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Biodiversity increases and decreases ecosystem stability

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45 **Losses and gains in species diversity affect ecological stability¹⁻⁷ and the sustainability**
46 **of ecosystem functions and services⁸⁻¹³. 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^{2,3,6,11,12,14}. How these stability components**
49 **covary is poorly appreciated¹⁵, as are diversity effects on overall ecosystem stability¹⁶,**
50 **conceptually akin to ecosystem multifunctionality^{17,18}. 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 components³. 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^{1,2,16}. 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 services¹⁻¹³. 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 production¹³. Positive effects of diversity on
74 resistance are common, though neutral and negative effects on resistance and resilience also
75 occur^{9,13,19,20}. While assessment of individual stability components is essential, a more
76 integrative approach to ecological stability could lead to clearer conceptual understanding¹⁵
77 and might improve policy guidance concerning ecological stability¹⁶.

78 Analogous to ecosystem multifunctionality^{17,18}, 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 flooding¹² or chemical stress²¹. 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 restrictive²².

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 [mg/°C/ log(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(richness) x temperature interaction of -0.0053 [units of
118 mg/mL/°C/log(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)¹⁶ (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 relationships³ 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^{23,24}, 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 components²³. 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 simultaneously¹⁶ (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 components²⁵. 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 others²⁶, 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 approach²⁷.

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 value²⁷. Similarly, different weightings of
191 ecosystem functions can alter which species and interactions are considered important for
192 multifunctionality²⁶. 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^{16,26,28,29}. 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 effect³⁰. 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 rates³¹. 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⁻¹ 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 release³².

225 Monocultures (species richness = 1) were initiated at a density of 3 individuals mL⁻¹
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 communities³³. 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 BEMOVI³⁴.

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/cm³). 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⁻¹), compared to our multi-species culture species which
251 started between 7 and 20 % carrying capacity (depending on richness), we aligned the

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

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

264 We did not quantify resilience since in a constant environment temporal variability is
265 in principle closely related to resilience³⁵. To understand potential drivers and mechanisms,
266 we investigated the role of statistical averaging and species asynchrony. Statistical averaging
267 is assessed by the scaling relationship between the species mean biomass and species
268 variance in biomass³⁶. Synchrony was assessed by a metric introduced by Gross et al.
269 (2014)³⁷ which calculates the average correlation between the biomass of each species and
270 the total biomass of all other species in the group. We used the R package *codyn*³⁸ to
271 calculate asynchrony.

272 Analyses

273 Analysis of total biomass used linear mixed effects models³⁹ (LMMs), with temperature
274 (linear, centred), species richness (log-linear), and their interaction as fixed effects (extended
275 data table 1a). Microcosm identity nested in composition was included as random factor to
276 account for the repeated measurements. Heterogeneity of residuals was accounted for by
277 estimating a composition-specific variance. AIC comparison consistently identified a model
278 with linear temperature effect, as opposed to when temperature was a factor, as most
279 parsimonious (delta AIC of model with nonlinear temperature term was greater than 2 in all
280 comparisons). A simpler analysis of the temporal average of total biomass of each individual
281 microcosm to test the effect of richness, temperature, and their interaction, including a
282 random effect for species composition, yielded quantitatively and qualitatively similar results
283 (see extended data table 1b). Figure 1c shows the estimated effects of LMMs fitted separately
284 for each day with temperature (linear, centred), species richness (log-linear), and their
285 interaction as fixed effects and composition as a random effect. Analyses of temporal
286 stability and resistance did not contain repeated measures and hence only accounted for
287 variation in composition with a random effect. We used the R package *nlme* for all linear
288 mixed effects models⁴⁰. To calculate associations between resistance and temporal stability
289 among and within richness levels, we calculated reduced major axis regressions (RMA) using
290 the R package *lmodel2*⁴¹ as both variables potentially contain measurement error.
291 Significance of RMA slopes deviating from zero was assessed by one-tailed permutation
292 tests. All analyses were done in R - the statistical computing environment⁴².

293 Review of empirical studies

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

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

305 Calculating overall ecosystem stability

306 An interactive web page
307 (https://frankpennekamp.shinyapps.io/Overall_ecosystem_stability_demo/) describes the
308 calculation of ecosystem multifunctionality (also known as overall ecosystem functioning) or
309 overall ecosystem stability and illustrates the following. The calculation requires that values
310 of an ecosystem function (e.g. biomass production) or of a stability component
311 (e.g. resistance to temperature) be converted into a common currency. The threshold
312 approach uses a step mathematical function⁴³; the averaging approach uses a linear
313 mathematical function (and both equalise relative contributions of different ecosystem
314 functions / stability components)²⁵; a principal component approach uses a specific linear
315 mathematical function for each ecosystem function or stability component⁴⁴; and Slade et al.
316 (2017)²⁶ propose step-like mathematical functions with more or less gradual changes from the
317 lower to higher value. The generalised logistic function (also known as the Richard's
318 function) is flexible enough to give a wide range of shapes of conversion function. If x is the
319 measured variable, and Y is the converted variable, the generalised logistic function is:
320

$$321 \quad Y = A + \frac{K - A}{(C + Qe^{-Bx})^{1/v}}$$

322

323 A is the lower asymptote.

324 K is the upper asymptote.

325 B is the gradient.

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

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

328 C is typically set to 1.

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

330

331 Overall ecosystem stability is then the sum of the standardised and converted stability
332 components $OES = f(z(\text{res})) + f(z(\text{ts}))$, where res is the measured resistance, ts is the
333 measured temporal stability, the function z() subtracts the mean and divides by the standard
334 deviation, and f() is the generalised logistic function. The parameters of f() were $A = -1$, $K =$
335 1 , $B = 5$, $v = 1$, $C = 1$ and Q was varied from 10^{-2} to 10^2 . These values were chosen to
336 produce converted stability measures that span the range A to K and to have a relatively
337 threshold-like change from A to K.

338 Standardisation prior to summation results in overall ecosystem stability with mean of
339 zero, emphasising that the units of valuation here are arbitrary (though generally need not
340 be). Standardisation also implies equal weights for different stability components; weighting
341 of functions needs to be further considered and may be specified according to the specific use
342 cases⁴⁵. Differential weightings, if desired and justified, can be incorporated into the
343 conversions functions. Suggestions regarding the choice of conversion functions for managed
344 systems can be found in Slade et al. 2017²⁶ and Manning et al. 2018²⁸.

345 Unimodal relationships can result from negative covariation among two stability
346 components. How does consideration of more than two components affect the unimodal
347 pattern? While the unimodal relationship is the most pronounced when equal numbers of
348 positive and negative relationships are considered, a unimodal relationship will persist as
349 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

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) 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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 455 of biodiversity for overall ecosystem functioning. *Ecology* **89**, 1223–1231 (2008).

456

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463

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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.

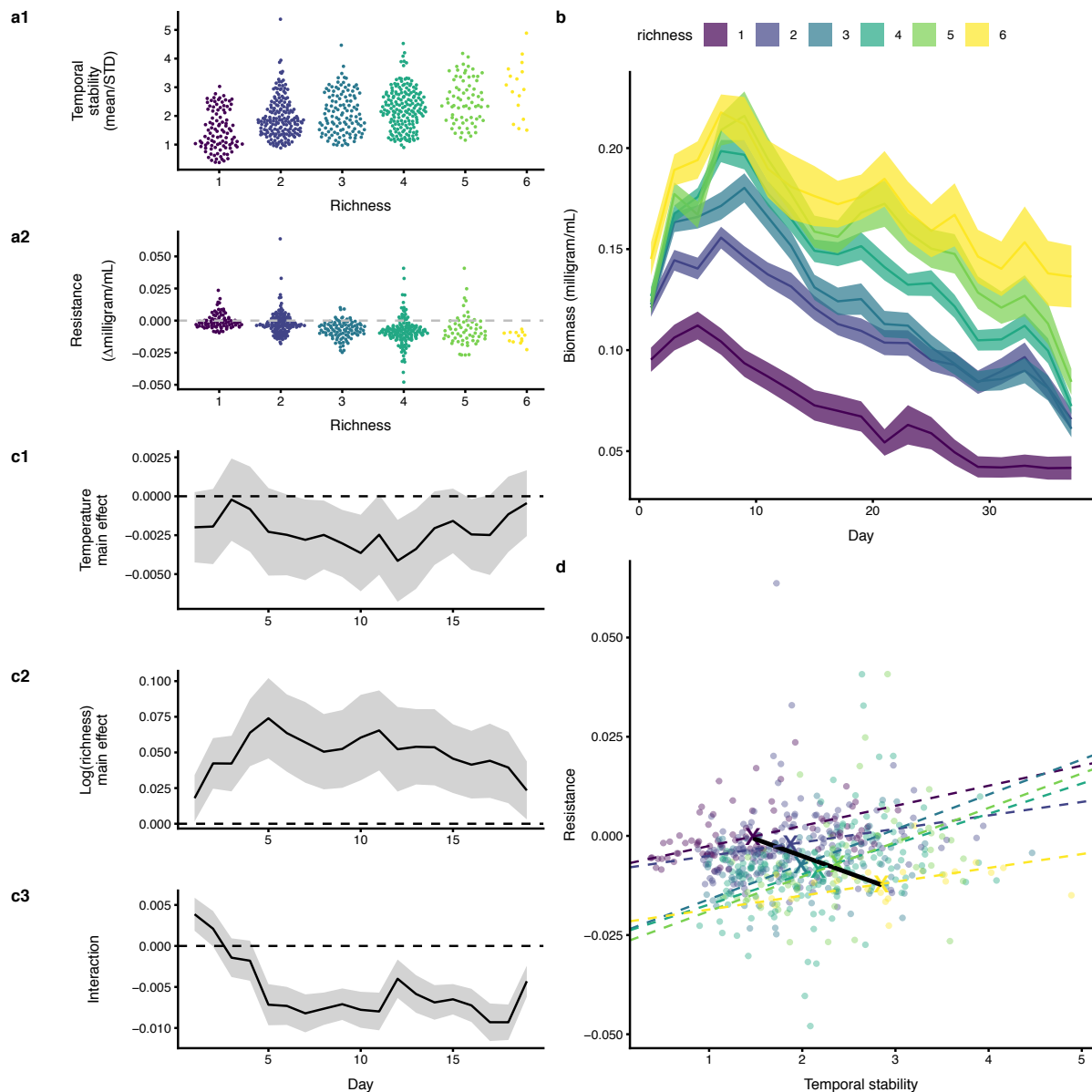
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476 **Correspondence and requests for materials** should be addressed to F.P. or O.P.

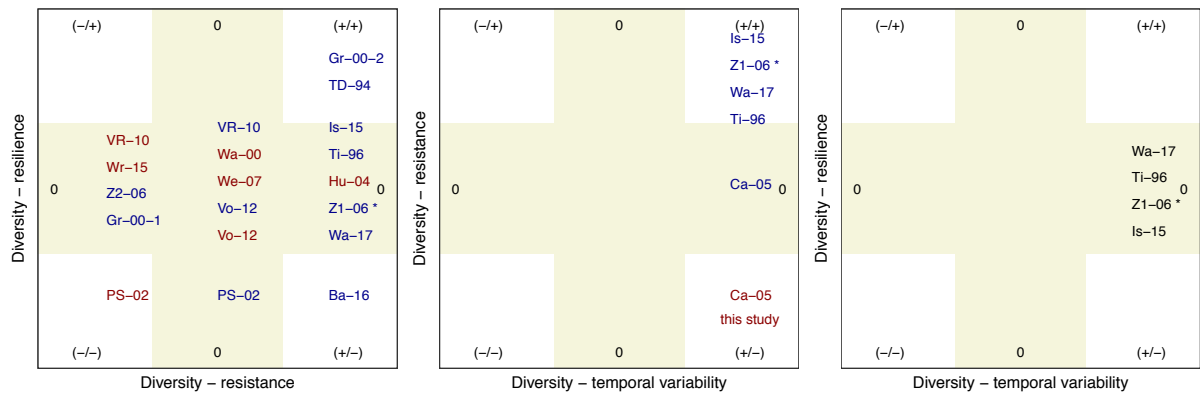
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479 **Figures**
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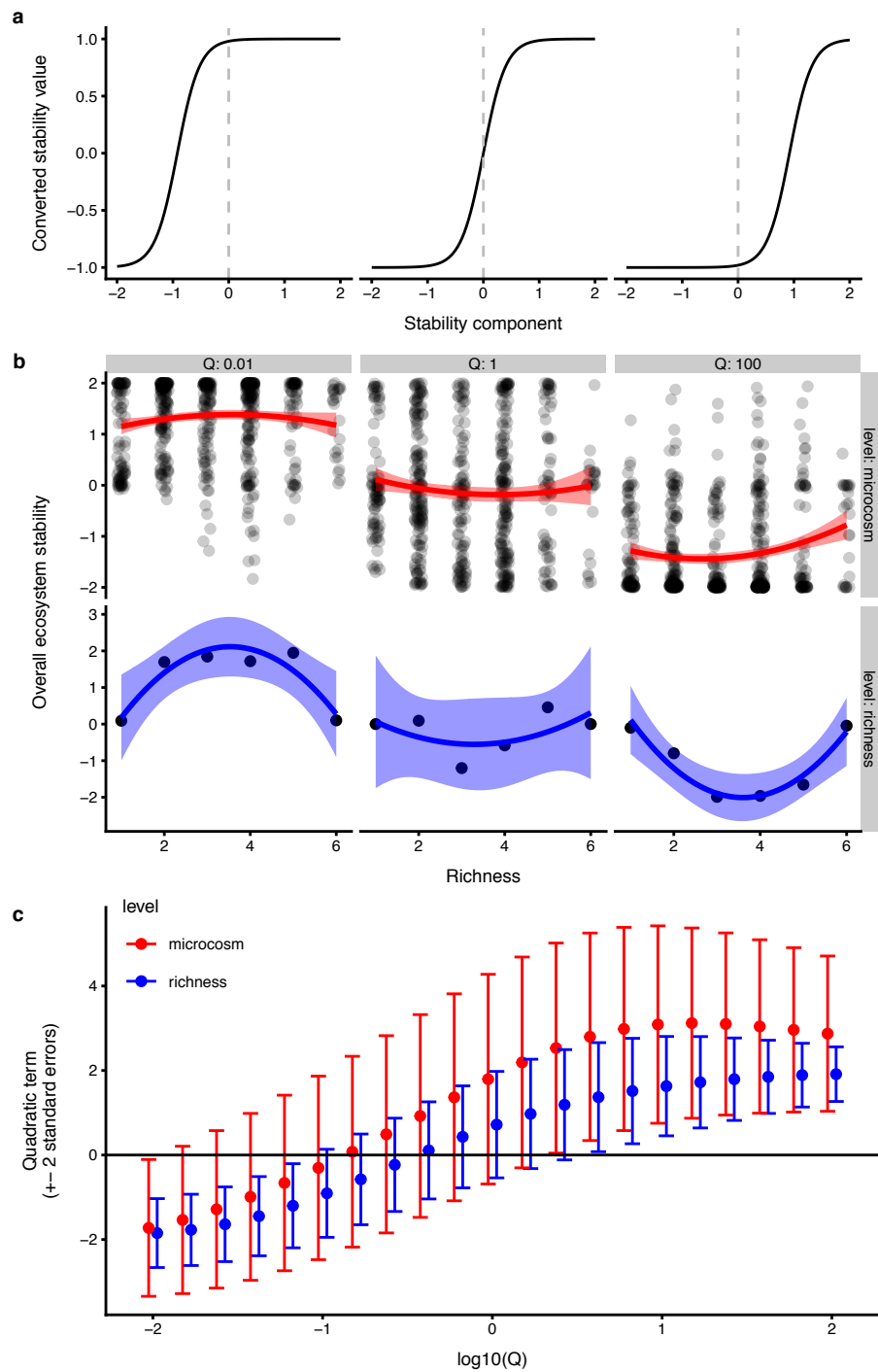


481
 482 **Figure 1: Biomass and stability in experimental microbial communities.** Richness increased temporal
 483 stability (a1, n=681 independent microcosms), but decreased resistance (a2, n = 567 independent microcosms).
 484 Average (± 1 standard error of the mean) biomass for each diversity level (b, n = 12939 microcosm x day
 485 combinations). Temporal dynamics of effect sizes (and 95% confidence intervals) of a linear mixed effects
 486 model of total biomass showed on average a negative effect of temperature (c1), a positive effect of diversity
 487 (c2), and a more negative effect of temperature at higher richness (persistent negative interaction term, c3) (n =
 488 681 independent microcosms per day). Resistance and temporal stability (n = 567 independent microcosms)
 489 covaried negatively across richness (d, solid line through centroid of each richness level, n = 6 independent
 490 richness levels) but positively within richness levels (dashed lines).
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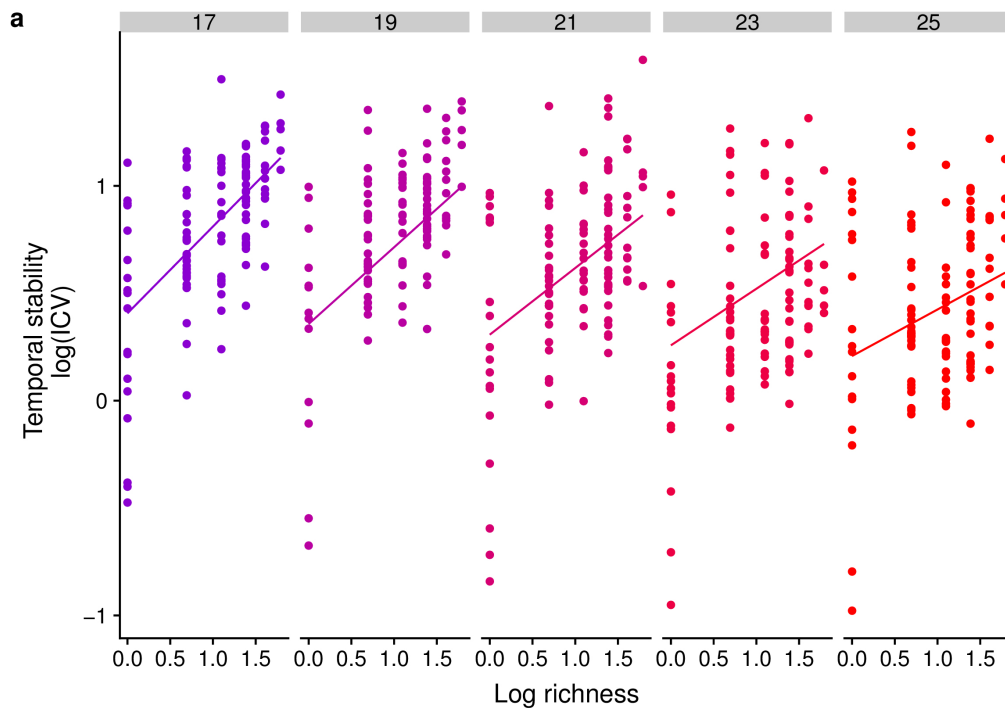
Figure 2: Positive, negative and neutral relationships among resistance, resilience and temporal variability in empirical studies with diversity manipulation. 30 bivariate relationships were reported by 17 independent studies (in addition to this study). Detailed information about individual studies (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).

511 **Extended data figures:**
 512



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

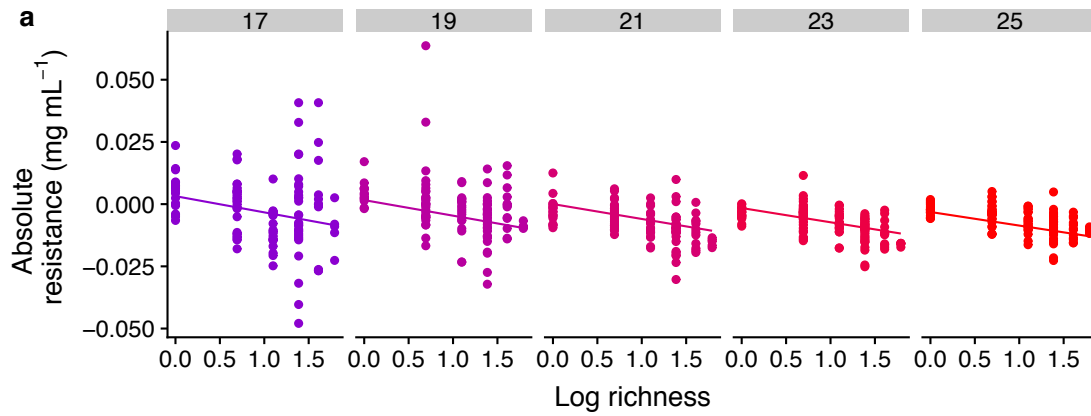
CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

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

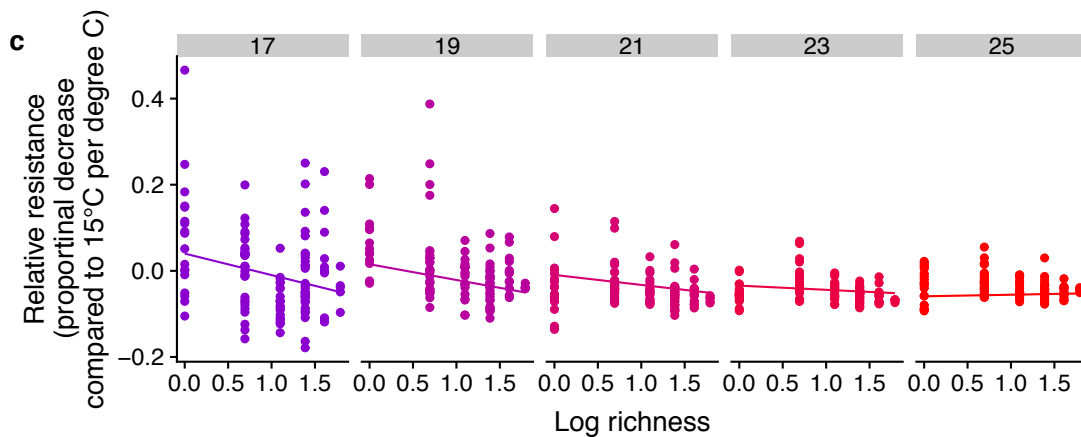
CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

513 **Extended data figure 1: Richness increased temporal stability across temperatures.** a) The
 514 stabilizing effect of richness was present across all temperatures, although temperature has a
 515 negative effect on mean stability. b) Result table for linear, mixed effects model of log
 516 richness, temperature and their interaction on temporal stability supporting the stabilizing
 517 effects of richness and the negative effect of temperature on temporal stability (n = 681
 518 independent microcosms). c) Result table for the same analysis as b) but without the
 519 monocultures. Results are qualitatively the same, indicating that the relationship between
 520 richness and temporal stability is not only driven by the monocultures (n = 580 independent
 521 microcosms).
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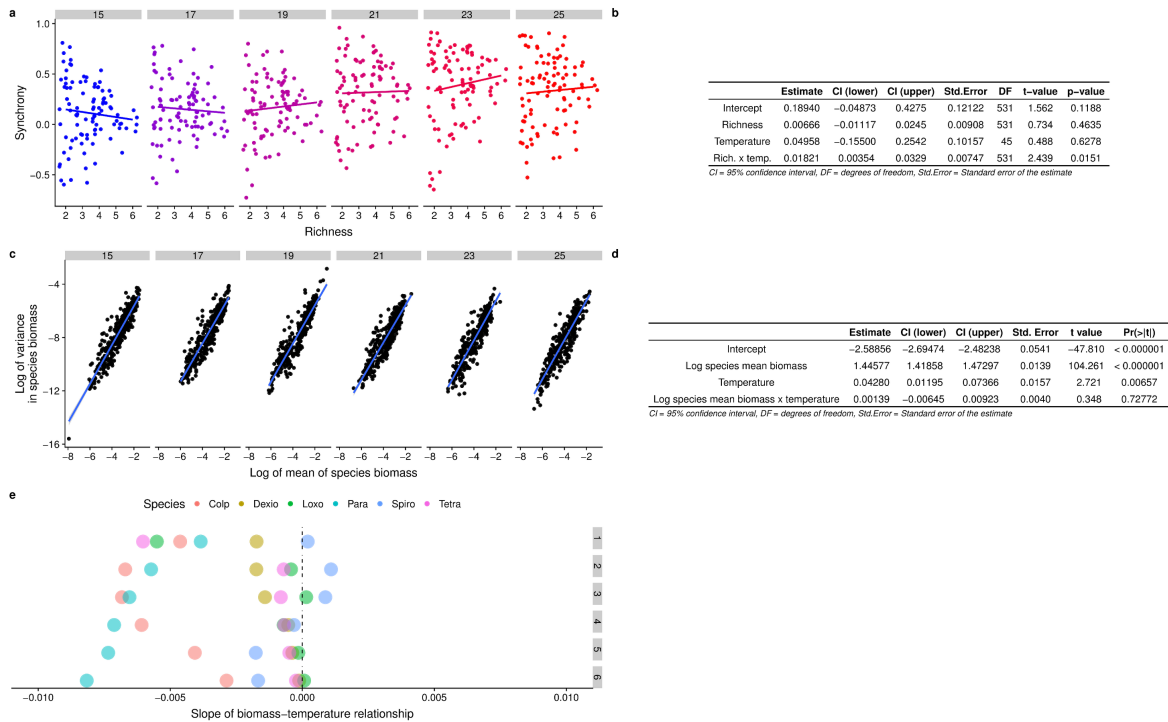
	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.000812	-0.003137	0.004760	0.002010	512	0.404	0.686407
Richness	-0.006115	-0.009710	-0.002520	0.001791	51	-3.415	0.001258
Temperature	-0.000796	-0.001215	-0.000376	0.000214	512	-3.726	0.000216
Rich. x temp.	0.000133	-0.000241	0.000507	0.000190	512	0.697	0.486295



d

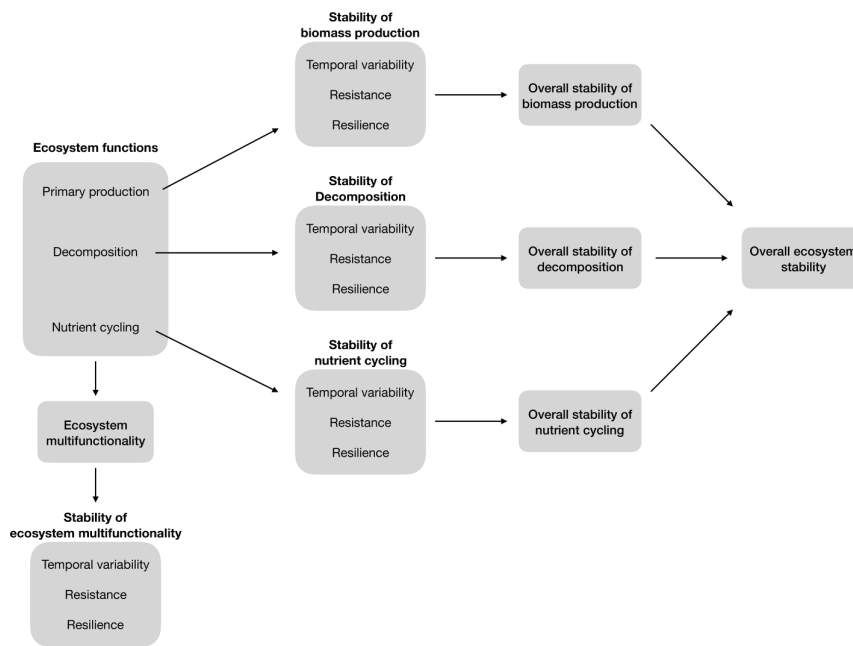
	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t-value	p-value
Intercept	0.00284	-0.02027	0.02595	0.01176	512	0.241	0.80951
Richness	-0.02980	-0.05085	-0.00875	0.01048	51	-2.842	0.00643
Temperature	-0.01241	-0.01544	-0.00937	0.00155	512	-8.023	< 0.000001
Rich. x temp.	0.00670	0.00399	0.00941	0.00138	512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

523
 524 **Extended data figure 2:** The effect of richness on absolute and proportional resistance. a, c)
 525 Richness decreased resistance, regardless whether its measured on the absolute or
 526 proportional scale. b, d) Result tables of linear, mixed effects model of richness, temperature
 527 and their interaction on absolute and proportional richness (n = 567 independent
 528 microcosms).
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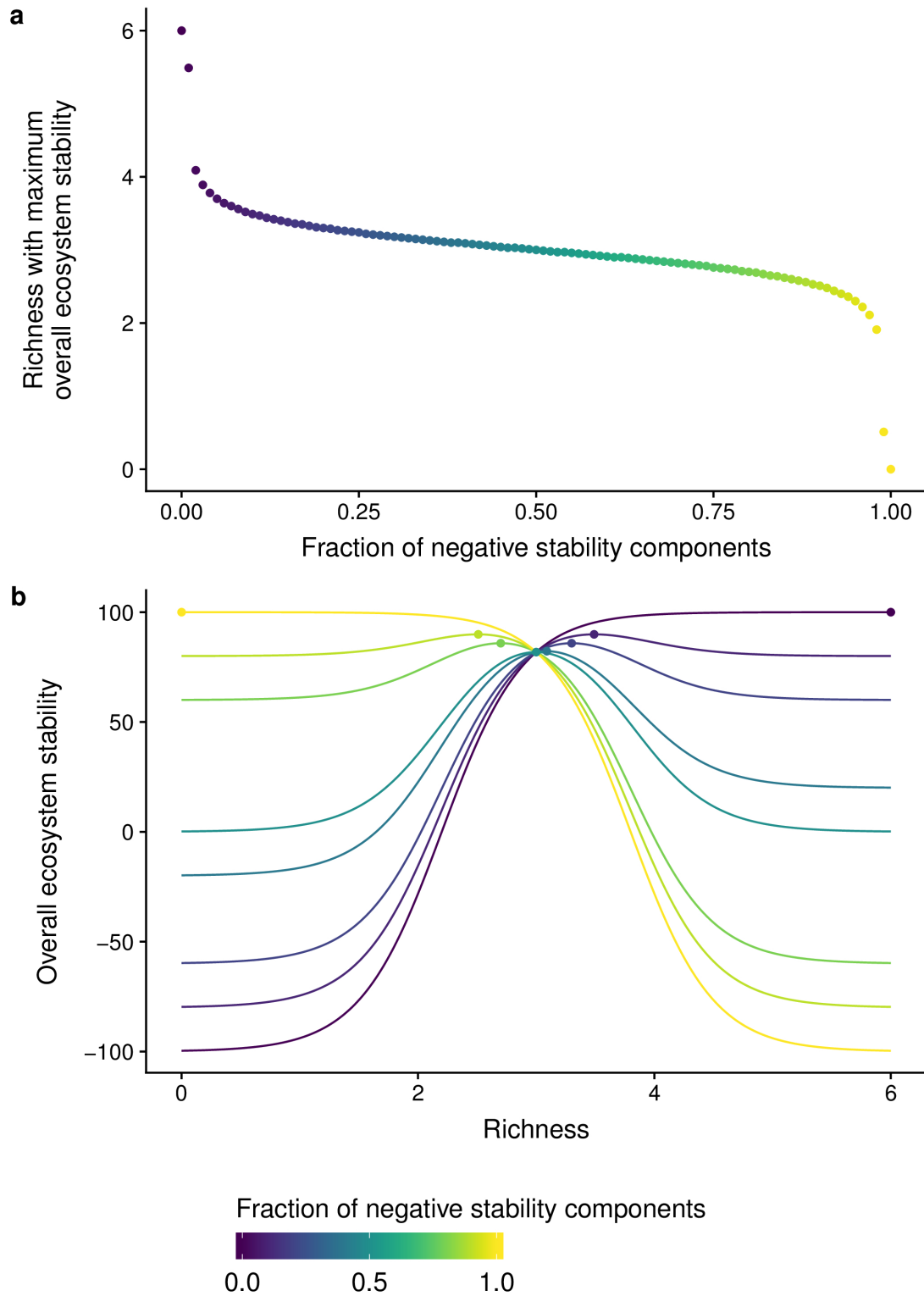
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Extended data figure 3: Niche complementarity and low response diversity were likely caused negative covariance of stability components. Niche complementarity and the resulting increase in total biomass with richness tended to increase temporal stability (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.



558
 559 **Extended data figure 5:** The effect of aggregating more than two stability components into
 560 overall ecosystem stability. The fraction of stability components with negative sign
 561 influences whether or not a unimodal pattern will result for a total of 100 stability
 562 components. a) A unimodal relationship between diversity and OES will result if at least one
 563 stability component is negative. b) However, the strength of the pattern depends on the
 564 relative balance of positive and negative relationships.
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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

568 **Extended data table 1:** Richness increased while temperature decreases biomass production.
 569 a) Result table for the linear, mixed effects model of richness, temperature and their
 570 interaction on the temporal dynamics of biomass (n = 12939 microcosm x day combinations).
 571 b) Result table for linear, mixed effects model of richness, temperature and their interaction
 572 with the time series aggregated to the average biomass for each microcosm (n = 681
 573 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 BIODDEPTH 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 BIODDEPTH 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 ₄) 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.

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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/negative	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-04	resistance/resilience	positive/positive	high response diversity	not stated	verbal	missing	relative
Ti-96	resistance/resilience	positive/neutral	high response diversity	not stated	verbal	missing	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	missing	absolute
VR-09	resistance/resilience	neutral/neutral	high response diversity	not stated	signals of mechanisms	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	insurance effect	verbal	verbal	relative
We-07	resistance/resilience	neutral/neutral	high response diversity	high response diversity	verbal	verbal	absolute
Wr-15	resistance/resilience	negative/neutral	selection effect; community composition	not stated	signals of mechanisms	missing	absolute
Z1-06 *	resistance/resilience	positive/neutral	high response diversity	not stated	verbal	missing	relative
Z1-06 *	resistance/temporal_var	positive/positive	high response diversity	statistical averaging	verbal	signals of mechanisms	relative
Z1-06 *	resilience/temporal_var	neutral/positive	not stated	statistical averaging	missing	signals of mechanisms	relative
Z2-06	resistance/resilience	negative/neutral	low response diversity	not stated	signals of mechanisms	missing	relative