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Estimating the Rock Volume Bias in Paleobiodiversity Studies

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To interpret changes in biodiversity through geological time, it is necessary first to correct for biases in sampling effort related to variations in the exposure of rocks and recovery of fossils with age. Data from New Zealand indicate that outcrop area is likely to be a reliable proxy of rock volume in both stable cratonic regions, where the paleobiodiversity record is strongly correlated with relative sea level, and on tectonically active margins. In contrast, another potential proxy, the number of rock formations, is a poor predictor of outcrop area or sampling effort in the New Zealand case.

Documenting and explaining large-scale patterns of biodiversity change through geological time is a key research agenda in paleobiology (*1*). Intuitively, however, it seems reasonable to expect that the number of fossil specimens and, therefore, taxa recovered from any particular interval of time will be determined, in part, simply by the amount of sedimentary rock available for sampling (*2*, *3*). Recent studies have corroborated this relation using data from North America and Western Europe (*4*–*6*). Clearly, correction for this bias underpins meaningful interpretation of the history of life.

Previous studies have used two proxies for available rock volume: the number of named geological formations of a given age (*4*, *5*, *7*) and approximations of outcrop area, based typically on equal-grid sampling methods (*6*). Both proxies apparently correlate with collection effort and standing biodiversity. They are, however, functions of many factors that interact in complex, nonlinear, and poorly understood ways, factors that also influence biodiversity and the nature of the fossil record (Fig. 1). To isolate and quantify these influences requires more complete compilations of data than have hitherto been available (*8*, *9*). Here we test the value of different proxies of rock volume and identify some of the underlying controls of rock volume and sampled biodiversity using new data from New Zealand (NZ).

We compiled independent estimates of the number of marine formations, outcrop area of marine sedimentary rocks, numbers of mollusc collections and species, and the proportion of mollusc species that inhabited shelf and bathyal depths or greater, for each of the 24 NZ Cenozoic stages (*10*). These estimates are considered reliable for several reasons.

(i) Through a nationwide research program, all Cenozoic sedimentary basins of NZ have been systematically described, mapped (at 1:250,000 scale), and sampled for fossils to a reasonable, uniform minimum standard. Although monographic biases cannot be discounted, we are confident that such effects will not distort large-scale trends in the collection data and that there are no major collection failures in either the fossil mollusc or sedimentary rock records. (ii) Since 1946, NZ paleontologists have developed the Fossil Record File (FRF), a register of all localities that have yielded macrofossils or have been sampled for microfossils. All government, industry, and university collectors, and many private collectors, have submitted information to this database. Since 1970, 65% of the FRF has been progressively computerized and there are now 56,000 locality records, 76,000 taxon lists, and >700,000 individual species occurrence records in the Fossil Record Electronic Database. These locality records have been used here to obtain a reliable estimate of sampling effort for Cenozoic marine molluscs in NZ (*10*). (iii) Over the past 50 years, geological age determinations in NZ have been given in terms of the local time scale. Although correlations with the international time scale have changed substantially, the system of local stages has remained largely stable (*11*). This means that the ages of collections, formations, and species can be readily and reliably compared, even when dealing with data of varying vintage.

For the purposes of our analysis, we treated the stages as ordered "bins" and the mollusc and rock data were not normalized for stage length, although the relative durations of stages were used to adjust the weightings of range-through collections (*10*). In addition to comparisons of the raw data, we also examined the first differences between successive stages (i.e., the value for a stage minus the value for the preceding stage). Comparisons of the raw data tend to emphasize similarities and differences in the general, long-term trends, whereas the first differences focus on short-term, stage-to-stage changes (*4*). To measure the degree of positive association between each of our four data sets, we used Pearson's linear product-moment correlation coefficient. Because our data are not normally distributed, however, we confirmed the statistical significance of these correlations using Spearman's rank correlation coefficient (*10*).

Our a priori expectation was that the number of marine formations, outcrop area, and number of collections would be signif-

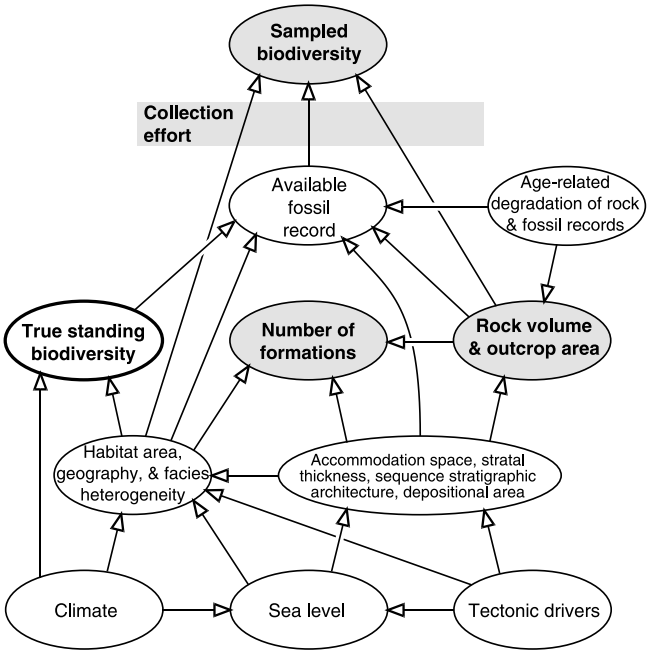


Fig. 1. Schematic diagram showing complex interrelationships between major physical determinants of fossil-record quality. Factors shown in bold and shaded are those examined here. "Collection effort" acts as a filter that influences through-going arrows in ill-defined ways. The true-standing biodiversity, the quantity of ultimate interest, is highlighted.

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icantly and positively correlated. It is immediately apparent from Fig. 2 and Table 1 that the number of formations is significantly but only weakly correlated with either outcrop area or collections for the raw data; these correlations are not significant for the first differences. In contrast, outcrop area and collections are relatively strongly and significantly correlated for both the raw data and their first differences. If one ignores the conflicting data for the youngest three stages, values of r for outcrop area and number of collections increase to 0.889 and 0.841 for the raw data and the first differences, respectively. These results indicate that, for Cenozoic marine strata in NZ, the number of named formations is a poor proxy for outcrop area, whereas outcrop area is a comparatively robust proxy for collection effort.

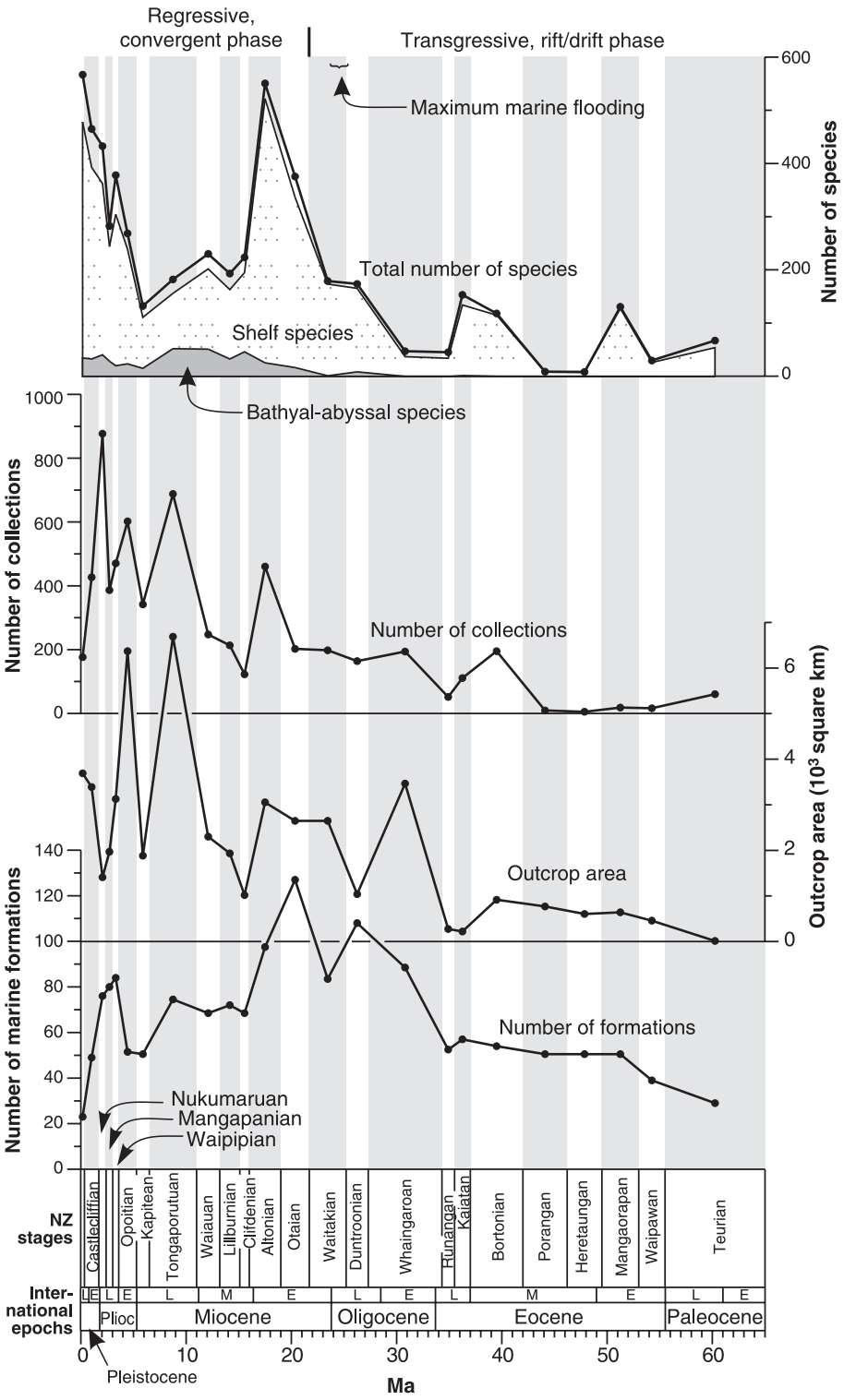


Fig. 2. Plots of number of marine formations, outcrop area of marine sedimentary rocks, number of mollusc-bearing fossil collections, and number of mollusc species (bivalves, gastropods, and scaphopods) for each stage of the NZ Cenozoic time scale (*10*) (table S1). The most recent NZ stage (not labeled) is the Haweran. Also shown (at top) are the major elements of the first-order sea-level on-lap curve (*12*, *13*). The species curve represents only the raw data in the biodiversity database, and no particular biological meaning is ascribed to this plot. Within the total species curve, cumulative proportions of taxa from inferred shelf and deep-water environments are shown.

Which, if any, of these proxies is likely to best inform us about the rock volume bias in the biodiversity record? Table 1 reveals that both outcrop area and number of collections are significantly correlated with large-scale biodiversity trends, whereas only the number of collections is significantly though comparatively weakly correlated with short-term changes in biodiversity (i.e., first differences). This indicates that there is, indeed, some relationship in NZ between large-scale patterns of recorded species diversity and rock volume, confirming results from Western Europe and North America. For the sake of argument, we assume that the collection curve recorded here is an accurate measure of total collection effort, that it reflects unbiased and systematic sampling across the NZ landmass, and therefore that it is a representative measure of rock available for sampling. If we are willing to accept this assumption, then we can say that outcrop area is a useful predictor of both collection effort and rock volume bias in the Cenozoic of NZ, whereas number of formations is not.

Our assumption, however, is clearly overly simplistic (Fig. 1) and makes no statement about direct causal relationships between rock volume, collections, and sampled biodiversity, or whether all three reflect some other, common, underlying causal factor(s) such as the species-area effect. Although we are not in a position yet to address this perplexing question, our data shed light on some of the other underlying, large-scale controls of sampled biodiversity. First, the shape of the formation curve appears to mirror closely the first-order, tectonically driven, sea-level on-lap curve (*12*, *13*). From the latest Cretaceous to Oligocene, the NZ microcontinent experienced passive thermal subsidence after its separation from Gondwanaland. During the Early Miocene, the modern Pacific-Australian plate boundary propagated through the region, and the current phase of uplift and deformation initiated. The greatest number of marine formations coincides, with a one-stage lag, to

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maximum flooding close to the Oligocene/Miocene boundary (Fig. 2) and to widespread deposition of carbonate rocks across the largely submerged NZ microcontinent. The post-Oligocene regression is characterized by a decline in the number of formations. This trend does not reflect greater stratigraphic lumping of units; instead, the opposite is true. For the Oligocene and Miocene, the average formation duration (±SD) is relatively constant at 16.0 million years (My) (±1.6 My), whereas for the Pliocene and Pleistocene, the average is only 3.2 My (±1.4 My). In contrast to the formation data, outcrop area shows a generally increasing trend in the post-Oligocene interval and does not seem to be related (at a first order) to degree of marine on-lap. Taken together, these observations indicate that, with decreasing age, formations become increasingly differentiated temporally and have increasing areal extent. We infer that this pattern simply reflects decreasing levels of deformation, dismemberment, and erosion of progressively younger units. Areal preservation of formations, not their number or level of differentiation, is the strongest predictor of fossil collection numbers in NZ. Our result does not reproduce the positive correlations between formations and outcrop area that have been observed in North America (*4*). One explanation for this discrepancy might lie in the relatively high levels of tectonic activity in NZ compared with large parts of North America. In tectonically active areas, high levels of uplift and erosion might expose large numbers of older formations as volumetrically small, spatially isolated, and differentiated units, thus causing the observed mismatch between outcrop area and formations.

Second, the shape of the NZ mollusc biodiversity curve is determined primarily by the number of sampled shelf taxa (Fig. 2), as opposed to bathyal and abyssal species, a finding that is consistent with data from Europe (*14*). The marked decline in sampled shelf diversity in the Middle to Late Miocene corresponds to an increasing trend in the number of collections. In other words, this apparent decline in diversity marks a true reduction in the average number of species per collection and is not simply an artefact of reduced collection effort. Although data are not available on the preservation of different paleoenvironments in the NZ rock record, the Middle and Late Miocene are characterized by rapid, local subsidence in basins around the emerging NZ landmass (*13*). Within these basins, subsidence rates exceeded sediment supply, and most deposition was at bathyal depths. Thus, the apparent decline in shelf diversity in the Miocene probably reflects two causes: cannibalization and erosional removal of shallow-water deposits on the emerging and deforming landmass, and a relative reduction in the original depositional area of shelf facies versus deeper basinal facies. As for the formation and outcrop data discussed above, therefore, patterns of sampled diversity seem to be influenced strongly by regional tectonics and show no simple relation to first-order sea-level per se.

Thus, we infer that tectonic regime plays an important role in determining which underlying factors have the greatest control on the rock volume bias to apparent paleobiodiversity. Diversity data sets that are derived largely from stable, cratonic areas are likely to reflect cyclical sea-level controls on the preservation of species-rich, shelf facies (*6*, *14*). In contrast, in data sets derived from tectonically active margins such as NZ, the sea-level signal may be obscured by regional or local tectonic effects (*12*). Although this conclusion appears self-evident, it has important implications for the compilation and interpretation of paleobiodiversity data. It is inappropriate to assume a single predictor or correction for the rock volume bias, such as a sea-level curve, across all regions, or to group data from different tectonic regimes within a single analysis. This caveat applies as much to regions that have changed tectonic regime through time as to geographically separated regions subject to different regimes. On a positive note, however, our results suggest that outcrop area may be a reasonably reliable estimator of the rock volume bias, irrespective of tectonic regime and in the absence of robust data on collection effort.

Table 1. Spearman's rank correlation coefficient (r_s) and Pearson's product-moment correlation coefficient (r) for the data shown in Fig. 2. An asterisk indicates values of r_s that are significant at the $P \leq 0.05$ level of confidence (*10*).

First differences	Raw data			
	Species	Collections	Outcrop	Formations
Species		$r_s = 0.748^*$ $r = 0.581$	$r_s = 0.660^*$ $r = 0.449$	$r_s = 0.321$ $r = 0.248$
Collections	$r_s = 0.396^*$ $r = 0.388$		$r_s = 0.736^*$ $r = 0.658$	$r_s = 0.442^*$ $r = 0.276$
Outcrop	$r_s = 0.082$ $r = 0.132$	$r_s = 0.508^*$ $r = 0.507$		$r_s = 0.354^*$ $r = 0.200$
Formations	$r_s = 0.241$ $r = 0.330$	$r_s = 0.266$ $r = 0.293$	$r_s = 0.011$ $r = 0.071$	

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15. The larger study of Cenozoic mollusc biodiversity, of which this is part, was conceived by J.S.C., A.G.B., and R.A.C. Mollusc species and paleoecological data were compiled by A.G.B., B.M., and P.A.M. into a database designed and managed by C.M.J. All other data were compiled by J.S.C., who also wrote the paper. R.A.C. contributed to the interpretation. We thank M. Rattenbury and I. Raine for assistance with FRED and geological map data extraction and R. Willink and D. Rhoades for statistical advice. The manuscript was reviewed by T. Naish, C. Hollis, M. Foote, and an anonymous referee. The research was supported by the Marsden Fund, administered by the Royal Society of New Zealand (contract GNS001).

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Materials and Methods
Table S1
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