

from the slab hydration source that permits refractory mantle to flow) that may have promoted the propagation of the CLSC to replace this system.

Spreading in the Lau back-arc basin is at present well-organized, as at mid-ocean ridges^{5,12}, but, as we have shown, the supply of magma is modulated by mantle wedge compositional controls and arc melt additions. Similar controls are indicated in the Mariana trough, even though the slab there is steeper, and rates of spreading and subduction are slower³⁰. In the northern Mariana trough¹⁶, the spreading centre varies from magmatically robust, to magma starved, to normal as it separates from the volcanic front, and in the southern trough the spreading centre changes from an axial valley to an axial high as it approaches the volcanic front³⁰. These variations in relative magma supply with proximity to the volcanic front are similar to those we report here for the Lau basin, and support the generality of our model of mantle wedge control on back-arc crustal accretion.

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The authors declare that they have no competing financial interests.

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Determinants of extinction in the fossil record

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The causes of mass extinctions and the nature of biological selectivity at extinction events are central questions in palaeobiology. It has long been recognized, however, that the amount of sedimentary rock available for sampling may bias perceptions of biodiversity^{1–7} and estimates of taxonomic rates of evolution^{5–8}. This problem has been particularly noted with respect to the principal mass extinctions^{5–12}. Here we use a new compilation of the amount of exposed marine sedimentary rock to predict how the observed fossil record of extinction would appear if the time series of true extinction rates were in fact smooth. Many features of the highly variable record of apparent extinction rates within marine animals can be predicted on the basis of temporal variation in the amount of exposed rock. Although this result is consistent with the possibility that a common geological cause determines both true extinction rates and the amount of exposed rock, it also supports the hypothesis that much of the observed short-term volatility in extinction rates is an artefact of variability in the stratigraphic record.

The highly variable rock record may distort the apparent timings of taxonomic origination and extinction both locally, at the outcrop scale, and globally, in taxonomic databases. For example, at outcrop and basin scales, principles of sequence stratigraphy imply that last occurrences of taxa should cluster artificially at temporal gaps and shifts in depositional environments that result from basin in-filling, eustatic sea-level variation, and crustal uplift and subsidence^{7,12–14}. To evaluate the relationship between global preservation potential, as reflected by rock availability, and the last sampled occurrences of taxa, we first compared the global, stage-level records of apparent genus extinction with our estimate of exposed marine rock (See Methods). Genus data are from Sepkoski's unpublished compen-

dium, and our measure of exposed rock is the number of marine sedimentary formations. The number of named formations is a useful proxy for the amount of rock because it reflects several relevant aspects of sampling, including exposed outcrop area (see Methods).

Figure 1 shows the stage-level records of genus extinction and the number of marine formations. The two time series are positively correlated in absolute value (Fig. 1a, $r = 0.304$) and when they are de-trended by analysing stage-to-stage changes (that is, first differences) in each (Fig. 1b, $r = 0.238$, $P = 0.056$). These correlations are weak, but there are important reasons to expect an imperfect relationship between the amount of rock and apparent extinction in the same time interval. Notably, many taxa that actually became extinct during an interval of time with a poor record are unlikely to be preserved during that interval and will therefore have spurious last occurrences, producing an artificially high extinction rate, in the

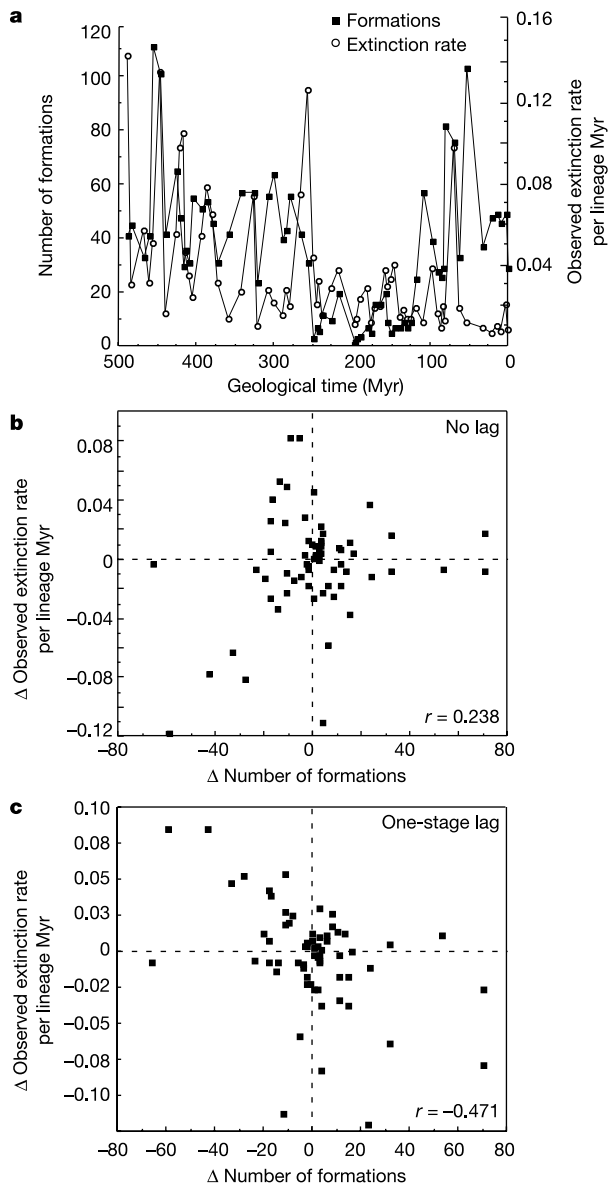


Figure 1 Observed extinction rate per lineage Myr (see Methods) and the number of marine formations in the combined data set. **a**, Time series. **b**, First differences (value for a stage minus the value for the previous stage) from **a**. **c**, Change in observed extinction rate from stage $i - 1$ to stage i versus change in amount of rock from stage i to stage $i + 1$. Myr, million years.

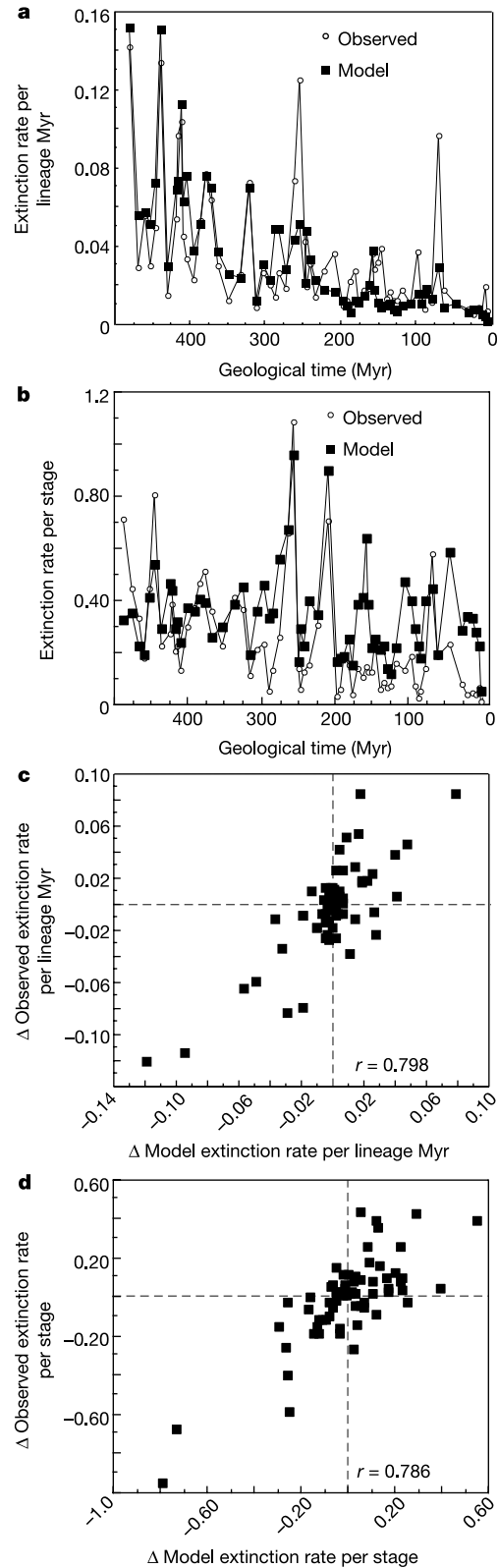


Figure 2 Observed extinction rates and predicted apparent extinction rates based on filtering a smooth extinction history through the empirically calibrated time series of preservation rates using the combined compilation. **a**, Time series for model with variable stage lengths and declining extinction rates. **b**, Time series for model with constant stage lengths and constant extinction rates. **c**, First differences from **a**. **d**, First differences from **b**. Correlations are significant ($P < 0.0005$) according to a formation randomization test. Observed extinction rates in **a** and **b** are identical, except that **a** expresses per capita rates per lineage Myr, whereas **b** expresses per capita rates per stage.

Table 1 Linear product-moment correlation coefficients

Formation compilation	Extinction model	Stage lengths	Recovery rate per formation (<i>R</i>)			
			<i>R</i> = 0.005	<i>R</i> = 0.01	<i>R</i> = 0.02	<i>R</i> = 0.04
Combined	Declining	Based on timescale	0.798	0.798	0.779	0.739
		Assumed constant	0.738	0.778	0.811	0.821
	Constant	Based on timescale	0.768	0.765	0.743	0.696
		Assumed constant	0.780	0.786	0.790	0.775
Lexicon*	Declining	Based on timescale	0.716	0.725	0.724	0.703
		Assumed constant	0.583	0.629	0.681	0.731
	Constant	Based on timescale	0.641	0.649	0.652	0.634
		Assumed constant	0.665	0.673	0.691	0.709
Literature†	Declining	Based on timescale	0.832	0.843	0.840	0.814
		Assumed constant	0.714	0.751	0.773	0.773
	Constant	Based on timescale	0.811	0.809	0.796	0.757
		Assumed constant	0.812	0.807	0.797	0.779

Data are product-moment correlation coefficients for de-trended empirical extinction rate time series and the predicted time series of extinction rates for different formation compilations, and for various model calibrations. The declining extinction model predicts true extinction rates that are equal to exponential fits to the empirical data. The constant extinction model assumes that rates are constant at the Phanerozoic mean. Stage lengths are assumed to be equal up-to-date calibrations^{27,28} or are assumed to be constant at unit duration. The probability of recovery per formation (*R*) was also allowed to vary. All correlations are significant at $P < 0.0005$ according to a formation randomization test.

* Taken from ref. 25.

† Taken from data published in the *Journal of Paleontology* and *Palaeontology* (see text for details).

preceding interval. Similarly, intervals with exceptionally good rock records will be preceded by artificially low extinction rates¹⁵.

To test the importance of this offset effect, we computed the correlation between the change in amount of rock from stage *i* to stage *i* + 1 versus the change in observed extinction rate from stage *i* - 1 to stage *i* (that is, first differences at a lag of one stage; Fig. 1c). As expected, this correlation is negative ($r = -0.471$, $P < 0.0001$) and stronger than that between the amount of rock and apparent extinction in the same stage. What is important to note in Fig. 1c is that substantial increases in observed extinction rate are generally followed by declines in exposed sedimentary rock, and major decreases in observed extinction rate tend to be followed by increases in exposed rock.

Although a negative correlation between extinction and preservation at a lag of one time interval constitutes *prima facie* evidence for artificial volatility in the extinction record, calculating correlations between the amount of rock and extinction rates does not

fully capture the potential effects of variability in the stratigraphic record. This is because the entire time series of the quality of preservation, as well as true variation in origination and extinction rates, affects the apparent extinction rate for each stage¹⁵. To assess the extent to which variation in extinction rates can be predicted by variation in the amount of rock, we therefore used a mathematical model to determine the expected pattern of extinction resulting from filtering a smooth extinction time series through the empirically calibrated time series of preservation. This model posits that true rates of extinction have varied smoothly over the Phanerozoic eon, and that observed volatility in extinction is partly an artefact of temporally heterogeneous preservation.

Figure 2 compares the empirical history of observed extinction rates with the model-predicted histories for two endmember models: one that assumes variable stage lengths and declining extinction rates (Fig. 2a, c), and one that assumes constant stage lengths and constant extinction rates (Fig. 2b, d). Within each endmember calibration, many features in the observed extinction data and the models agree. Although details of the model predictions vary, model–data correlations are similar for a wide range of model calibrations and for each compilation of formations (Table 1).

To test the statistical significance of the de-trended model–data correlations shown in Fig. 2 and Table 1, we generated null distributions of correlation coefficients by randomizing the formation time series and then recalculating the correlation between model and observations. Null distributions for the models shown in Fig. 2 are presented in Fig. 3. The null distribution for the variable stage-length scheme is not zero-centred. The offset reflects the shared timescale used to calculate both model and observed extinction rates. By contrast, the null distribution for the constant stage-length model is zero-centred. In every case, the observed formation data yield a correlation stronger than the distribution of 2,000 correlations generated by randomizing the formation data. Estimating the proportion of variance in apparent extinction rates that is potentially explained by the model would require knowledge of which model and which parameter values for that model are most realistic. Although these requirements cannot yet be met, we have shown results for a broad range of models and calibrations likely to represent reality. Regardless of the model assumed and the parameter values used to calibrate the model, the observed time series of formation numbers has a statistically significant ($P < 0.0005$) ability to predict variation in apparent extinction rate.

The extent to which deviations between our model and data reflect true biological anomalies, errors in Sepkoski's taxonomic data, inadequacies in our measure of rock quantity, and other

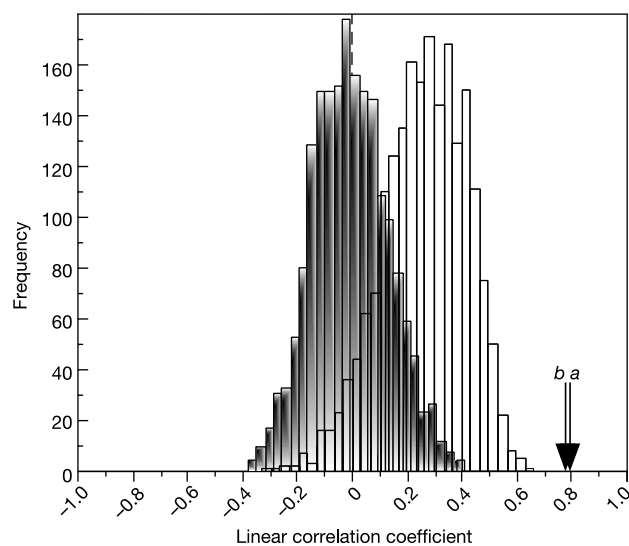


Figure 3 Null distributions of linear product-moment correlation coefficients generated by randomizing the combined formation time series. Open distribution shows model with variable stage lengths and declining extinction rates (a); shaded distribution shows model with constant stage lengths and constant extinction rates (b). Arrows indicate observed correlation coefficients, which are completely outside the range of their respective null distributions ($P < 0.0005$).

aspects of model calibration, is as yet unknown. Model results should therefore be interpreted as statistical descriptions of the potential effects of variable preservation on short-term volatility in apparent extinction rates, rather than as predictions of the absolute values of extinction rates. For example, whether the end-Permian (approximately 251 million years (Myr) ago) and end-Triassic (about 200 Myr ago) extinction peaks deviate from model predictions depends on whether true extinction rate is modelled as constant or declining (Fig. 2). Similarly, the scaling of the model–data relationship depends on the hypothesized time series of true extinction and the assumed per-formation probability of preservation. For the results shown in Fig. 2a, for example, the regression of de-trended observed rates on de-trended model rates has a slope of 1.04. Increasing or decreasing the assumed probability of preservation (see Methods) leads to a corresponding change in this slope. For the 48 model calibrations in Table 1, slopes range from 2.24 to 0.63, with a mean of 1.05 and a median of 0.91. Because the amplitude of variation in rates varies with model parameters, we choose to focus on the strength of the model–data correlation, which measures the agreement in the temporal pattern of rates. In this respect, our results are insensitive to model calibrations and to the hypothesized time series of extinction.

There are two explanations for the agreement between observed and model-predicted de-trended rates of genus extinction. The first is that the apparent volatility in extinction is largely spurious. Although our results suggest that there is an artificial overprint on the empirical data, some extinction events, such as the end-Permian, may involve a greater loss of genera than expected on the basis of known gaps in the record¹⁶. Despite the raw magnitude of such extinction events, it is possible that spurious termination of lineages by taxonomic practice, or pseudo-extinction, is prevalent near gaps in the stratigraphic record and at times of apparent increase in extinction rate¹⁷. Although the magnitude of pseudo-extinction at apparent mass extinctions is generally unknown, this effect would only serve to strengthen the artefact hypothesis.

The second explanation for the match between model and data is that a common cause affects both extinction and the amount of rock preserved and exposed at the Earth's surface. The most obvious candidate is sea level, a decline in which is expected to cause a drop in the number of preserved formations and potentially an increase in true extinction through the elimination of shallow marine habitats and overall reduction in habitable area^{18,19}. Although sea-level change may be a viable mechanism for extinction, the relationship between sea level, extinction, and preservation is potentially more complex than suggested by a simple common-cause hypothesis. For example, sea-level increase has been invoked as a causal agent of extinction through the spread of anoxic environments¹⁹, and increases in sea level can also have deleterious impacts on stratigraphic sampling⁷.

Regardless of the reason for the correlation, the agreement between observed rates of extinction and those predicted from stratigraphic data must affect our understanding of large-scale evolution in the Phanerozoic. If the correlation arises because the record has imposed a strong bias on fossil data, then the marine biosphere may have been substantially more stable than previously supposed. Testing this hypothesis and correcting biases in the record will be facilitated by additional work on sampling standardization²⁰, model-based fitting of rates²¹, phylogenetic standardization of taxonomy across stratigraphic boundaries¹⁷, and more complete, global compilations of the amount of sedimentary rock, its quality, and its stratigraphic context. If, instead, extinction rates and the amount of preserved sedimentary rock share a common cause, then our results may serve to constrain the mechanisms and timing of extinction, reducing the likelihood, for example, that bolide impacts^{22–24} are the principal cause of most extinction events.

Although we suspect that some extinction episodes may ultimately prove too severe to be explained entirely as stratigraphic artefacts, our analyses provide a measure of quantitative support for the hypothesis^{5,7} that a significant component of the observed variation in rates of genus extinction may be spurious. □

Methods

Marine formation data

We used ref. 25 to compile the number of named lithostratigraphic rock units in the United States and its territories for each of 77 conventional Phanerozoic stratigraphic intervals, principally stages, having an average duration of 7.1 Myr. Formation was chosen as the unit of sedimentary rock because it has a standardized definition (lithologically distinct and mappable at a scale of 1:24,000) and is not erected on the basis of fossil content. A total of 1,051 marine formations could be assigned to stratigraphic stages.

To supplement our compilation of formations from ref. 25 with world-wide data, we included a formation compilation derived by systematically surveying the palaeontological literature. This continuing survey currently covers data published over the past 10 years in the *Journal of Paleontology* and the past three years in *Palaentology*. Each marine formation was counted only once. When de-trending data by analysing stage-to-stage changes (that is, first differences), we find that the literature- and ref. 25-derived time series are positively correlated ($r = 0.751$, $P < 0.0001$). A total of 56.4% of 830 formations in the literature compilation and 27.5% of 1,700 formations in the combined compilation are from outside the United States. The de-trended time series of these formations outside of the United States is positively correlated with that for the United States-only formations from ref. 25 ($r = 0.456$, $P < 0.001$). Thus, our formation tabulations repeat similar patterns when compiled from different sources and for different geographical regions.

In addition to testing for agreement between formation compilations, we tested our data against independent estimates of global marine outcrop area. The Paleogeographic Atlas Project provided outcrop area data for 12 Mesozoic and Cenozoic stages. Area was measured as the number of equal-area grids occupied by at least one marine outcrop—grid size was 0.5×0.5 degrees at the equator, but other grid sizes yield similar results. The three formation compilations are positively correlated with global outcrop area (Spearman coefficients range from 0.752 to 0.813 and are significant at $P < 0.02$). In addition to providing an estimate of absolute outcrop area, formations may also reflect other relevant aspects of sampling including research effort and range of habitat preservation⁶.

Extinction data

We tabulated empirical rates of genus extinction using data on animals and animal-like protists from the global compendium of Sepkoski²⁶. In total, we used 30,379 marine genera with both first and last fossil appearances resolved at least to the stage level. Extinction was measured as the instantaneous, per capita rate of extinction per lineage per million years (lineage Myr)¹⁵. Stage lengths were based on a number of up-to-date sources^{27,28}. Because Cambrian formations could rarely be confidently assigned to stages using ref. 25, we present results only for the post-Cambrian Phanerozoic.

Extinction model

For the hypothesized declining extinction model, we fitted an exponential decline through the observed rates for the Palaeozoic era and again through the Mesozoic and Cenozoic eras²⁹. We chose to fit smooth curves to the observed data because the long-term empirical rate is expected to be approximately equal to the true long-term rate, no matter how biased short-term fluctuations may be by incomplete sampling¹⁵. This fitting procedure is an imperfect approximation, and the observed decline has even been claimed to reflect bias in taxonomic procedure³⁰. We nevertheless find consistent results if we ignore the long-term trend in extinction rates and assume that true extinction is constant at the Phanerozoic mean (Fig. 2 and Table 1). For simplicity, we assumed that origination and extinction rates are equivalent for each stage, but we obtain consistent results if we assume instead that origination rates are equal to their observed values.

We next used our formation data to derive a time series of instantaneous preservation rates per genus per Myr—by preservation we mean all events leading to the inclusion of a genus in a taxonomic database, including burial in sediments, collection and publication. We assumed a uniform probability of recovery per genus per formation. This is a simplification, but, provided that recovery probabilities vary stochastically over time, with or without a long-term trend¹⁵, this simplification should not bias our results. If R is the probability of recovery per formation, x is the rate of preservation per genus per Myr, F is the number of formations, and Δt is the duration of the stage, then $x = -F \ln(1 - R) / \Delta t$. This is because the probability that a genus ranging through a time interval will not be sampled is equal to $\exp(-x\Delta t)$ and to $(1 - R)^F$. Spreading a given number of formations over a longer interval of time therefore yields a lower rate of fossil recovery per unit time.

The value of R was chosen to yield a long-term average value of x comparable to those that have been empirically determined previously for the same genus data, namely about 0.05 per genus per Myr (ref. 21). However, correlation coefficients are consistent for a wide range of values of R (Table 1).

The goal of the forward model is to predict apparent rates of extinction given the temporal pattern of preservation and of hypothesized rates of origination and extinction. Let $p(T)$, $q(T)$ and $x(T)$ be time-specific rates of origination, extinction and preservation per genus per Myr, respectively. Consider an interval of time from $T = t$ to $T = t + \Delta t$.

Let X_b be the number of genera observed to cross the beginning boundary of the time interval, and X_{bt} be the number observed to cross both the beginning and terminal interval boundaries. Let N_b and N_{bt} be the corresponding true numbers. N_b is proportional to $\exp\{\int_0^t [p(T) - q(T)]dT\}$. If \bar{q} is the true mean extinction rate through the interval, then N_{bt} is equal to $N_b \exp(-\bar{q} \Delta t)$; thus $N_{bt}/N_b = \exp(-\bar{q} \Delta t)$ and $\bar{q} = -\ln(N_{bt}/N_b)/\Delta t$. The corresponding apparent rate of extinction is equal to $-\ln(X_{bt}/X_b)/\Delta t$. X_b and X_{bt} can be predicted from N_b and N_{bt} and the probabilities of being preserved before and after a given boundary, which in turn depend on the time series of $p(T)$, $q(T)$ and $x(T)$. A more detailed explanation of the model is given in ref. 15, and model source code is provided in the Supplementary Information.

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Patterns of colonization in a metapopulation of grey seals

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The colonization of a new habitat is a fundamental process in metapopulation biology¹, but it is difficult to study. The emigration of colonists from established populations might be induced by resource competition owing to high local population density^{2,3}. Migration distances are also important because they determine the frequency and scale of recolonization and hence the spatial scale of the metapopulation⁴. Traditionally, these factors have been investigated with demographic approaches that are labour-intensive and are only possible in amenable species. In many cases, genetic differentiation is minimal, preventing traditional genetic approaches from identifying the source of colonists unambiguously. Here we present a bayesian approach that integrates genetic, demographic and geographic distance data. We apply the method to study the British metapopulation of grey seals, which has been growing at 6% per year over the last few decades⁵. Our method reveals differential recruitment to three newly founded colonies and implicates density-dependent dispersal in metapopulation dynamics by using genetic data.

One-third of the world population of grey seals breeds at about 50 colonies around the British Isles, mostly on offshore islands to the north and west of Scotland. Although the population is growing exponentially, individual colonies exhibit diverse dynamics, including fluctuation around a long-term trend, exponential or logistic increase, decrease to extinction and a few recent colonizations. Grey seals breed colonially in autumn. Each female's single offspring is recruited to the adult population at the age of 5–7, and females seem to show strong philopatry⁶. The Orkney Isles (Fig. 1) comprise

Table 1 Inferences for contribution of sources to founding groups, x

Source	Mean percentage contribution (confidence interval)		
	Stromsay	Copinsay	Calf of Eday
Faray	14.91 (5.44, 26.57)	22.06 (7.55, 41.68)	24.54 (9.90, 43.28)
Holm of Huip	32.57 (17.61, 48.65)	14.03 (5.30, 25.03)	12.85 (3.65, 23.57)
Holm of Spurness	25.63 (13.08, 39.27)	17.52 (7.14, 29.00)	20.64 (9.70, 34.94)
Muckle Greenholm	12.14 (1.64, 23.34)	21.29 (9.79, 35.31)	13.59 (4.67, 24.30)
Ruskholm	9.52 (2.68, 18.15)	8.63 (1.80, 17.65)	11.59 (3.03, 20.95)
Stroma	2.57 (0.00, 13.19)	7.89 (1.42, 16.83)	7.72 (0.01, 20.21)
Swona	2.66 (0.00, 12.83)	8.58 (0.18, 18.98)	9.07 (0.03, 24.75)

Confidence intervals correspond to the 95% equal-tailed intervals of the posterior distributions for x.