

# The role of extinction in large-scale diversity–stability relationships

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More-diverse communities are thought to be ecologically stable because a greater number of ecological interactions among members allows for the increases in robustness and resilience. Diversity–stability relationships have mostly been studied on short ecological time scales but one study has identified such patterns over million-year time scales in reef communities. Here we propose and test a hypothesis for the mechanism of large-scale diversity–stability relationships in reefs. The extinction of community members destabilizes the community as a whole, unless there is sufficient diversity to buffer the community from the stochastic loss of members, thereby preventing collapse. If genera have high extinction rates, any variation in diversity among communities will result in a diversity–stability relationship. Conversely, in the absence of other mechanisms, the stability of low extinction communities is expected to be independent of diversity. We compare the extinction rates of six reef-building metazoan taxa to patterns of reef community stability and reef volume. We find that extinction of reef-builders occurs independent of reef volume, and that the strength of the diversity–stability relationship varies positively with extinction rate.

**Keywords:** extinction; coloniality; diversity–stability relationship; corals; reefs

## 1. INTRODUCTION

Over geological time, reef communities are notoriously volatile. New reef communities, with distinct members and structure, commonly arise, proliferate and disappear (Wood 1998; Kiessling 2009). One important pattern emerges from this volatility. Over most of the Phanerozoic (the last 540 Myr), reefs with a high species richness of reef-building taxa are more stable in ecological properties such as growth density and community composition than less-diverse reefs (Kiessling 2005). The time scales of stability are long enough that constituent genera or species often go extinct before the communities change.

Diversity–stability relationships are common patterns on short ecological timescales and an increase in the robustness and resilience of networks of ecological interactions among the whole community is generally considered to be their cause (McGrady-Steed *et al.* 1997; Tilman *et al.* 1998; Tilman 1999; McCann 2000; Cardinale *et al.* 2009). The specific mechanisms proposed for small-scale diversity–stability relationships, however, are inadequate for explaining the large-scale patterns observed in reefs because of species turnover.

On geological time scales, a more general mechanism for generating a diversity–stability relationship is needed. We propose a new mechanism for diversity–stability relationships that is driven only by the extinction of constituent species within communities (figure 1). Communities containing species with high extinction rates will not persist for long if they have low diversity, because the communities are sensitive to stochastic extinction of constituent species. However, the communities can

persist if they have a sufficiently high diversity to buffer them from the stochastic extinction of member species. Buffering of the community will increase with diversity, so that stability increases with diversity. Thus, communities with high rates of extinction must show a diversity–stability relationship. Communities with low extinction can be stable or unstable independent of their diversity, and so do not necessarily show a diversity–stability relationship. If they do show a diversity–stability relationship, it must be generated by some mechanism other than our buffering hypothesis.

Although the extinction buffering mechanism may occur in any community, we expect it to be particularly important in communities like reefs, where a non-random subset of species affects the whole community. Because reefs are built by the growth of skeletal organisms, reef-builders play a disproportionate role in structuring the community. Thus, their extinction is expected to be more detrimental to the ecosystem than the extinction of reef-dwelling organisms (Jackson & Coates 1986). The continual loss of reef-building species by extinction is expected to lead to instability of the community as a whole. If, for example, a reef community consists of a single reef-building species, the extinction of the reef-builder would lead to the collapse of the whole community, independent of the diversity of reef-dwelling species. A high diversity of reef-builders would therefore buffer the community from the stochastic loss of reef-building species so that the extinction of any one reef-building species would not lead to the collapse of the community.

This mechanism makes several falsifiable predictions that we test in this paper. First, the diversity–stability relationship should be observable in only the reef-building members of the community. For example, the diversity–stability relationship should still be detectable

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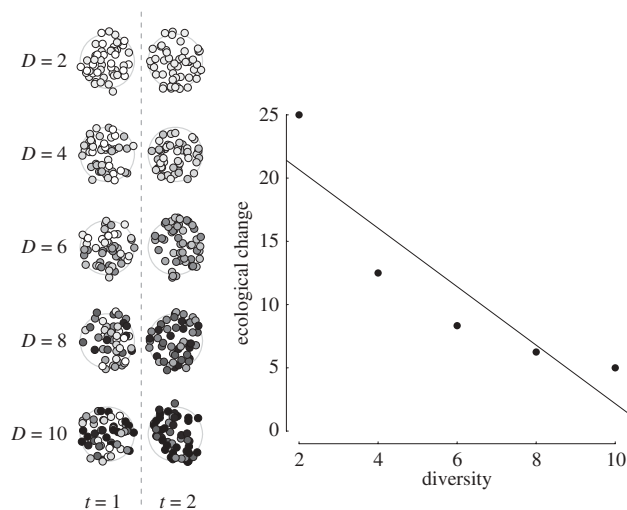


Figure 1. An illustration of how high extinction rates can generate a diversity–stability relationship. Five reef communities with varying diversities are sampled at two time intervals. They each lose half of their species from one interval to the next. Ecological change is measured as the difference in community composition (number of species and their abundances) across intervals.

if taxa such as fish, crabs and snails that dwell in reefs are ignored because the community should be more sensitive to the extinction of structurally important reef-builders. Second, the magnitude of extinction rates of reef-building organisms should correlate with the strength of the diversity–stability relationship. This is because more diversity is needed to buffer communities from the more frequent extinction of member species. In effect, as the extinction rate increases, low-diversity communities will become increasingly unstable, while high-diversity communities will maintain their stability. Third, extinction of reef-building organisms must occur continuously when reefs are present and must not be clustered together coincident with the termination of the reef community.

In this paper we test the above hypotheses by first estimating the extinction rates in all five reef-building taxa and testing whether reef-builder extinctions are continuously distributed in time relative to the expansion and contraction of reef habitats. We then test whether the diversity–stability relationship is strongest when reef-builder extinction rates are high.

## 2. MATERIAL AND METHODS

Two independent datasets are used in this paper, one for reef volume and community stability, and the other for estimating rates and patterns of extinction in reef-building organisms.

The globally preserved reef volume at a given time was calculated using the dimensions of reef sites as indicated in the PaleoReefs database (PARED; Kiessling *et al.* 2000). Volumes were calculated for each temporal interval based on the database as of March 2009 and exclude microbial components. Diversity–stability relationships are also based on the PARED (Kiessling 2005). Ecological change is measured as the Euclidean distance between consecutive time intervals in reef type. Reef types are expressed as the percentage of reefs dominated by a particular group of reef-builders and include microbes, calcareous algae, corals,

calcareous sponges, siliceous sponges, bivalves and bryozoans.

Extinction rate analyses are conducted using environmentally resolved taxonomic occurrences from the Paleobiology Database (PaleoDB; <http://paleodb.org>). Data were downloaded on 5 May 2009 and are comprised of 360 838 genus occurrences with information on taxonomy, geology and stratigraphy. We downloaded all occurrence data from the marine invertebrate working group except for vertebrates and genera with uncertain identifications (i.e. names listed in quotation marks, or qualified as ‘?’ , ‘cf.’ or ‘aff.’). Uncertain genera are excluded because they tend to be wastebasket taxa with long temporal ranges due only to the pooling of many unrelated occurrences (Plotnick & Wagner 2006). Temporal resolution was set to be the PaleoDB 10 Myr bins. Occurrences are classified as reef occurrences if ‘reef, buildup or bioherm’, ‘intrashelf/intraplatform reef’, ‘platform/shelf-margin reef’, ‘slope/ramp reef’, ‘basin reef’ or ‘perireef or subreef’ is included in the environmental calls. All other environments are considered non-reef.

Included in the extinction rate analyses are six reef-building metazoan taxa: calcareous sponges, which were important reef-builders through the Palaeozoic and Mesozoic; tabulate and rugose corals, which were important reef-builders in the Palaeozoic; scleractinian corals, which have been dominant reef-builders since the Late Triassic; and bivalves and stenolaemate bryozoans, which played a subordinate role as reef-builders. We categorize genera within each taxon into either reef-builders or reef-dwellers, and use the estimates of reef-builder extinction rates to test the diversity–stability hypothesis. The six taxa we use in this analysis have distinct bauplans, each of which requires slightly different criteria for partitioning between reef-building and reef-dwelling organisms (table 1). We include the classes Stomatoporoidea and Calcarea, as well as the Demospongia orders Agelasida, Axinellida, Chaetetida, Hadromerida, Permosphincta and Tabulospongida, as reef-building sponges. We consider scleractinian and Palaeozoic rugosan reef-builders to be highly integrated and colonial, whereas reef-dwellers are solitary or low-integration dendroid, phaceloid or fasciculate colonies. Palaeozoic tabulate corals and stenolaemate bryozoans were all colonial, so we restrict reef-dwellers to low-integration encrusting or vine-like forms, and reef-builders are highly integrated, erect or massive forms. Finally, rudist bivalves were fast-growing solitary bivalves that were major reef-builders during the Cretaceous (Steuber 1996). Growth forms used for the classification of genera into reef-building or reef-dwelling for each genus are listed in the electronic supplementary material.

We excluded from the analysis those genera that do not preferentially live in reefs, because they potentially experience very different selective environments and because differences in preservation potential among environments may lead to biased estimates of extinction. We consider a marine genus to be a reef taxon when the observed proportions of reef occurrences are significantly greater than the proportion of non-reef occurrences. This protocol automatically excludes very rare genera and minimizes artefactual range truncations. Because the numbers of reef and non-reef habitats change over time, the number of occurrences for each genus is compared with the total number of reef and non-reef environments over its stratigraphic range. Reef affinities are estimated using a Bayesian posterior

Table 1. A comparison of life-history attributes for reef-builders and reef-dwellers. +, present or high; -, absent or low; 0, mixed; ?, unknown. Abbreviations: determ., determinate growth; asex., asexual reproduction; sex., sexual reproduction; disp., dispersal ability; recruit., recruitment rate; photosymb., photosymbiosis.

taxa	ecology	growth						reproduction larvae					
		clonal	colonial	determ.	rate	form	size	asex.	sex.	disp.	recruit.	patchiness	photosymb.
Rugosa	reef-dweller	-	0	+	-	0-1 <sup>a</sup>	-	0	+	?	?	-	?
	reef-builder	+	+	-	+	2-4 <sup>a</sup>	+	+	+	?	?	+	?
Tabulata	reef-dweller	+	+	-	-	1 <sup>a</sup>	-	0	+	?	?	-	?
	reef-builder	+	+	-	+	2-4 <sup>a</sup>	+	+	+	?	?	+	?
Scleractinia	reef-dweller	0	0	0	-	0-1 <sup>a</sup>	-	0	+	-	+	-	-
	reef-builder	+	+	-	+	2-4 <sup>a</sup>	+	+	+	+	-	+	+
Stenolaemata	reef-dweller	+	+	-	-	1 <sup>b</sup>	-	0	+	-	+	-	-
	reef-builder	+	+	-	+	2-3 <sup>b</sup>	+	+	+	+	-	+	-
Bivalvia	reef-dweller	-	-	+	-	0	-	-	+	0	+	-	-
	reef-builder	-	-	-	+	0-1	+	-	+	?	?	+	?

<sup>a</sup>Levels of colonial integration; 0, solitary; 1, gregarious, dendroid, phaceloid or fasciculate; 2, cerioid or plocoid; 3, thamnasteroid or asteroid; 4, meandroid.

<sup>b</sup>Levels of colonial integration measured by growth form: 1, encrusting or vine-like; 2, erect; 3, massive.

Table 2. A comparison of two models of extinction derived from the distribution of longevities of extinct genera with reef affinities for five reef-building higher taxa. Preferred model is shown in bold.

taxa	model	growth form	mean duration (Ma)	$\hat{q}$	$\ln L$	$n$	$K$	$\Delta AICc$	$w_i$
Rugosa	single rate	all	40	0.025	-635	137	1	8.97	0.011
	<b>two rate</b>	<b>reef-builders</b>	<b>32.26</b>	<b>0.031</b>	<b>-142.07</b>	<b>33</b>	<b>2</b>	<b>0</b>	<b>0.988</b>
		<b>reef-dwellers</b>	<b>41.67</b>	<b>0.024</b>	<b>-487.37</b>	<b>104</b>			
Tabulata	single rate	all	55.55	0.018	-401.39	81	1	9.78	0.007
	<b>two rate</b>	<b>reef-builders</b>	<b>50</b>	<b>0.02</b>	<b>-219.43</b>	<b>46</b>	<b>2</b>	<b>0</b>	<b>0.992</b>
		<b>reef-dwellers</b>	<b>66.67</b>	<b>0.015</b>	<b>-176.02</b>	<b>35</b>			
Scleractinia	single rate	all	47.62	0.021	-396.4	244	1	7.64	0.021
	<b>two rate</b>	<b>reef-builders</b>	<b>45.45</b>	<b>0.022</b>	<b>-177.5</b>	<b>148</b>	<b>2</b>	<b>0</b>	<b>0.978</b>
		<b>reef-dwellers</b>	<b>47.62</b>	<b>0.021</b>	<b>-214</b>	<b>96</b>			
Stenolaemata	single rate	all	71.43	0.014	-177.8	35	1	9.23	0.01
	<b>two rate</b>	<b>reef-builders</b>	<b>66.67</b>	<b>0.015</b>	<b>-149.98</b>	<b>30</b>	<b>2</b>	<b>0</b>	<b>0.99</b>
		<b>reef-dwellers</b>	<b>111.11</b>	<b>0.009</b>	<b>-22.08</b>	<b>5</b>			
Bivalvia	single rate	all	40	0.025	-370.9	80	1	13.24	0.001
	<b>two rate</b>	<b>reef-builders</b>	<b>32.26</b>	<b>0.031</b>	<b>-236.81</b>	<b>54</b>	<b>2</b>	<b>0</b>	<b>0.999</b>
		<b>reef-dwellers</b>	<b>58.82</b>	<b>0.017</b>	<b>-125.61</b>	<b>26</b>			

probability (Simpson & Harnik 2009). The prior probability is estimated from the proportion of global reef and non-reef occurrences during the stratigraphic range of the genus. The null hypothesis is no affinity, where there is an equal chance of being found in reef and non-reef environments. Genera with posterior probabilities of less than 0.5 are considered to have reef affinity.

Analyses were conducted at the genus level. A time series of extinction rates ( $q$ ) are estimated using boundary-crossing genera (Foote 2000):  $\hat{q} = \log[N_{bt}/(N_{bL} + N_{bt})]$ , where  $N_{bt}$  denotes the number of genera that cross the bottom and the top boundary of an interval, and  $N_{bL}$  is the number of genera that only cross the bottom boundary before going extinct in that interval. We also estimate a single extinction rate for each taxon from the frequency distribution of temporal durations of reef-building genera, assuming an exponential model of extinction (Van Valen 1973). Under this model, the maximum-likelihood extinction rate estimate is  $\hat{q} = 1/\bar{d}$ , where  $\bar{d}$  is the mean duration of genera.

Extinction rates commonly vary within as well as among taxa, and it is possible that reef-building genera have

systematically different extinction rates than their reef-dwelling counterparts (Jackson & Coates 1986). We tested whether reef-builders have distinct rates by comparing two models of extinction: one where builders and dwellers have independent rates and one where they share the same rate. We ranked models using Akaike's weights ( $w_i$ ) based on Akaike's modified information criterion (Burnham & Anderson 2002). The sample-size-corrected Akaike's information criterion is  $AICc = -2 \ln L(\text{Model}) + 2K[n/(n - K - 1)]$ , where  $K$  is the number of parameters (i.e. separate extinction rates),  $n$  is the number of data points and  $L$  is the maximum likelihood of the extinction model given the data. The likelihood is attained analytically by taking the first derivative of the extinction rate equation. For the temporal pattern of extinction, the likelihood is given by  $L = N_{bt} \log(N_{bt}/N_b) + N_{bL} \log(N_{bL}/N_b)$ , where  $N_b$  is the total number of genera that crosses the interval. For the extinction rate estimated from the duration distributions, the likelihood is a function of the number of genera ( $n$ ) and the sum of genus durations ( $d$ ):  $L = n \log(\hat{q}) - \hat{q} \sum_{i=1}^n d_i$ . Akaike's weight ( $w_i$ ) for each

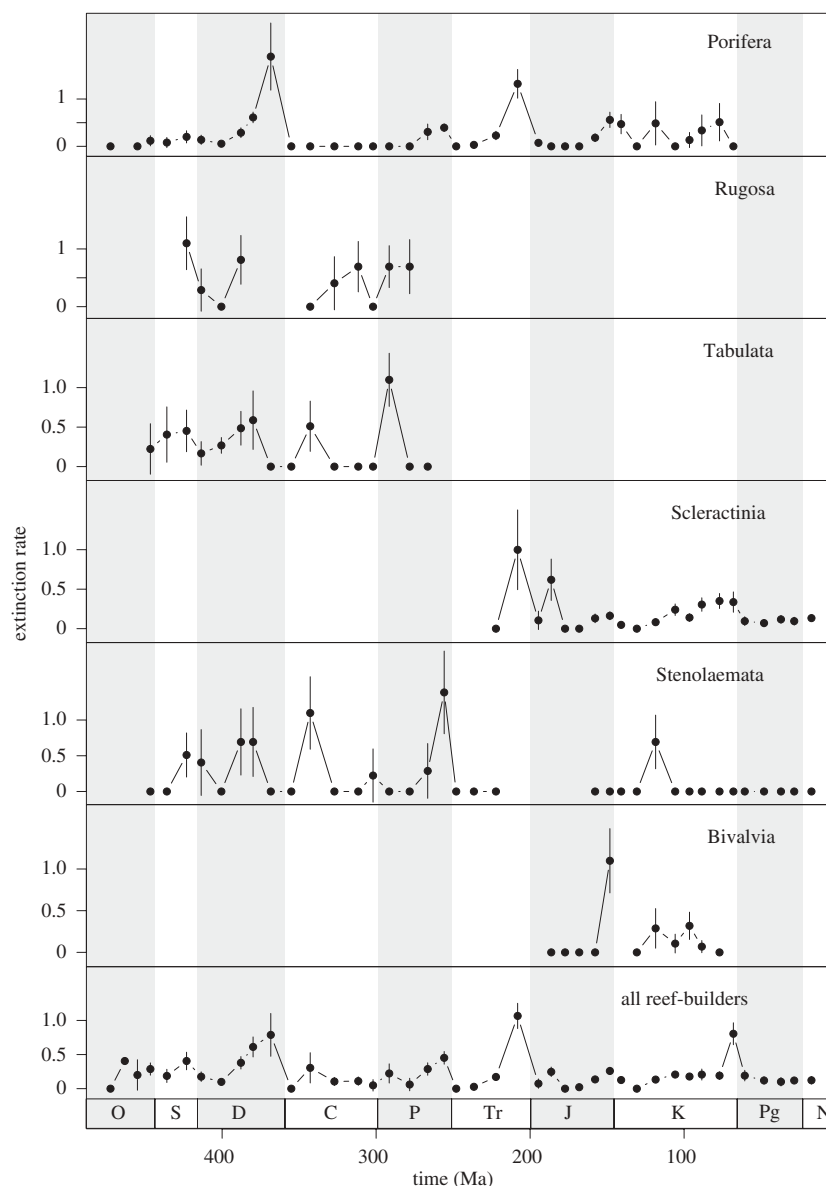


Figure 2. Time series of extinction rates for all reef-building genera with reef affinities for the six higher taxa. Per-interval extinction rates are estimated from boundary-crossing genera, hence genera restricted to a single interval are excluded (Foote 2000). The rugosan and tabulate lineages went extinct at the end of the Permian and rudists at the end of the Cretaceous. Their infinite extinction rate is not shown in these intervals. Error bars are estimated from 1000 bootstrap replicates. O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; N, Neogene.

hypothesis is  $\omega_i = (e^{-\Delta_i/2}) / \sum (e^{-\Delta_i/2})$ , where  $\Delta_i$  is the difference between the AICc of the best model and that of the model  $i$  (Burnham & Anderson 2002). The Akaike's weight of each model is proportional to the probability of hypothesis given the data, corrected for the number of parameters and data points. Using 0.89 for the cut-off of model preference is similar to using a likelihood criterion of rejecting hypotheses when an outcome is eight times less probable for one model than for the other (Wagner *et al.* 2006).

The maximum decrease in reef volume over time is constrained by the volume of the previous interval, but the maximum increase in volume is not. To ensure the potential for changes to be symmetrically distributed around zero, we use the log return to describe the temporal pattern of reef volume changes. The log return is  $\Delta V_i = \log(V_i/V_{i-1})$ , where  $V$  is the global reef volume per interval  $i$ .

### 3. RESULTS AND DISCUSSION

#### (a) Extinction rates

We find that reef-building genera have higher extinction rates, when estimated as a function of genus longevity, than reef-dwellers of the same higher taxa, with the exception of scleractinian corals, which have indistinguishable rates even though the two-rate model has higher support (table 2). These results pool genera that go extinct in all time intervals and exclude those that survive until the recent, but the same basic results are achieved when episodes of mass extinctions (defined to have extinction rates greater than a standard deviation above the mean extinction rate) are excluded. A separate temporal pattern of extinction rates for reef-builders is also supported. For the six reef-building taxa, the two-rate model is preferred (Porifera, multirate  $\Delta\text{AICc} = 0$ ,  $\omega_i = 1$ ; Rugosa, multirate  $\Delta\text{AICc} = 0$ ,



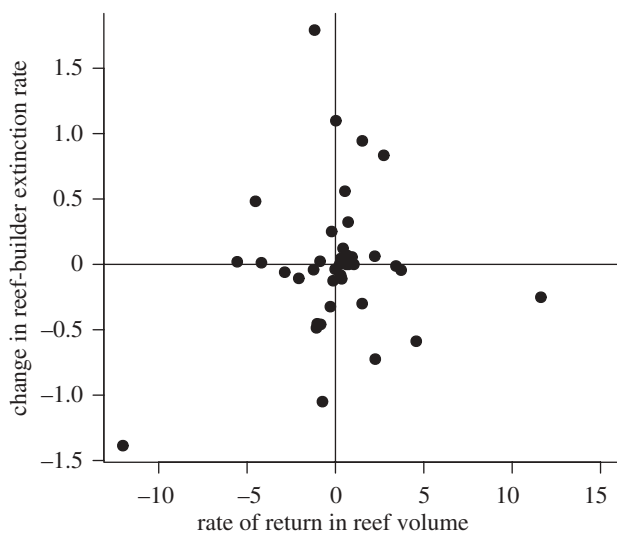


Figure 3. Log return of reef volume compared with changes in reef-builder extinction. Extinction rates are estimated by pooling reef-building genera from the six reef-building taxa. The lack of any correlation suggests that extinctions occur independent of global reef proliferation.

$w_i = 0.9982$ ; Tabulata,  $\Delta\text{AICc} = 0$ ,  $w_i = 1$ ; Scleractinia,  $\Delta\text{AICc} = 0$ ,  $w_i = 0.9999$ ; Stenolaemata,  $\Delta\text{AICc} = 0$ ,  $w_i = 0.9972$ ; Bivalvia,  $\Delta\text{AICc} = 0$ ,  $w_i = 1$ ). All subsequent analyses use only the time series of estimated reef-builder extinction rates (figure 2).

#### (b) Diversity–stability

If the high extinction rate of reef-builders underpins the observed diversity–stability relationship, extinctions need to be continuously occurring even if reefs are widespread. Alternatively, extinction risk of reef-builders could be reduced during times of global expansion and increased during global reef crises, defined here as times of substantially reduced reef volume. Global reef volume (Kiessling *et al.* 2000) and extinction rates should be negatively cross-correlated under this scenario. We observe no significant correlation between the log return in globally preserved reef volume and the change in extinction rates of reef-builders for any temporal subset of the data over time (figure 3; Spearman's  $\rho = 0.0305$ ,  $p = 0.846$ ; Palaeozoic only, Spearman's  $\rho = -0.1002$ ,  $p = 0.6832$ ; post-Palaeozoic only, Spearman's  $\rho = 0.1983$ ,  $p = 0.3529$ ). This supports the contention that continual turnover of reef-building genera occurs even during times of reef expansion.

In order to test whether the strength of the diversity–stability relationship depends on extinction rates, we partition the diversity–stability data in two ways. First, we compare the diversity–stability relationship in the Palaeozoic (with a mean *per capita* extinction rate of 0.2568) to that observed in the post-Palaeozoic (mean *per capita* extinction rate of 0.1959). The diversity–stability relationship is weaker in the post-Palaeozoic (figure 4; Palaeozoic: slope =  $-0.1203$ , Spearman's  $\rho = -0.475$ ,  $p = 0.019$ ; post-Palaeozoic: slope =  $-0.0893$ , Spearman's  $\rho = -0.261$ ,  $p = 0.2174$ ). A more direct test is to compare the diversity–stability relationship between intervals with high and low extinction. We partition intervals into high or low extinction intervals based on the first

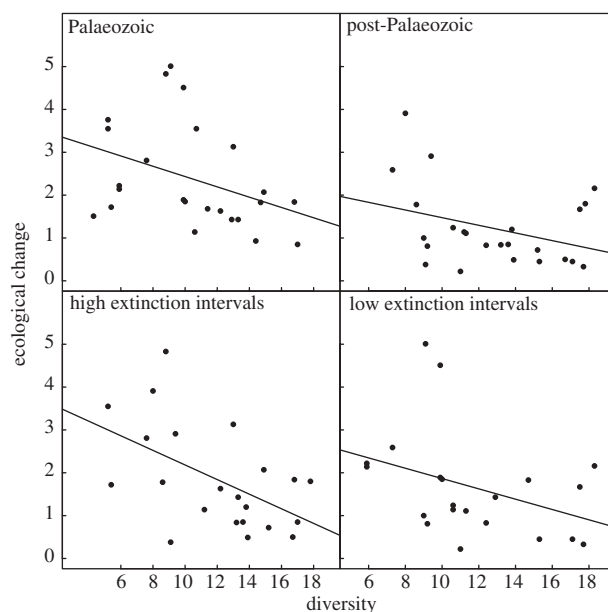


Figure 4. A comparison of the change in generic diversity and the change in reef stability as measured by Euclidean distance of changes in community composition for those compared between the Palaeozoic and post-Palaeozoic and between high and low extinction intervals. Diversity is based on the number of reef-building species. Community stability is measured as the Euclidean distance between the compositions of reef communities from one interval to other. Community compositions are derived from the proportion of microbes, algae, sponges, bryozoans, corals and other builders (reproduced data from Kiessling 2005).

differences of extinction rates over time in order to control the background rates. We use the median change in *per capita* extinction rate for all Phanerozoic reef-builders (0.0215) as the cut-off between high and low extinction intervals. The diversity–stability relationship is strongest when the change in extinction rates is high (figure 4), although the scatter in the data prevents this from being seen in the non-parametric correlation tests (high extinction communities: slope =  $-0.1704$ , Spearman's  $\rho = -0.4496$ ,  $p = 0.0358$ ; low extinction communities: slope =  $-0.1204$ , Spearman's  $\rho = -0.4701$ ,  $p = 0.0315$ ). The buffering effect of high diversity is stronger when extinction rates are high. Five time intervals have an estimated extinction rate equal to zero. The slope of the regression of ecological change on diversity for no-extinction intervals (based on the five intervals where the extinction rate is equal to zero) is equal to  $-0.1267$  (Spearman's  $\rho = -0.6593$ ,  $p = 0.2261$ ). It is then possible that other mechanisms are operating in addition to our extinction buffering hypothesis.

#### 4. CONCLUSIONS

The high turnover of reef-building genera leads to community instability, which is buffered by high diversity. This results in a large-scale diversity–stability relationship over all reef communities in the Phanerozoic (Kiessling 2005), and also occurs in the Palaeozoic, but is weaker in the post-Palaeozoic, when reef-builders tend to have low extinction rates. Furthermore, the diversity–stability relationship is strong in those intervals with high extinction

and weak in times with low extinction rates. These patterns, together with the observation that reef-building genera go extinct even while reefs expand, support our proposed mechanism of large-scale diversity–stability relationships.

The mechanism of diversity–stability relationships on evolutionary time scales is decidedly different from those on ecological time scales. Thus diversity–stability relationships can emerge from different mechanisms, and it will be an exciting research to look at their interactions at different time scales.

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