low response diversity were likely caused negative covariance of stability components. Niche complementarity and the resulting increase in total biomass with richness tended to increase temporal stability (figure 1 in main text). a, b) We found little evidence for an effect of population asynchrony on temporal stability (linear mixed effects model with composition as random effect and log richness and temperature as fixed effects;  $n = 681$  independent microcosms). c, d) In contrast, statistical averaging contributed to stabilization (linear regression between mean species biomass and the variance of species biomass;  $n = 2077$  species mean-variance biomass observations). e) Low response diversity was inferred because the biomass of most species decreased or was unaffected by temperature (linear regression between temperature and species biomass;  $n = 972$  species biomass x temperature observations). Consequently, when there were more species, there was greater total biomass, greater temporal stability, but greater biomass loss with temperature increase. Thus, niche complementarity (i.e. effect diversity) likely caused a positive effect of diversity on temporal stability but in the absence of high response diversity, also had a negative effect of diversity on resistance. However, this explanation cannot apply within richness levels, where there was positive covariance among stability components.



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**Extended data figure 4:** Overview of terms and the overall ecosystem stability concept. Measured ecosystem functions (left most upper box) can each have multiple components of stability (e.g. temporal variability, resistance, and resilience of biomass production), which can each be combined into a measure of overall stability. When, as in our study, there is only one ecosystem function, this overall stability of a specific function is also the overall ecosystem stability. In studies of more than one ecosystem function, the overall stability of several functions could be combined to give overall ecosystem stability. Alternatively, one could first calculate ecosystem multifunctionality, and then measure its stability components.



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**Extended data figure 5:** The effect of aggregating more than two stability components into overall ecosystem stability. The fraction of stability components with negative sign influences whether or not a unimodal pattern will result for a total of 100 stability components. a) A unimodal relationship between diversity and OES will result if at least one stability component is negative. b) However, the strength of the pattern depends on the relative balance of positive and negative relationships.

566 **Extended data table captions:**

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**a**

	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.07286	0.05182	0.093890	0.010731	12258	6.79	< 0.000001
Richness	0.04977	0.03058	0.068958	0.009559	51	5.21	0.000003
Temperature	-0.00205	-0.00315	-0.000948	0.000561	626	-3.65	0.000281
Rich. x temp.	-0.00534	-0.00634	-0.004345	0.000507	626	-10.54	< 0.000001

CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

**b**

	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.07323	0.05206	0.094407	0.010782	626	6.79	< 0.000001
Richness	0.04959	0.03031	0.068872	0.009603	51	5.16	0.000004
Temperature	-0.00220	-0.00351	-0.000892	0.000667	626	-3.30	0.00102
Rich. x temp.	-0.00547	-0.00664	-0.004296	0.000596	626	-9.18	< 0.000001

CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

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**Extended data table 1:** Richness increased while temperature decreases biomass production.

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a) Result table for the linear, mixed effects model of richness, temperature and their interaction on the temporal dynamics of biomass (n = 12939 microcosm x day combinations).

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b) Result table for linear, mixed effects model of richness, temperature and their interaction with the time series aggregated to the average biomass for each microcosm (n = 681 independent microcosms).

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richness	Intercept	Slope	P-perm (1-tailed)	N
1	-0.00760617400951036	0.00506367932695562	0.01	84
2	-0.00843466390669893	0.00339781153057296	0.02	148
3	-0.0247877029765781	0.00880722901581866	0.04	100
4	-0.0249323685277533	0.00762486814778502	0.01	150
5	-0.027634192253533	0.0086737833813624	0.01	60
6	-0.0220565962582076	0.00349526254239345	0.04	25

P-perm = permutation-based p value

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578 **Extended data table 2:** Reduced major axis regression revealed positive relationships  
579 between temporal stability and resistance within each of the six richness levels (p value based  
580 on one-tailed permutation tests; N = sample size for each richness level).

Code	Description	Abbreviated reference
Ca-05	Diversity manipulation of grassland plants (Portuguese BIODEPTH site) analysing temporal variability and resistance to natural perturbation (frost and low precipitation) of biomass production.	Caldeira et al (2005) <i>Oikos</i> , 110, 115
PS-02	Diversity manipulation of grassland plants (Swiss BIODEPTH site) analysing resistance and resilience of biomass production to experimental drought perturbation.	Pfister & Schmid (2002) <i>Nature</i> , 416, 84
Z2-06	Diversity manipulation of unicellular algae analysing resistance and resilience of biomass production to experimental cold perturbation.	Zhang & Zhang (2006) <i>Oikos</i> , 112, 218
Z1-06 *	Diversity manipulation of unicellular algae analysing temporal variability and resistance to experimental cold perturbation of biomass production.	Zhang & Zhang (2006) <i>Oikos</i> , 114, 385
Is-15	Forty-six diversity manipulations of grassland plants analysing temporal variability, resistance, and resilience to natural perturbations (drought and wet events) of biomass production.	Isbell et al (2015) <i>Nature</i> , 526, 574
VR-09	Diversity manipulation of plants, analysing resistance and resilience to natural perturbation (drought) of biomass production.	Van Ruijven & Berendse (2009) <i>Journal of Ecology</i> , 98, 81
Ba-16	Diversity manipulation of diatoms, analysing resistance and resilience to perturbation (chemical stressor, atrazine) of biomass production.	Baert et al (2016) <i>Ecology</i> , 97, 3433
Gr-00-1	Diversity manipulation by fumigation of soil microorganisms, analysing resilience to perturbation (heating) and resistance to perturbation (heating) of respiration.	Griffiths et al (2000) <i>Oikos</i> , 2, 279
Gr-00-2	Diversity manipulation by fumigation of soil microorganisms, analysing resilience to perturbation (chemical stress) and resistance to perturbation (chemical stress, CuSO <sub>4</sub> ) of respiration.	Griffiths et al (2000) <i>Oikos</i> , 2, 279
TD-94	Diversity manipulation by fertilisation of plants, analysing resistance and resilience of biomass production to natural perturbation (drought).	Timan & Downing (1994) <i>Nature</i> , 367, 363
Wa-00	Diversity manipulation of plants, analysing resistance and resilience to experimental perturbation (drought) of various ecosystem functions.	Wardle et al (2000) <i>Oikos</i> , 98, 11
Hu-04	Analysis of diverse studies of marine ecosystems, some of which examined diversity-resistance and some diversity-resilience relationships for various ecosystem functions.	Hughes & Stachwicz (2004), <i>PNAS</i> , 101, 24
Vo-12	Diversity manipulation of grassland plants. Analysis of resistance and resilience of biomass production to drought perturbation.	Vogel et al (2012) <i>PLoS One</i> , 7, e36992
Wr-15	Diversity manipulation of grassland plants. Analysis of temporal variability and resilience of biomass production to drought perturbation.	Wright et al (2015) <i>Nature Communications</i> , 6, 6092
We-07	Manipulation of soil microbial diversity by serial dilution. Analysis of resistance and resilience of denitrification and nitrite oxidation to a temperature perturbation.	Wertz et al (2007) <i>Environmental Microbiology</i> , 9, 2211
Wa-17	Diversity manipulation of grassland plants. Analysis of temporal variability and resilience of biomass production to drought perturbation.	Waag et al (2017) <i>Ecology</i> , DOI: 10.1002/ecy.2003
Ti-96	Diversity manipulation of grassland plants via fertilisation. Analysis of temporal variability, resilience and resistance of biomass production to natural drought perturbation.	Tilman (1996) <i>Ecology</i> , 77, 350

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**Extended data table 3:** Studies used for literature survey (figure 2). The individual study code, a short description and the abbreviated reference for each study is shown. \* denotes studies that examine intrinsic stability alongside response to a disturbance.

**Extended data table 4:** Putative mechanisms and type of evidence reported for all bivariate diversity-stability relationships.

Code	diversity_stability_relation	direction	mechanism1	mechanism2	evidence1	evidence2	scale
Ba-16	resistance/resilience	positive/negative	low response diversity	selection effect	signals of mechanisms	signals of mechanisms	relative
Ca-05	resistance/temporal_var	negative/positive	selection effect	increased evenness, synchrony; statistical averaging	signals of mechanisms	signals of mechanisms	absolute
Ca-05	resistance/temporal_var	neutral/positive	selection effect	increased evenness, synchrony; statistical averaging	signals of mechanisms	signals of mechanisms	relative
Gr-00-1	resistance/resilience	negative/neutral	not stated	not stated	missing	missing	relative
Gr-00-2	resistance/resilience	positive/positive	insurance effect	insurance effect	verbal	verbal	relative
Hu-04	resistance/resilience	positive/neutral	trade-offs in response diversity among stressors	not a sampling effect	signals of mechanisms	signals of mechanisms	absolute
Is-15	resistance/resilience	positive/neutral	not stated	not stated	missing	missing	relative
Is-15	resistance/temporal_var	positive/positive	not stated	not stated	missing	missing	relative
Is-15	resilience/temporal_var	neutral/positive	not stated	not stated	missing	missing	relative
Ps-02	resistance/resilience	negative/positive	high response diversity; evenness	species composition	signals of mechanisms	signals of mechanisms	absolute
Ps-02	resistance/resilience	neutral/negative	high response diversity; evenness	species composition	signals of mechanisms	signals of mechanisms	relative
TD-94	resistance/resilience	positive/positive	high response diversity	not stated	missing	missing	relative
Ti-96	resistance/resilience	positive/neutral	high response diversity	not stated	verbal	verbal	relative
Ti-96	resistance/temporal_var	positive/positive	high response diversity	high response diversity; competition	verbal	signals of mechanisms	relative
Ti-96	resilience/temporal_var	neutral/positive	not stated	high response diversity; competition	missing	signals of mechanisms	relative
Vo-12	resistance/resilience	neutral/neutral	not stated	not stated	missing	missing	absolute
Vo-12	resistance/resilience	neutral/neutral	not stated	not stated	missing	missing	relative
VR-09	resistance/resilience	negative/neutral	high response diversity	not stated	signals of mechanisms	signals of mechanisms	absolute
VR-09	resistance/resilience	neutral/neutral	high response diversity	not stated	missing	missing	relative
Wa-00	resistance/resilience	neutral/neutral	species composition	species composition	verbal	verbal	absolute
Wa-17	resistance/resilience	positive/neutral	insurance effect	insurance effect	verbal	verbal	relative
Wa-17	resistance/temporal_var	positive/positive	insurance effect	insurance effect	verbal	verbal	relative
Wa-17	resilience/temporal_var	neutral/positive	insurance effect	high response diversity	high response diversity	verbal	relative
We-07	resistance/resilience	neutral/neutral	selection effect; community composition	not stated	signals of mechanisms	signals of mechanisms	absolute
Wr-15	resistance/resilience	negative/neutral	high response diversity	high response diversity	verbal	verbal	absolute
Z1-06 *	resistance/resilience	positive/neutral	positive/positive	high response diversity	not stated	missing	relative
Z1-06 *	resistance/temporal_var	positive/positive	positive/positive	high response diversity	statistical averaging	signals of mechanisms	relative
Z1-06 *	resilience/temporal_var	neutral/positive	not stated	not stated	statistical averaging	signals of mechanisms	relative
Z2-06	resistance/resilience	negative/neutral	low response diversity	not stated	signals of mechanisms	signals of mechanisms	relative