

10. Giggenbach, W. F. In *Monitoring and Mitigation of Volcano Hazards* (eds Scarpa, R. & Tilling, R.) (Springer, Berlin, 1996).

11. Mori, T. *et al.* Remote detection of fumarolic gas chemistry at Vulcano, Italy, using an FT-IR spectral radiometer. *Earth Planet. Sci. Lett.* **134**, 219–224 (1995).

12. Francis, P. W., Burton, M. & Oppenheimer, C. Remote measurements of volcanic gas compositions by solar FTIR spectroscopy. *Nature* **396**, 567–570 (1998).

13. Burton, M., Oppenheimer, C., Horrocks, L. A. & Francis, P. W. Field measurement of CO₂ and H₂O emissions from Masaya Volcano, Nicaragua, by Fourier transform spectrometry. *Geology* **28**, 915–918 (2000).

14. Burton, M., Allard, P., Murè, F. & Oppenheimer, C. In *Volcanic Degassing* (eds Oppenheimer, C., Pyle, D. & Barclay, J.) 281–293 (Special Publication 2213, Geological Society, London, 2003).

15. Allard, P. *Géochimie Isotopique et Origine de l'eau, du Carbone et du Soufre dans les Gaz Volcaniques: Zones de Rift, Marges Continentales et Arcs Insulaires*. Thesis, Paris 7 Univ. (1986).

16. Allard, P. *et al.* Eruptive and diffuse emissions of carbon dioxide from Etna volcano. *Nature* **351**, 387–391 (1991).

17. Pennisi, M. & Le Cloarec, M. F. Variations of Cl, F, and S in Mount Etna's plume, Italy, between 1992 and 1995. *J. Geophys. Res.* **B 103**, 5061–5070 (1998).

18. Allard, P. *Monitoring Volcanic Risk by Remote Sensing Techniques: Airborne Plume Validation* (Final Rep. MVRSS RTD Contract, ENV4960288, CEE-DGXII, Bruxelles, 1999).

19. Métrich, N., Allard, P., Spilliaert, N., Andronico, D. & Burton, M. 2001 flank eruption of the alkali- and volatile-rich primitive melt responsible for Mount Etna's evolution in the last three decades. *Earth Planet. Sci. Lett.* **228**, 1–17 (2004).

20. Spilliaert, N., Allard, P., Métrich, N. & Sobolev, A. A new step in modelling magma degassing processes and eruptive dynamics at Mount Etna: the 2002–2003 eruption. *Geophys. Res. Abstr.* **6**, 04189 (2004).

21. Alparone, S., Andronico, D., Lodato, L. & Sgroi, T. Relationship between tremor and volcanic activity during the Southeast Crater eruption on Mount Etna in early 2000. *J. Geophys. Res.* **108**, 2241, doi:10.1029/2002JB001866 (2003).

22. Allard, P. *et al.* Source process of cyclic fire fountaining at Mt. Etna in 2000: a multidisciplinary study of the June 14 (63rd) event. *Geophys. Res. Abstr.* **5**, 13079 (2003).

23. World Data Centre for Greenhouse Gases, Japan Meteorological Agency. <http://gaw.kishou.go.jp/wdogg.html>.

24. Métrich, N. & Clacchiatti, R. Sulfur abundance and its speciation in oxidized alkaline melts. *Geochim. Cosmochim. Acta* **60**, 4151–4160 (1996).

25. Naughton, J. J., Derby, J. V. & Glover, R. B. Infrared measurements on volcanic gas and fume: Kilauca eruption, 1968. *J. Geophys. Res.* **74**, 3273–3277 (1969).

26. Métrich, N., Clacchiatti, R., Mosbah, M. & Chaussidon, M. The 1989–1990 activity of Etna magma mingling and ascent of H₂O-Cl-S-rich basaltic magma. Evidence from melt inclusions. *J. Volcanol. Geotherm. Res.* **59**, 131–144 (1993).

27. Allard, P., Burton, M., Brusca, L. & Murè, F. *Geochemical Monitoring of Sicilian Volcanoes* (Second Rep., July–December 2000, Sistema Poseidon, Nicolosi, Italy, 2000).

28. Rodgers, C. D. Retrieval of atmospheric temperature and composition from remote measurements of thermal radiation. *Rev. Geophys. Space Phys.* **14**, 609–624 (1976).

29. Rothman, L. S. *et al.* The HITRAN molecular spectroscopic database and HAWKS (HITRAN Atmospheric Workstation): 1996 edition. *J. Quant. Spectrosc. Radiat. Transfer* **60**, 665–710 (1998).

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Long-term relationships between ecological stability and biodiversity in Phanerozoic reefs

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High biodiversity has been shown to enhance ecological stability on small spatial scales and over intervals of weeks to decades^{1–4}. It remains unclear, however, whether this diversity–stability relationship can be scaled up to regional scales, or to longer timescales⁵. Without empirical validation at larger scales, the implications of the diversity–stability relationship for both ecology and long-term conservation strategies cannot readily

be resolved. Here I show that in biogenic reefs, ecological stability is related to taxonomic diversity on million-year timescales. The higher the mean reef diversity in a particular time interval, the smaller the change in skeletal density, style of reef building and biotic reef types in the subsequent time interval. Because the relationships apply to a wide spectrum of disturbance regimes and reef types, these results support the hypothesis that species richness itself promotes ecological stability³. Carbonate production by reefs, while closely correlated with reef diversity without temporal lag, is not stabilized by reef diversity over these long timescales. This suggests that ecological stability and productivity may be decoupled in natural ecosystems.

Reefs, broadly defined as laterally confined structures built by the growth and/or metabolic activity of sessile benthic organisms in an aquatic environment, are an excellent tool for tracking long-term ecological changes, because they have an outstanding fossil record reaching back at least two billion years and because they yield a number of attributes, other than taxonomic richness, that permit the identification of ecological traits. Reefs changed substantially in abundance, composition, palaeogeographic distribution, geometric attributes and biodiversity during the Phanerozoic eon (the past 542 million years, Myr), but these changes are rarely linearly correlated with global environmental changes—at least as inferred from the geological record^{6,7}. Biological controls seem either to buffer the reef system (the combined traits of all reefs recorded within a time interval) or to amplify responses to global change on timescales of millions of years^{7,8}. Using a database of more than 3,300 Phaner-

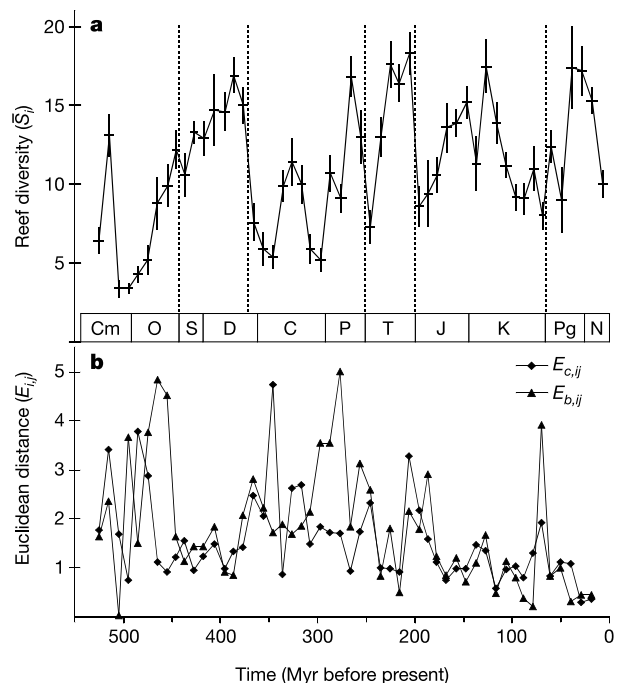


Figure 1 Time series of mean reef diversity and two measures of ecological change resolved to 10-Myr intervals. **a**, Reef diversity expressed as the mean species richness (number of species) of reef-builders within individual reef complexes per time interval. Vertical bars indicate one standard error of the mean in each direction. Horizontal bars demarcate the spans of time intervals. Vertical dashed lines mark the big five mass extinction events of the Phanerozoic. Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene. **b**, Ecological changes between consecutive time intervals ($i-j$, plotted in i) expressed as the euclidean distances of constructional styles ($E_{c,ij}$) and biotic reef types ($E_{b,ij}$).

ozoic reef complexes, I show that on these long timescales, reef diversity itself forms an important control of ecological stability.

Relationships between reef diversity and ecological stability were tested through correlations between reef diversity in one time interval (*i*) and the change of ecological traits between this initial interval and the succeeding interval (*j*). Reef diversity (\bar{S}_i) was measured by the average number of reef-building species within individual reefs per time interval (Fig. 1a). Ecological change (D_{ij}) was assessed by euclidean distances (E_{ij} , Fig. 1b) and Mahalanobis distances (M_{ij}) among variables divided into four sets (see Methods) that reflect: (1) changes in the density of skeletal reef builders (*d*), relative to matrix and cement, $E_{d,ij}$ and $M_{d,ij}$; (2) changes in reef architecture (*a*), $E_{a,ij}$; (3) changes in reef construction styles (*c*), a combination of (1) and (2), $E_{c,ij}$ and $M_{c,ij}$; and (4) changes in biotic reef types (*b*), $E_{b,ij}$. Changes in carbonate production (*p*), $D_{p,ij}$, were measured by the change in one variable: the volume of preserved reef carbonate per million years (ref. 9). Analyses of the relationship between reef diversity and ecological changes were performed on three time series at differing sample resolutions: (1) traditional stages or epochs (73 intervals), largely defined by global changes of fossil assemblages; (2) regularly spaced 10-Myr intervals (53 intervals); and (3) supersequences (32 intervals), defined by nearly global breaks in the sedimentary record¹⁰. Because reef diversity and several measures of ecological change are serially correlated, all time series were de-trended to $\Delta\bar{S}_i$ and ΔD_{ij} before correlation tests (see Methods). Owing to space constrictions, only 10-Myr time series are plotted. A full set of graphs is available as Supplementary Information.

Initial tests of the relationship between $\Delta\bar{S}_i$ and ΔD_{ij} rarely

yielded significant linear relationships. Except for $\Delta D_{p,ij}$, all plots of $\Delta\bar{S}_i$ versus ΔD_{ij} show a negative slope—implying that greater reef diversity tends to reduce ecological change—but several outliers prevent conclusive statements (Fig. 2). Exceptions are $\Delta\bar{S}_i$ versus $\Delta E_{c,ij}$, which, applying Spearman's Rho (r_s), is initially significant at all three temporal resolutions. Outliers, detected by least-trimmed square regressions and visual inspection of $\Delta\bar{S}_i$ - ΔD_{ij} plots, vary among analyses and temporal resolutions but are usually associated with major mass extinction events, or lie in the Cambrian period. Uncertainties of estimates of both reef diversity and ecological changes in the predominantly microbial reef system of the Cambrian, and the high volatility of diversity dynamics in this period^{11,12}, justify an exclusion from further analyses. The outlying mass extinctions are characterized by large ecological changes following times of high reef diversity. The ability of mass extinction events to cause disruption to regular evolutionary patterns has long been noted¹³. However, it is not reasonable to exclude all mass extinctions from the correlation analyses. Although mass extinctions may break the persistence stability (ability to withstand perturbations) on shorter timescales, resilience stability (potential for recovery from perturbations) on longer timescales is probably responsible for the observation that even the strongest mass extinctions are not recognized as outliers in all time series. The Permian–Triassic mass extinction provides an instructive example: at the stage/epoch level, great ecological distances are noted between all stages from the Late Permian to the Middle Triassic (Anisian), owing to a complete but transient destruction of metazoan reefs. At the supersequence level, however, great ecological similarities have been noted previously between Middle–Late Permian and Middle Triassic reefs¹⁴.

When the Cambrian period and outlying mass extinctions are excluded from the analyses, significant negative correlations between $\Delta\bar{S}_i$ and ΔD_{ij} are evident in all three time series and for nearly all measures of ecological change, except for $\Delta D_{p,ij}$ (Table 1). If reef diversity is higher than average in one time interval, lower

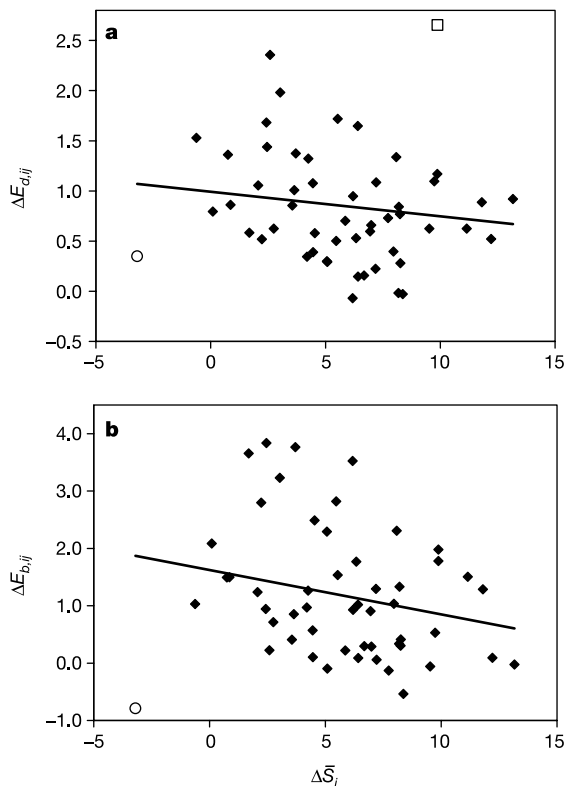


Figure 2 Examples of initial relationships between de-trended reef diversity ($\Delta\bar{S}_i$) and de-trended measures of ecological change in 10-Myr intervals. Marked outliers are: open circles, Middle–Late Cambrian boundary; open square, Triassic–Jurassic boundary (late Norian/Rhaetian–Hettangian/Sinemurian). **a**, Correlation with changes in skeletal framework density; **b**, correlation with changes in biotic reef types.

Table 1 Correlations between initial reef diversity and ecological changes

Ecological trait	r_s	<i>P</i>
Supersequences (<i>n</i> = 27)		
Framework density ($E_{d,ij}$)	-0.63	<0.001
Framework density ($M_{d,ij}$)	-0.53	0.005
Reef architecture ($E_{a,ij}$)	-0.70	<0.001
Constructional style ($E_{c,ij}$)	-0.76	<0.001
Constructional style ($M_{c,ij}$)	-0.56	0.002
Biotic reef type ($E_{b,ij}$)	-0.35	0.070
Carbonate production ($D_{p,ij}$)	0.20	0.314
Carbonate production ($ D_{p,ij} $)	0.43	0.025
10-Myr intervals (<i>n</i> = 47)		
Framework density ($E_{d,ij}$)	-0.36	0.012
Framework density ($M_{d,ij}$)	-0.34	0.020
Reef architecture ($E_{a,ij}$)	-0.50	<0.001
Constructional style ($E_{c,ij}$)	-0.59	<0.001
Constructional style ($M_{c,ij}$)	-0.32	0.027
Biotic reef type ($E_{b,ij}$)	-0.41	0.004
Carbonate production ($D_{p,ij}$)	0.11	0.461
Carbonate production ($ D_{p,ij} $)	0.27	0.066
Stages/epochs (<i>n</i> = 65)		
Framework density ($E_{d,ij}$)	-0.29	0.018
Framework density ($M_{d,ij}$)	-0.23	0.070
Reef architecture ($E_{a,ij}$)	-0.22	0.077
Constructional style ($E_{c,ij}$)	-0.34	0.006
Constructional style ($M_{c,ij}$)	-0.35	0.004
Biotic reef type ($E_{b,ij}$)	-0.29	0.020
Carbonate production ($D_{p,ij}$)	0.06	0.631
Carbonate production ($ D_{p,ij} $)	0.14	0.285

Spearman rank order correlations are based on normalized values and de-trended time series, and exclude the following intervals and boundaries. In the supersequences, I excluded the Cambrian (two intervals), the Frasnian–Famennian boundary (Givetian/Frasnian–Famennian/early Viséan) and the Triassic–Jurassic boundary (late Carnian/Rhaetian–Hettangian/early Aalenian). In the 10-Myr intervals, I excluded the Cambrian (four intervals) and the Triassic–Jurassic boundary (late Norian/Rhaetian–Hettangian/Sinemurian). In the stages/epochs, I excluded the Cambrian (five intervals), the Permian–Triassic boundary (Changhsingian–Scythian) and the Triassic–Jurassic boundary (Rhaetian–Hettangian/Sinemurian).

than average ecological changes occur in the subsequent time interval with respect to the density of skeletal organisms, reef architecture, reef construction style and biotic reef types. Although some individual variables defining ecological change are inevitably correlated with $\Delta\bar{S}_i$ (for example, \bar{S} is significantly higher in intervals with many coral reefs than in intervals with a prevalence of microbial reefs), the combinations of variables used to define ecological distances are largely independent of reef diversity. Cross-correlations confirmed that significant correlations listed in Table 1 only occur at lag 1 (Fig. 3), that is, reef diversity in one time interval is related to ecological change in the subsequent interval, and not the converse.

The basic conclusion is that high reef diversity in one time interval predicts low ecological change in the subsequent time interval, whereas low-diversity reefs were more prone to ecological changes. The variance explained by $\Delta\bar{S}_i$ for individual measures of ΔD_{ij} is low enough (5%–58%) to leave space for environmental influences to control ecological changes, but, with the exception of major mass extinctions, environmental perturbations rarely forced substantial changes of large-scale ecological attributes of a high-diversity reef system. These results provide strong support for the existence of diversity–stability relationships on very long timescales, and also help to pinpoint their underlying causes. Because the diversity–stability relationship is evident through a wide range of reef types growing under variable physicochemical and biological disturbance regimes⁸, we may conclude that species richness itself had a stabilizing effect. This supports the diversity insurance hypothesis^{3,15}, which states that a high-diversity system is: (1) more likely to have species able to tolerate environmental perturbations; and (2) more likely to have functional redundancy so that ecologically important species can be readily replaced after a perturbation. The alternatives, that individual species traits and ecological history are more crucial to diversity–stability relationships^{16,17}, are unlikely for these long timescales.

The second conclusion is that reef diversity has little effect on long-term changes of carbonate production (Fig. 3). $\Delta\bar{S}_i$ is strongly correlated with concurrent carbonate production (Δp_{ij}) at all three sample resolutions ($r_s = 0.39$ – 0.52 , $P < 0.001$ – 0.004). This suggests that either reef carbonate production and reef diversity are driven by related controls, or that diversity itself promotes productivity. The latter view is known as the diversity–productivity hypothesis, which is supported by theoretical models and grassland experiments^{18,19}. However, the future development of reef carbonate production is apparently not predictable from reef diversity. There is even a tendency for absolute values of $\Delta D_{p,ij}$ to increase, after intervals with high $\Delta\bar{S}$ (Table 1). This is consistent with the results of

small-scale experiments where species-poor systems were shown to be more stable against perturbations in terms of biomass, although diversity and biomass were initially positively correlated²⁰. Here, the contradiction can be partly explained by the recognition of reefs as multi-stable ecosystems, able to achieve high rates of carbonate production with different consortia of communities²¹. Turning this argument around could mean that substantial fluctuations in carbonate production can occur in ecologically stable reefs; an interpretation supported by the record of coral reefs from the Pleistocene epoch²².

Because my results largely agree with findings from smaller-scale studies, it seems that diversity–stability relationships scale up from short observation periods and laboratory scales to millions of years and global scales. Although the validity of diversity–stability relationships at intermediate timescales—within the range of long-term ecosystem management—remains to be demonstrated, these analyses emphasize the urgency with which current threats to coral reef diversity and function^{23,24} need to be addressed. Although coral reefs are relatively diverse at present, this high biodiversity is not likely to protect them against productivity declines, because standing diversity appears to be uncoupled from productivity changes in these systems. Furthermore, if coral reefs and their biodiversity continue to decline as current trends predict, reef behaviour may eventually become unpredictable and unmanageable. The fossil record shows that even in the worst cases, reef destruction does not last forever, but a re-emerging reef system will probably look very different from today's tropical paradises. □

Methods

Database

Data were extracted from PaleoReefs, a palaeogeographic database of pre-Pleistocene Phanerozoic reefs that encompasses quantitative data on biogenic and petrographic composition, (palaeo-)geography, environmental setting and geometric attributes²⁵. An individual reef in the database is represented by an isolated reef of more than 20 km in maximum diameter, a reef transect 20 km in length (if the reef is more than 20 km in maximum diameter), or data lumped from reefs spaced less than 20 km apart (if the reefs are of the same age and environment).

The relevant variables for analyses are: diversity (see subsection 'Assessment of reef diversity'); matrix (carbonate mud or sand) and spar (carbonate cement) content, relative to the concentration of skeletal reef builders (ordinal values); architecture of a reef based on its inferred syndepositional relief, ranging from true rigid reef with maximum relief to biostromes with no relief (ordinal values); the dominant group of fourteen groups that construct reefs (supra-order groups, except for *Tubiphytes*, a reef builder of disputed taxonomic affinity; nominal values); and length, width and thickness (ordinal and scale values).

The database is available online at <http://193.175.236.205/paleo> (id = paleo, password = reefs). Taxonomic data of the database are deposited in the Paleobiology Database (<http://paleodb.org/>). All analyses exclude non-tropical reef types.

Assessment of reef diversity

Each diversity value in the database represents the total number of species, S , contributing to the construction of a reef (reef builders). The species richness of the dominant modern reef builders (scleractinian corals) has been shown to correlate with the diversity of reef-dwelling organisms²⁶ and thus may serve as a proxy of total reef diversity. Metric diversity values could be extracted for 650 reefs. Broad diversity intervals (low, moderate, high) were defined to include reefs with incomplete taxonomic data but with estimates of total diversity in the published literature (1,736 values). Ordinal values were transformed into scale values to permit the calculation of means on the basis of the empirical relationship: low diversity = 3 species; moderate diversity = 12 species; high diversity = 30 species. A maximum of 45 reef-building species was allowed for individual reefs, to adjust for monographic effects.

Assessment of ecological change

For euclidean distances, relevant attributes were first aggregated globally per time interval (mean or percentage values for ordinal values, percentage values for nominal values). Individual sets of variables comprise: (1) mean density, d , of skeletal reef builders (mean matrix, mean spar); (2) reef architecture, a (percentages of true reefs, reef mounds and mud mounds); (3) reef construction styles, c (variables of 1 and 2 combined); and (4) biotic reef type, b , expressed as the percentage of reefs dominated by a particular group of reef builders (microbes, calcareous algae, corals, calcareous sponges, siliceous sponges, bivalves, bryozoans or *Tubiphytes*). An euclidean distance matrix of standardized (rescaled to unit variance, z-scores) sets of variables was computed and the distances between consecutive time intervals (E_{ij}) were tabulated.

To adjust for covariances in the variables, Mahalanobis distances between individual populations of reefs within time intervals (M_{ij}) were also computed for sets of ordinal

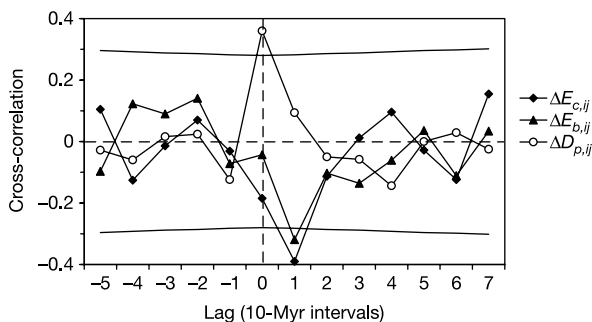


Figure 3 Cross-correlation between reef diversity and selected measures of ecological change in ten-Myr intervals. Cambrian omitted, but the outlier at the Triassic–Jurassic boundary is included to preserve a complete time series. Curved lines indicate the upper and lower 95% confidence bounds. Positive lags indicate ecological change lagging diversity.

variables (matrix content, spar content, reef architecture) after conversion to z-scores. Because this measure requires listwise deletion of data, considerably fewer data are available than for the computation of means and percentages.

In contrast to reef diversity and the other methods of ecological change, recorded reef volume is strongly dependent on the available rock record and exploration intensity, but it is unlikely that $D_{p,ij}$ is completely obscured by heterogeneities of the geological record⁹.

Time series

Stages or epochs with fewer than ten reefs were combined with the subsequent time interval. The 10-Myr intervals were slightly adjusted (± 2 Myr for individual intervals) to avoid lumping data across major extinction events (see Supplementary Information). Lag 1 autocorrelations were removed by calculating generalized differences of the time series data²⁷:

$$\Delta x = x_t - r_A(x_{t-1})$$

where x_t is the original value and r_A is the lag 1 autocorrelation. The first point in the time series was modified to:

$$\Delta x_1 = x_1 \sqrt{1 - r_A^2}$$

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1. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).
2. McGrady-Steed, J., Harris, P. M. & Morin, P. J. Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165 (1997).
3. Naeem, S. & Li, S. Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509 (1997).
4. McCann, K. S. The diversity–stability debate. *Nature* **405**, 228–233 (2000).
5. Loreau, M. *et al.* Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808 (2001).
6. Webb, G. E. Was Phanerozoic reef history controlled by the distribution of non-enzymatically secreted reef carbonates (microbial carbonate and biologically induced cement)? *Sedimentology* **43**, 947–971 (1996).
7. Kiessling, W. in *Phanerozoic Reef Patterns* (eds Kiessling, W., Flügel, E. & Golonka, J.) 625–690 (SEPM Special Publication 72, Tulsa, 2002).
8. Wood, R. *Reef Evolution* (Oxford Univ. Press, Oxford, 1999).
9. Kiessling, W., Flügel, E. & Golonka, J. in *Carbonate Platform Systems: Components and Interactions* (eds Insalaco, E., Skelton, P. W. & Palmer, T. J.) 191–215 (Geological Society Special Publication 178, London, 2000).
10. Golonka, J. & Kiessling, W. in *Phanerozoic Reef Patterns* (eds Kiessling, W., Flügel, E. & Golonka, J.) 11–20 (SEPM Special Publication 72, Tulsa, 2002).
11. Kirchner, J. W. & Weil, A. Delayed biological recovery from extinctions throughout the fossil record. *Nature* **404**, 177–180 (2000).
12. Alroy, J. Are Sepkoski's evolutionary faunas dynamically coherent? *Evol. Ecol. Res.* **6**, 1–32 (2004).
13. Jablonski, D. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science* **231**, 129–133 (1986).
14. Flügel, E. in *Phanerozoic Reef Patterns* (eds Kiessling, W., Flügel, E. & Golonka, J.) 391–463 (SEPM Special Publication 72, Tulsa, 2002).
15. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl Acad. Sci USA* **96**, 1463–1468 (1999).
16. Sankaran, M. & McNaughton, S. J. Determinants of biodiversity regulate compositional stability of communities. *Nature* **401**, 691–693 (1999).
17. Bellwood, D. R., Hoey, A. S. & Choat, J. H. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol. Lett.* **6**, 281–285 (2003).
18. Tilman, D. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–1474 (1999).
19. Tilman, D. *et al.* Diversity and productivity in a long-term grassland experiment. *Science* **294**, 843–845 (2001).
20. Pfisterer, A. B. & Schmid, B. Diversity-dependent production can decrease the stability of ecosystem functioning. *Nature* **416**, 84–86 (2002).
21. Nyström, M., Folke, C. & Moberg, F. Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.* **15**, 413–417 (2000).
22. Pandolfi, J. M. Response of Pleistocene coral reefs to environmental change over long temporal scales. *Am. Zool.* **39**, 113–130 (1999).
23. Pandolfi, J. M. *et al.* Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**, 955–958 (2003).
24. Bellwood, D. R., Hughes, T. P., Folke, C. & Nyström, M. Confronting the coral reef crisis. *Nature* **429**, 827–833 (2004).
25. Kiessling, W. & Flügel, E. in *Phanerozoic Reef Patterns* (eds Kiessling, W., Flügel, E. & Golonka, J.) 77–92 (SEPM Special Publication 72, Tulsa, 2002).
26. Bellwood, D. R. & Hughes, T. P. Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**, 1532–1535 (2001).
27. McKinney, M. L. & Oyen, C. W. Causation and nonrandomness in biological and geological time series: temperature as a proximal control of extinction and diversity. *Palaïos* **4**, 3–15 (1989).

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Stage-structured cycles promote genetic diversity in a predator–prey system of *Daphnia* and algae

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Competition theory predicts that population fluctuations can promote genetic diversity when combined with density-dependent selection^{1,2}. However, this stabilizing mechanism has rarely been tested, and was recently rejected as an explanation for maintaining diversity in natural populations of the freshwater herbivore *Daphnia pulex*³. The primary limitation of competition theory is its failure to account for the alternative types of population cycles that are caused by size- or stage-dependent population vital rates—even though such structure both explains the fluctuating dynamics of many species⁴ and may alter the outcome of competition⁵. Here we provide the first experimental test of whether alternative types of cycles affect natural selection in predator–prey systems. Using competing *Daphnia* genotypes, we show that internally generated, stage-structured cycles substantially reduce the magnitude of selection (thereby contributing to the maintenance of genetic diversity), whereas externally forced cycles show rapid competitive exclusion. The change in selection is ecologically significant, spanning the observed range in natural populations³. We argue that structured cycles reduce selection through a combination of stalled juvenile development and stage-specific mortality. This potentially general fitness-equalizing mechanism may reduce the need for strong stabilizing mechanisms to explain the maintenance of genetic diversity in natural systems.

The maintenance of genetic diversity is a central problem in biology. It is particularly acute when considering populations composed of asexual clones with extensive niche overlap. Natural populations of zooplankton, such as *Daphnia*, are a good example because they are rich in genotypic diversity^{3,6–10}, and observations of correlated dynamics in fecundity among clones^{11,12} suggest that genotypes have high resource overlap. Diversity is maintained in spite of the fact that coexisting genotypes often show strong fitness differences in the laboratory^{11,13}. These observations have been declared the second ‘paradox of the plankton’¹⁴ because they contradict the principle of competitive exclusion¹⁵, which postulates that only a single competitor should remain at equilibrium.

Competition theory offers a compelling solution to this paradox. It proposes that combining density-dependent selection with fluctuating population dynamics could allow coexistence among competitors^{1,2}. This mechanism requires that the relative fitness among competitors changes as the resource abundance changes, such that fluctuations in resource generate fluctuations in selection. Genetic diversity is thus maintained through fluctuating selection, which is considered a stabilizing mechanism that allows for coexistence by balancing fitness differences over time¹⁶. Recently, one of the first tests of this hypothesis in natural systems has been performed³ by analysing numerous time series of *Daphnia* genotype frequencies and population dynamics. No evidence was found for the maintenance of genetic diversity in *Daphnia* populations by fluctuating selection, suggesting that coexistence is more likely explained by an equalizing mechanism that reduces fitness differences among genotypes¹⁶.

Competition theory was largely developed under the assumption that populations can be modelled without considering the natural