Biodiversity increases and decreases ecosystem stability

Frank Pennekamp, Mikael Pontarp, Andrea Tabi, Florian Altermatt, Roman Alther, Yves Choffat, Emanuel A Fronhofer, Pravin Ganesanandamoorthy, Aurélie Garnier, Jason Griffiths, et al.

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Frank Pennekamp[a] - email: frank.pennekamp@ieu.uzh.ch
Mikael Pontarp[a, b] - mikael.pontarp@ieu.uzh.ch
Andrea Tabi[a] - andrea.tabi@ieu.uzh.ch
Florian Altermatt[a,c] - florian.altermatt@eawag.ch
Roman Alther[a,c] – roman.alther@eawag.ch
Yves Choffat[a] - yves.choffat@ieu.uzh.ch
Emanuel A. Fronhofer[a,c,g] – emanuel.fronhofer@umontpellier.fr
Pravin Ganesanandamoorthy[a, c] – pravin.ganesanandamoorthy@eawag.ch
Aurélie Garnier[a] - aurelie.garnier.research@gmail.com
Jason I. Griffiths[f] - jasonigriff@gmail.com
Suzanne Greene[a,e] - segreene@mit.edu
Katherine Horgan[a] – katherine.horgan@ieu.uzh.ch
Thomas M. Massie[a] - thomas.massie@outlook.com
Elvira Mächler[a,c] - elvria.maechler@eawag.ch
Gian-Marco Palamara[a,h] - gianmarco.palamara@gmail.com
Mathew Seymour[c, d] - m.seymour@bangor.ac.uk
Owen L. Petchey[a] - email: owen.petchey@ieu.uzh.ch

Affiliations:
[a]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
[b]Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden
[c]Department of Aquatic Ecology, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Überlandstrasse 133, 8600 Dübendorf, Switzerland
[f]Department of Mathematics, University of Utah, Salt Lake City, UT, 84112,USA

Present addresses:
[d]Molecular Ecology and Fisheries Genetics Laboratory, School of Biological Sciences, Environment Centre Wales Building, Bangor University, Bangor, Gwynedd, UK
[e]Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, MA USA
[g]ISEM, Université de Montpellier, CNRS, IRD, EPHE, Montpellier, France
[h]Department Systems Analysis, Integrated Assessment and Modelling, Eawag: Swiss Federal Institute of Aquatic Science and Technology, Überlandstrasse 133, 8600 Dübendorf, Switzerland

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Losses and gains in species diversity affect ecological stability[1–7] and the sustainability of ecosystem functions and services[8–13]. Experiments and models reveal positive, negative, and no effects of diversity on individual components of stability such as temporal variability, resistance, and resilience[2,3,6,11,12,14]. How these stability components covary is poorly appreciated[15], as are diversity effects on overall ecosystem stability[16], conceptually akin to ecosystem multifunctionality[17,18]. We observed how temporal variability, resistance, and overall ecosystem stability responded to diversity (i.e. species richness) in a large experiment involving 690 micro-ecosystems sampled 19 times over 40 days, resulting in 12939 samplings. Species richness increased temporal stability but decreased resistance to warming. Thus, two stability components negatively covaried along the diversity gradient. Previous biodiversity manipulation studies rarely reported such negative covariation despite general predictions of negative effects of diversity on individual stability components[3]. 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. Effects of diversity on ecosystem multifunctionality would also be hump- or U-shaped if diversity has positive effects on some functions and negative effects on others. Linking the ecosystem multifunctionality concept and ecosystem stability can transform perceived effects of diversity on ecological stability and may assist translation of this science into policy-relevant information.

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

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

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

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

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

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

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

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

A general mechanistic understanding of why different studies find different correlations would be a major step forward. Of the 30 pairs of stability components, only seven were accompanied by quantitative analyses of mechanism for both diversity-stability relationships (extended data table 4). Response diversity was implicated in five of these seven. Indeed, response diversity has been identified as an important driver of the resilience of ecological systems[23,24], and correlation among effect (i.e. high biomass production) and response (e.g. response to an environmental driver) traits, at least in the absence of strong interspecific interactions, might predict covariance among stability components[23]. None of the studies involved manipulation of mechanism.

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

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

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

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

The chosen mathematical conversion function and its parameter values are therefore important. Ecosystem multifunctionality-diversity relationships can be negative, neutral or positive depending on the chosen threshold value[27]. Similarly, different weightings of ecosystem functions can alter which species and interactions are considered important for multifunctionality[26]. Other types and parameterisations of conversion functions might conceivably result in other diversity-stability relationships. For instance, weighting one ecosystem function (or stability component) highly, would lead to a multifunctionality / overall ecosystem stability measure that is essentially univariate. We view the choice and parameterization of conversion functions as an opportunity to tailor estimates of ecosystem multifunctionality and overall ecosystem stability to their policy and decision making applications[16,26,28,29]. These conversion functions and estimates of overall ecosystem stability can then transform the perceived importance of biodiversity change for the sustainable delivery of multiple ecosystem services and may assist in translating the results of scientific studies into actionable information.

Methods section

Experimental methods

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

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

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

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

We derived community biomass by summing the biovolume of all individuals of a given species in a given community and multiplying biovolume with a constant density equal to water (i.e. $1g/cm^3$). For each community, this resulted in a time series of community biomass. To avoid analysing monoculture time series whilst starting at a low fraction of the carrying capacity (3 individuals mL^{-1}), compared to our multi-species culture species which 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[35]. 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[36]. Synchrony was assessed by a metric introduced by Gross et al. (2014)[37] 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[38] to calculate asynchrony.

Analyses

Analysis of total biomass used linear mixed effects models[39] (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[40]. 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[41] 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[42].

Review of empirical studies

Based on the review by Donohue et al. (2016)[16] 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/) 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[43]; the averaging approach uses a linear mathematical function (and both equalise relative contributions of different ecosystem functions / stability components)[25]; a principal component approach uses a specific linear mathematical function for each ecosystem function or stability component[44]; and Slade et al. (2017)[26] 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:

$$\mathrm{Y} = \mathrm{A} + \frac{\mathrm{K} - \mathrm{A}}{(\mathrm{C} + \mathrm{Q}e^{-\mathrm{B}x})^{1/\mathrm{v}}}$$

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 $\mathrm{OES} = f(z(res)) + f(z(ts))$, 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[45]. 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[26] and Manning et al. 2018[28].

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).

Code availability

Code to reproduce the analyses and figures is accessible on Github https://github.com/pennekampster/Code_and_data_OverallEcosystemStability (DOI: 10.5281/zenodo.1345557).

Data availability

The experimental data that support the findings of this study are available in Github (https://github.com/pennekampster/Code_and_data_OverallEcosystemStability) with the identifier (DOI: 10.5281/zenodo.1345557).). Source data for figures 1-3 are provided with the paper.

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Author Contributions:

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

Analysed data: FP, OP, MP, AT, MS
Wrote the first draft: FP, OP
Contributed to revisions of the manuscript: all

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

Figures

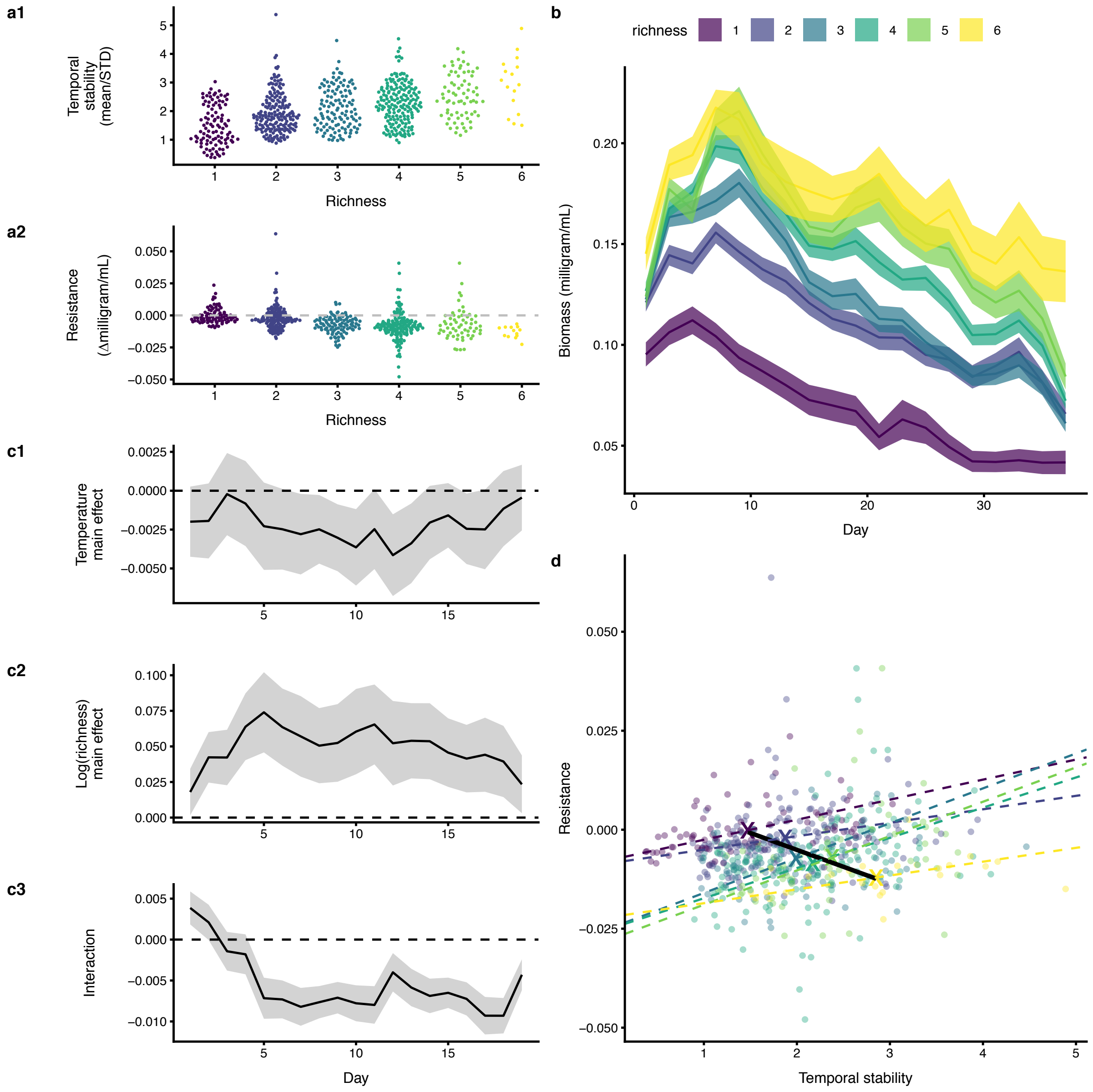


Figure 1: Biomass and stability in experimental microbial communities. Richness increased temporal stability (a1, n=681 independent microcosms), but decreased resistance (a2, n = 567 independent microcosms). Average (±1 standard error of the mean) biomass for each diversity level (b, n = 12939 microcosm 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).

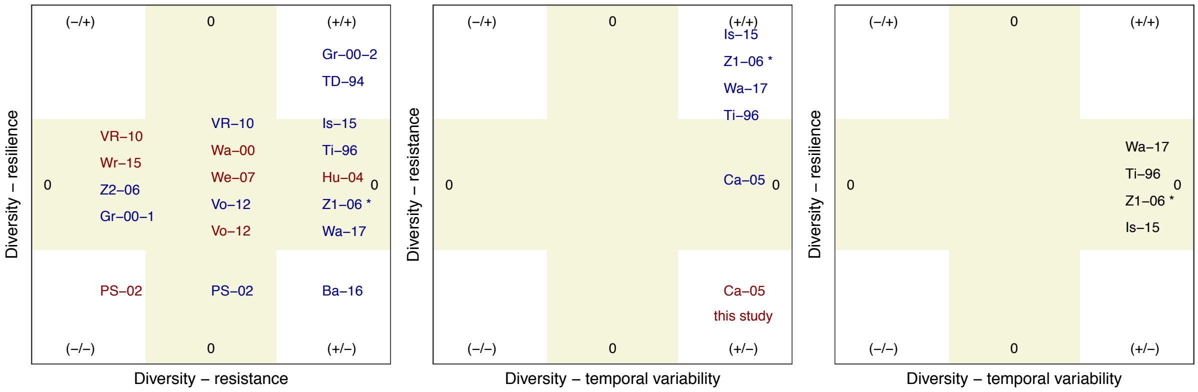


Figure 2: Positive, negative and neutral relationships among resistance, resilience and temporal variability in empirical studies with diversity manipulation. 30 bivariate relationships were reported by 17 independent studies (in addition to this study). Detailed information about individual studies (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.

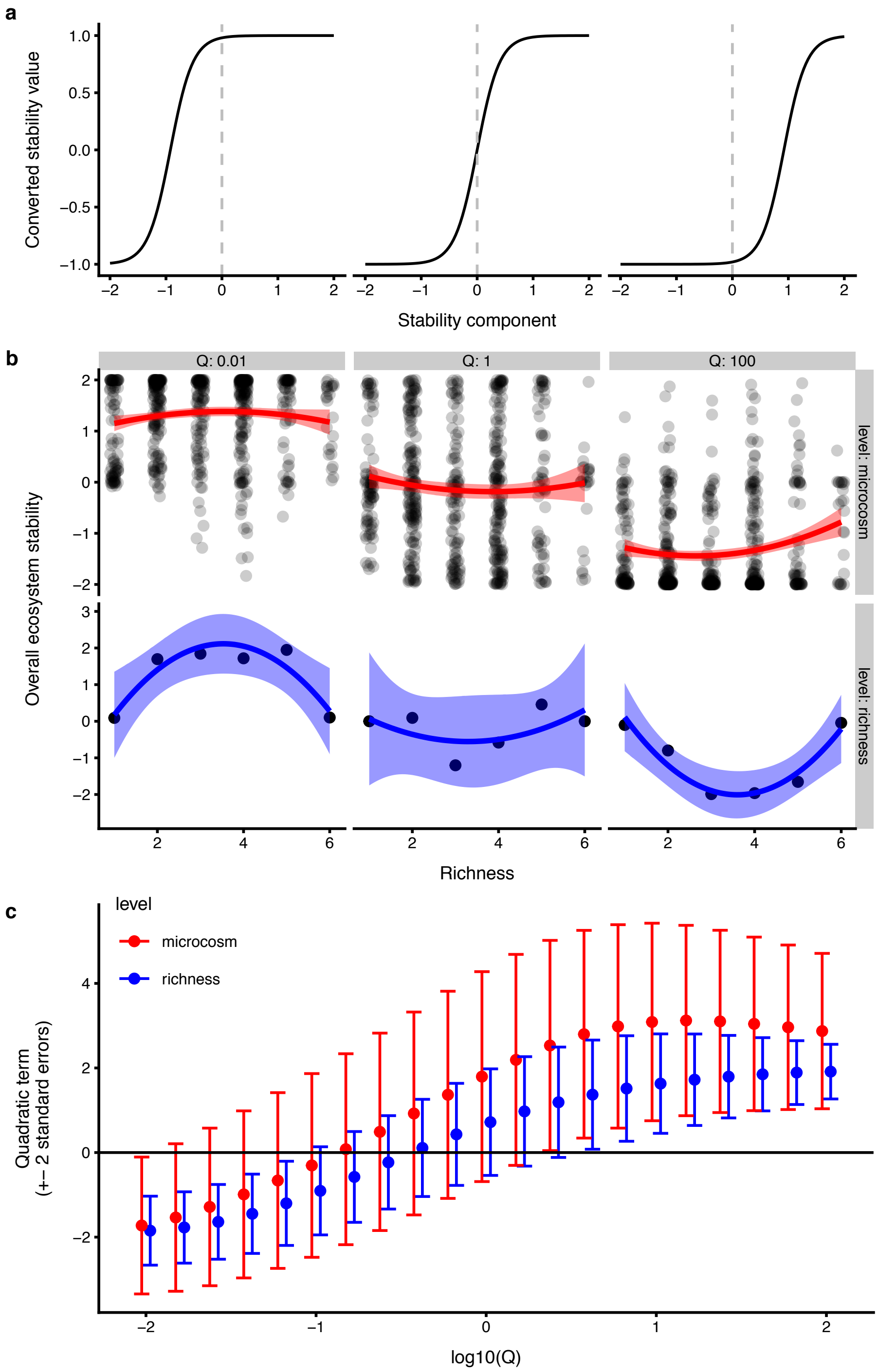
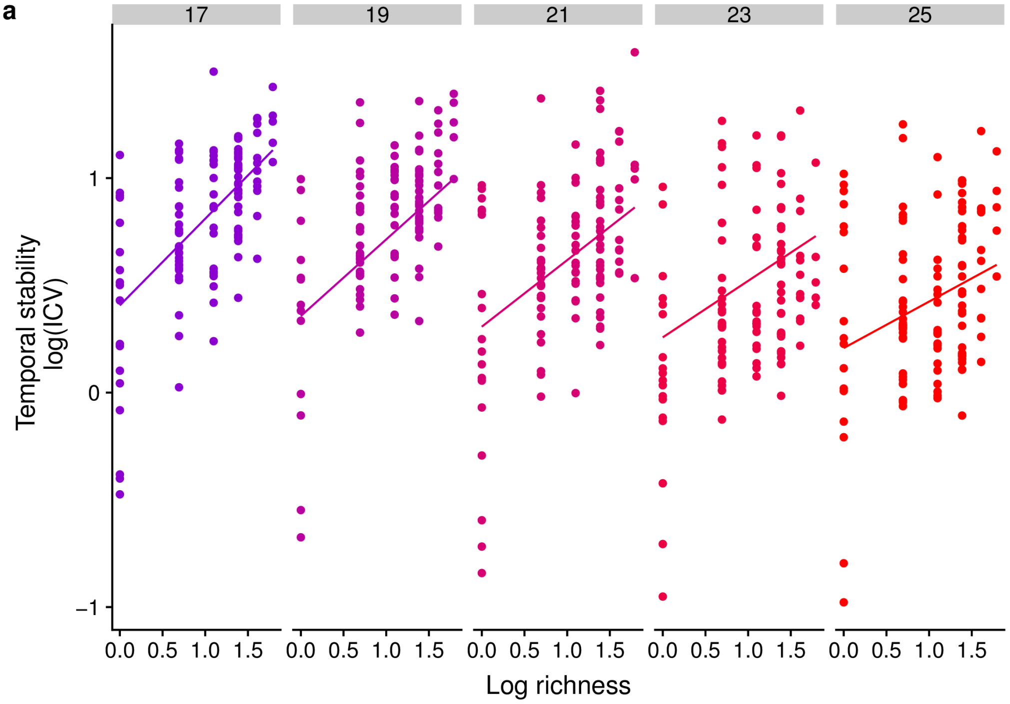


Figure 3: Hump- and U-shaped diversity-stability relationships. The intercept of the generalised logistic to convert measured stability components into a common currency varies with parameter *Q* (a). The non-aggregated (n = 567 independent microcosms) or aggregated (n = 6 richness levels) data exhibits 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).

Extended data figures:

a



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

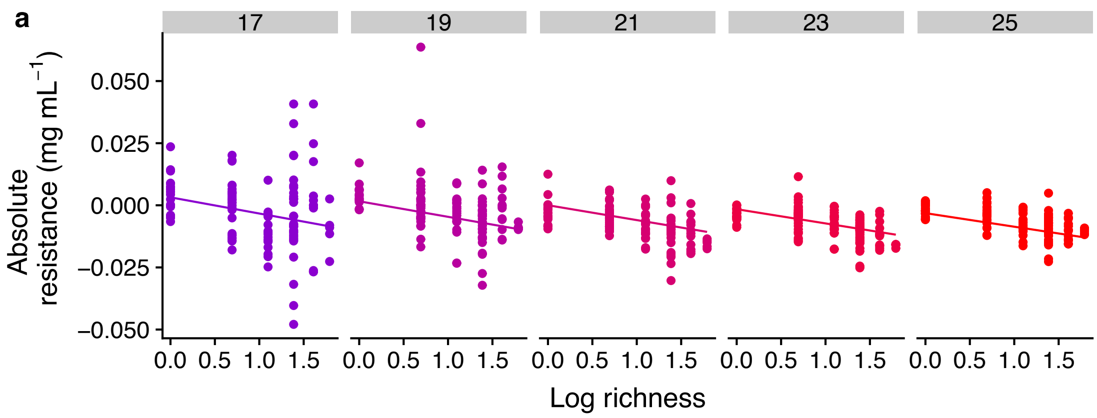
CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

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

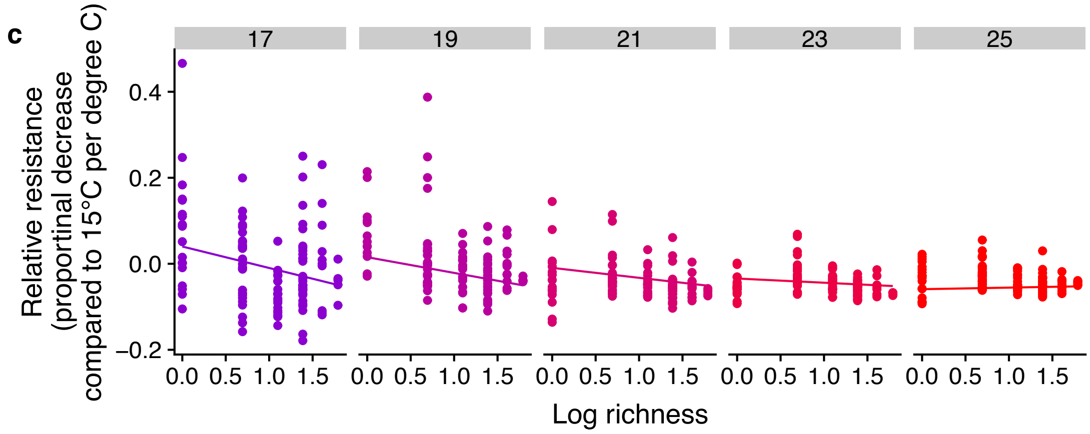
CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

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

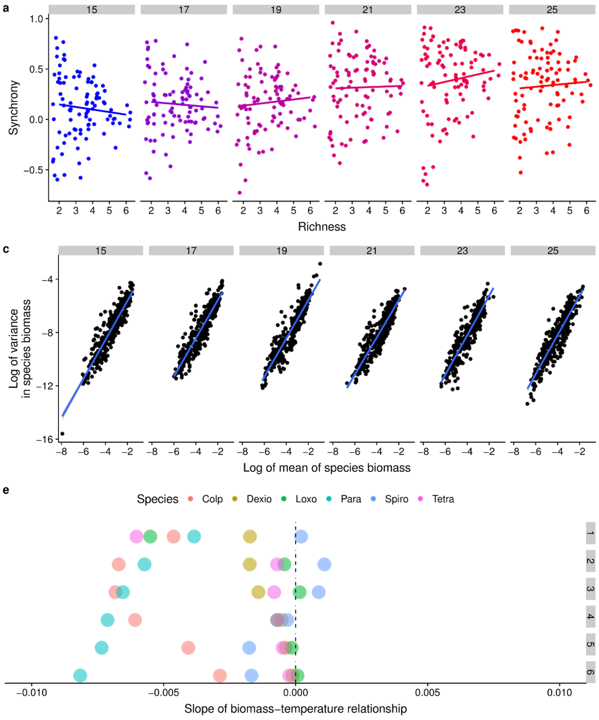
	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t−value	p−value
Intercept	0.000812	−0.003137	0.004760	0.002010	512	0.404	0.686407
Richness	−0.006115	−0.009710	−0.002520	0.001791	51	−3.415	0.001258
Temperature	−0.000796	−0.001215	−0.000376	0.000214	512	−3.726	0.000216
Rich. x temp.	0.000133	−0.000241	0.000507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



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

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).



b

	Estimate	CI (lower)	CI (upper)	Std.Error	DF	t−value	p−value
Intercept	0.18940	−0.04873	0.4275	0.12122	531	1.562	0.1188
Richness	0.00666	−0.01117	0.0245	0.00908	531	0.734	0.4635
Temperature	0.04958	−0.15500	0.2542	0.10157	45	0.488	0.6278
Rich. x temp.	0.01821	0.00354	0.0329	0.00747	531	2.439	0.0151

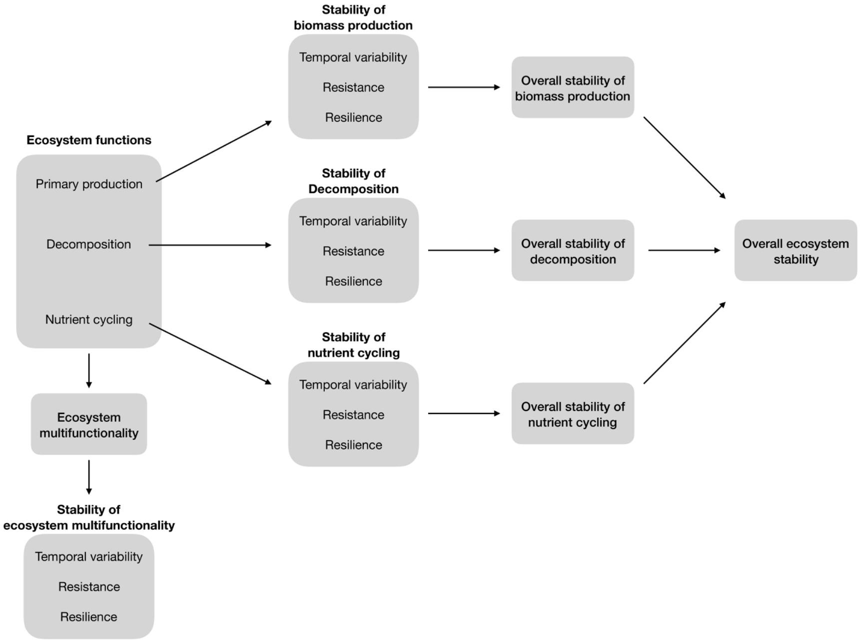
CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

d

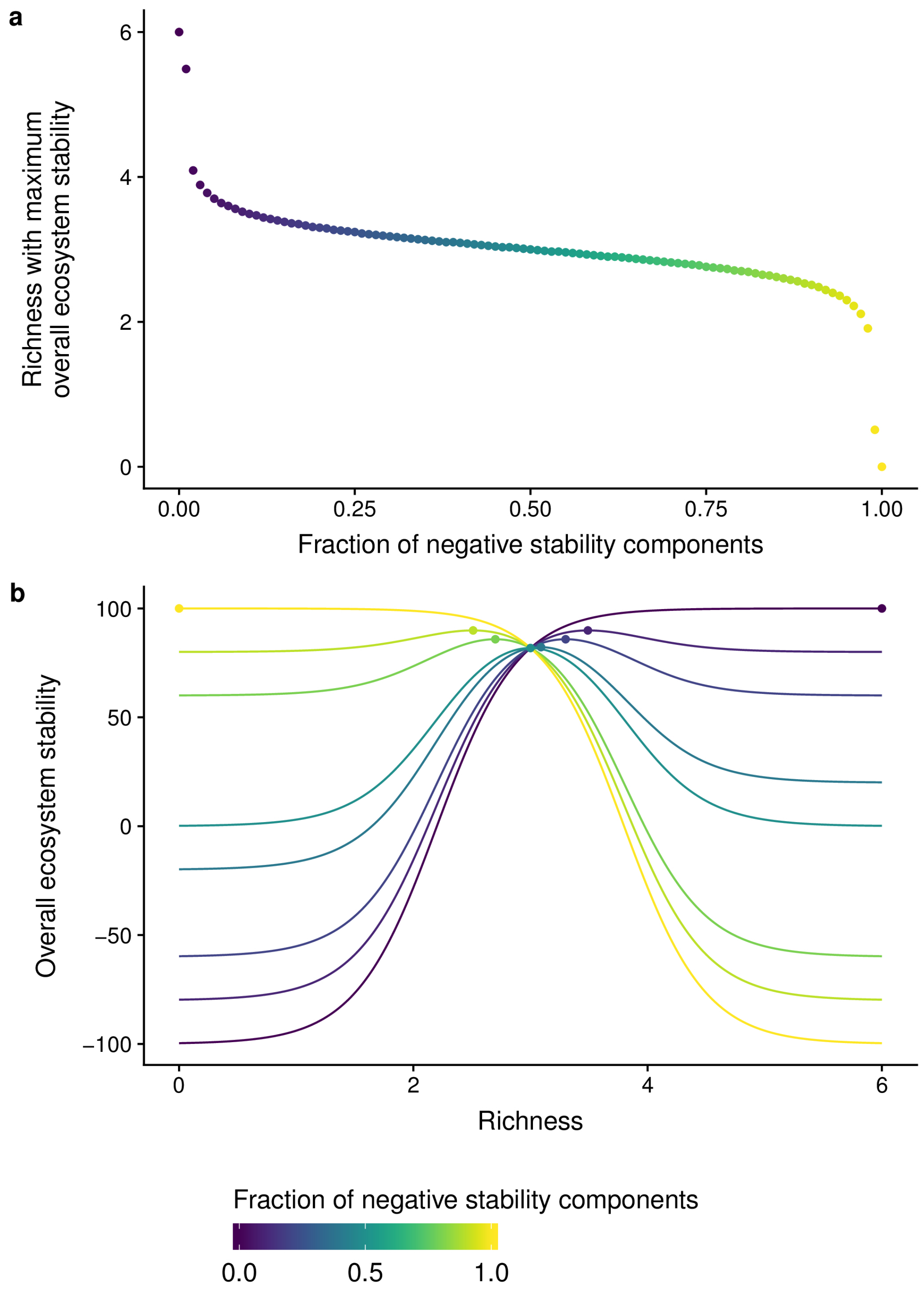
	Estimate	CI (lower)	CI (upper)	Std. Error	t value	Pr(>|t|)
Intercept	−2.58856	−2.69474	−2.48238	0.0541	−47.810	< 0.000001
Log species mean biomass	1.44577	1.41858	1.47297	0.0139	104.261	< 0.000001
Temperature	0.04280	0.01195	0.07366	0.0157	2.721	0.00657
Log species mean biomass x temperature	0.00139	−0.00645	0.00923	0.0040	0.348	0.72772

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

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.



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.



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.

Extended data table captions:

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

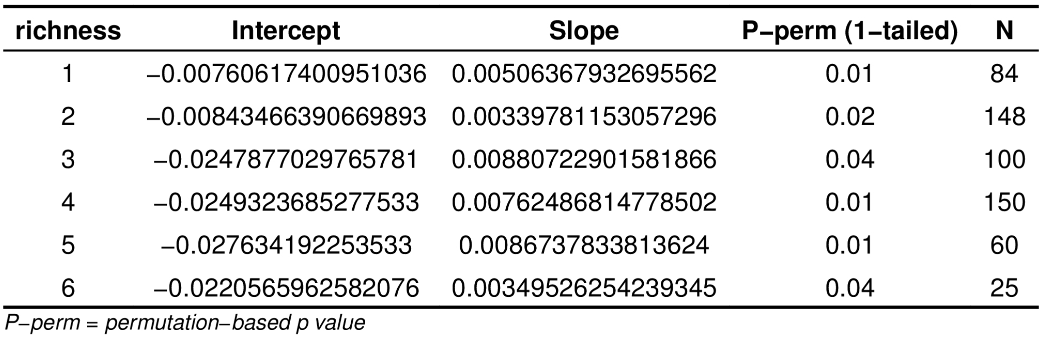
CI = 95% confidence interval, DF = degrees of freedom, Std.Error = Standard error of the estimate

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

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



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

Extended data table 2: Reduced major axis regression revealed positive relationships between temporal stability and resistance within each of the six richness levels (p value based 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) Oikos, 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) Nature, 416, 84
Z2−06	Diversity manipulation of unicellular algae analysing resistance and resilience of biomass production to experimental cold perturbation.	Zhang & Zhang (2006) Oikos, 112, 218
Z1−06 *	Diversity manipulation of unicellular algae analysing temporal variability and resistance to experimental cold perturbation of biomass production.	Zhang & Zhang (2006) Oikos, 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) Nature, 526, 574
VR−09	Diversity manipulation of plants, analysing resistance and resilience to natural perturbation (drought) of biomass production.	Van Ruijven & Berendse (2009) Journal of Ecology, 98, 81
Ba−16	Diversity manipulation of diatoms, analysing resistance and resilience to perturbation (chemical stressor, atrazine) of biomass production.	Baert et al (2016) Ecology, 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) Oikos, 2, 279
Gr−00−2	Diversity manipulation by fumigation of soil microorganisms, analysing resilience to perturbation (chemical stress) and resistance to perturbation (chemical stress, CuSO4) of respiration.	Griffiths et al (2000) Oikos, 2, 279
TD−94	Diversity manipulation by fertilisation of plants, analysing resistance and resilience of biomass production to natural perturbation (drought).	Timan & Downing (1994) Nature, 367, 363
Wa−00	Diversity manipulation of plants, analysing resistance and resilience to experimental perturbation (drought) of various ecosystem functions.	Wardle et al (2000) Oikos, 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), PNAS, 101, 24
Vo−12	Diversity manipulation of grassland plants. Analysis of resistance and resilience of biomass production to drought perturbation.	Vogel et al (2012) PLoS One, 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) Nature Communications, 6, 6092
We−07	Manipulation of soil microbial diversity by serial dilution. Analysis of resistance and resilience of denitrification and nitrite oxidisation to a temperature perturbation.	Wertz et al (2007) Environmental Microbiology, 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) Ecology, 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) Ecology, 77, 350

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.

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	
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−94	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	
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	
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	
Z2−06	resistance/resilience	negative/neutral	low response diversity	not stated	signals of mechanisms	missing	relative

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