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Evolutionary speed limits inferred from the fossil record

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The dynamics of extinction and diversification determine the long-term effects of extinction episodes¹. If rapid bursts of extinction are offset by equally rapid bursts of diversification, their biodiversity consequences will be transient. But if diversification rates cannot accelerate rapidly enough, pulses of extinction will lead to long-lasting depletion of biodiversity^{2,3}. Here I use spectral analysis of the fossil record to test whether diversification rates can accelerate as much as extinction rates, over both short and long spans of geological time. I show that although the long-wavelength variability of diversification rates equals or exceeds that of extinctions, diversification rates are markedly less variable than extinction rates at wavelengths shorter than roughly 25 million years. This implies that there are intrinsic speed limits that constrain how rapidly diversification rates can accelerate in response to pulses of extinction.

To measure how fossil extinction and origination rates fluctuate across different timescales, I used spectral analysis methods^{4,5} specially designed for unevenly spaced data such as the fossil record. Spectral analysis decomposes a time series into its component frequencies and measures each of their amplitudes (expressed as their square, the spectral power). My source data are Sepkoski's compilations of Phanerozoic fossil marine animal families⁶ and genera⁷. Because the suitability of different extinction and origination metrics is sometimes disputed^{8,9}, I analysed all four that are in common use: (1) counts of first or last occurrences per stratigraphic interval; (2) counts per million years (counts in each stratigraphic interval, divided by interval length); (3) percentages per interval (counts divided by total diversity); and (4) percentages per million years (counts divided by total diversity and interval length). This yields a total of eight data sets (two taxonomic levels times four metrics) for both extinctions and originations.

Spectral analysis shows that across all eight data sets, extinctions and originations have fundamentally different scaling behaviour (Fig. 1; and Supplementary Information). From the shortest resolvable timescale (~10 Myr, twice the average sampling interval) to the longest (~500 Myr, the length of the data set), the spectral power of extinction rates usually lies within the confidence limits for white noise, as estimated by randomly shuffling and re-analysing the

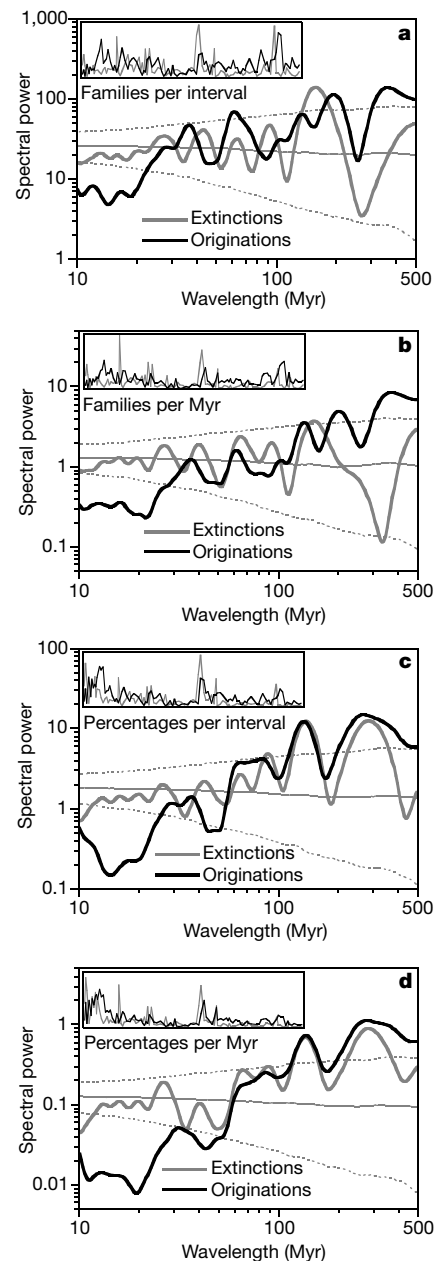


Figure 1 Fourier power spectra for extinction and origination rates of fossil marine families. Four different metrics were used: families per stratigraphic interval (a) and per million years (b), and percentages of total diversity per stratigraphic interval (c) and per million years (d). Insets show the raw time series. Spectra are smoothed over a window spanning 5% of the width of each plot. Fine lines are the median and 90% confidence limits for spectral power of random white noise at each wavelength, estimated by repeating the same analysis on 10,000 random re-shuffles of the original extinction data. Spectral power is the square of amplitude at each wavelength; thus, the relative placement of extinction and origination spectra is not arbitrary. Origination rates have markedly lower spectral power than extinction rates at wavelengths less than roughly 25 Myr, indicating that they are much less variable over short timescales. Spectra for genera are similar (see Supplementary Information).

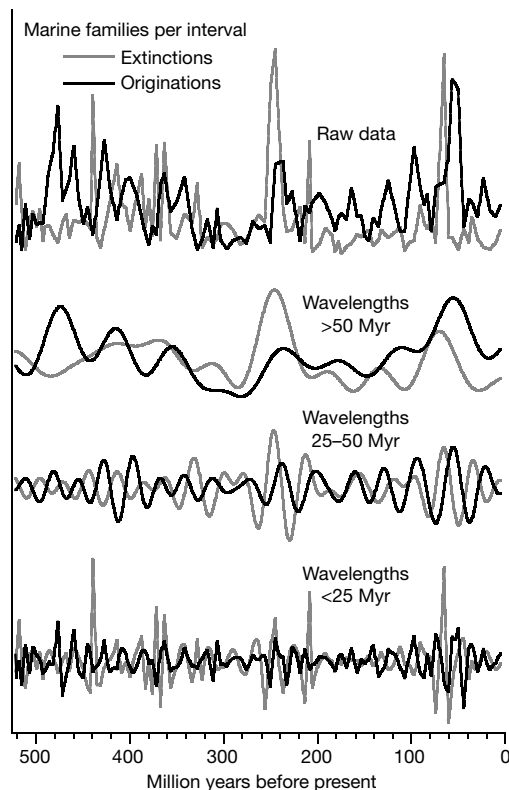


Figure 2 Fossil extinction and origination rates, separated into long-wavelength (> 50 Myr), intermediate-wavelength (25–50 Myr) and short-wavelength (< 25 Myr) components by Fourier filtering²⁶. Long-wavelength variations in origination and extinction rates are similar in size, but short-wavelength fluctuations in extinction rates are

larger and more abrupt than those in origination rates. Counts are shown of fossil marine families originating or going extinct in each stratigraphic interval; plots for other extinction and origination metrics are similar (see Supplementary Information).

original data. (Extinction rates that are expressed as percentages of total diversity have greater spectral power than expected by chance at wavelengths greater than 100 Myr, but this may reflect long-wavelength patterns resulting from changes in diversity through time, rather than long-term patterns in extinction rates *per se*.)

Compared with extinction rates, origination rates (Fig. 1, black lines) have equal or greater spectral power at long wavelengths (> 100 Myr), but much lower spectral power at short wavelengths (< 25 Myr). That is, origination rates fluctuate less than extinction rates over short timescales, even though over long timescales they fluctuate as much as, or more than, extinction rates. Fossil origination rates are known to vary less than extinction rates^{9,10}. My analysis shows that this results from the markedly lower short-term variability of originations, because on longer timescales origination rates vary at least as much as extinction rates do.

The average spectral power in the 10–25-Myr wavelength band is

3.4 times lower for origination rates than for extinction rates (averaged across the eight data sets), implying that short-wavelength fluctuations are 1.8 times smaller in originations than in extinctions. This difference in fluctuation scaling can also be seen in the statistics of the time series themselves. Across the eight data sets analysed here, origination rates are 30% higher, on average, than extinction rates (consistent with the overall growth in diversity through time), but are a factor of 1.6 less variable between adjacent stratigraphic intervals (Table 1). Furthermore, the greatest increases in origination rates from one stratigraphic interval to the next are a factor of 2.3 smaller, on average across the eight data sets, than the greatest increases in extinction rates (Table 1). Thus, by several different measures, origination rates show substantially less short-term variability than extinction rates.

The difference in scaling behaviour between originations and extinctions can be visualized by using Fourier filtering to separate

Table 1 Fossil origination and extinction rate statistics

Taxonomic level and metric	Average rates			Rate changes (r.m.s.)*			Maximum increases†		
	Ext.	Orig.	Ratio	Ext.	Orig.	Ratio	Ext.	Orig.	Ratio
Families									
per interval	25.1	34.8	0.72	34.5	22.8	1.5	130	54	2.4
per Myr	5.3	7.1	0.74	39.7	20.8	1.7	32.8	8.9	3.7
% per interval	6.0	7.8	0.78	37.7	29.7	1.3	19.0	18.8	1.0
% per Myr	1.4	1.7	0.81	9.1	7.7	1.4	6.4	4.1	1.6
Genera									
per interval	149	197	0.76	1,049	787	1.6	900	396	2.3
per Myr	30.4	39.2	0.78	228.8	145.4	1.7	192.0	77.3	2.5
% per interval	13.4	16.0	0.84	60.8	42.6	1.6	38.8	25.0	1.6
% per Myr	2.9	3.4	0.86	16.9	12.8	1.6	14.1	6.0	2.4

* Root mean-square average of changes in rates between adjacent stratigraphic intervals.

† Maximum increase in rates from one interval to the next. Ext., extinctions; Orig., originations.

the original time series' fluctuations into specified ranges of wavelengths (Fig. 2; and Supplementary Information). Fluctuations in originations and extinctions are generally similar in amplitude (although they often do not coincide in time) at wavelengths longer than 25 Myr (Fig. 2). But at wavelengths shorter than 25 Myr, extinction rates show large, abrupt fluctuations that are not observed in origination rates.

Whereas the power spectra of extinction rates generally lie within the confidence limits for random white noise, the power spectra of origination rates generally lie well outside those confidence limits at wavelengths shorter than about 25 Myr (Fig. 1; and Supplementary Information). The log-log slopes of the extinction power spectra are generally small, and often statistically indistinguishable from white noise, whereas the log-log slopes of the origination power spectra are markedly steeper, and statistically highly significant (Table 2). The coarseness of the stratigraphic timescale makes it impossible to measure accurately fluctuations on wavelengths shorter than about 10 Myr (see Methods), but if the scaling trends shown in Fig. 1 were to continue at shorter wavelengths, they would imply that the discrepancy between short-term fluctuations in originations and extinctions should grow as the temporal resolution becomes finer.

Why are diversification rates less variable than extinction rates over short timescales? Uneven preservation and sampling through geological time^{11,12} should affect measurements of origination and extinction rates to similar degrees, and thus are unlikely to account for origination rates' markedly smaller short-term variability. Instead, this phenomenon implies either that the processes regulating originations have more inertia than those driving extinctions, or that origination events tend to be diverse and local, whereas extinctions (particularly mass extinctions) tend to be coherent and global^{19,13,14}. If extinctions are driven primarily by external shocks^{2,15} they are unlikely to be intrinsically rate-limited, whereas originations of new taxa may be limited by sparse opportunities for reproductive isolation and thus speciation. Alternatively, the process of diversification may be inhibited by harsh environmental conditions during and after extinction events², or by biotic disruptions resulting from the extinctions themselves³. To the extent that extinctions entail the collapse of niches rather than the emptying of them, they restrict opportunities for future diversification^{16,17}. Furthermore, the dynamics of evolutionary ecology are likely to be intrinsically asymmetrical; the web of ecological relationships that supports a collection of organisms may be constructed gradually, but then collapse rapidly as its component species are lost. These evolutionary mechanisms may help to explain the greater short-term inertia of origination rates as compared with diversification rates.

These results imply that evolutionary responses to extinction events are constrained by intrinsic speed limits. It has been shown previously that evolutionary responses to extinction events are delayed in time¹⁶; the current analysis shows that they are also strongly damped in amplitude. Although some groups of fossil taxa

radiate rapidly after extinction episodes^{1,13,18}, this analysis indicates that the overall response by origination rates is attenuated, and thus biodiversity is slow to recover. If the continuing anthropogenic extinction episode^{19–21} turns out to be comparable to those in the fossil record (which is not yet clear^{22,23}), my analysis shows that diversification rates are unlikely to accelerate enough to keep pace with it. Thus, widespread depletion of biodiversity would probably be permanent on multimillion-year timescales. □

Methods

Spectral methods

Conventional Fourier methods should not be applied to the fossil record, because its stratigraphic boundaries are unevenly spaced in time. Nor should one simply even out the spacing by interpolating within each stratigraphic interval, because this introduces artefactual correlation among the interpolated points^{24,25}. Instead, I used the date-compensated discrete Fourier transform⁴ and the Lomb-Scargle Fourier transform⁵, two algorithms that have similar statistical behaviour to the conventional Fourier transform, but can be applied directly to unevenly spaced data. Both techniques yielded similar results. Each spectrum was smoothed over a window spanning about 5% of the width of the spectrum plots; this reduces the noise in the spectrum, but preserves the average spectral power at each wavelength. This is appropriate because my analysis concerns the broadband spectral properties of the fossil record rather than narrow spectral peaks, such as would be used to identify periodicities. I limited my analysis to wavelengths longer than 10 Myr (corresponding to the Nyquist frequency), because tests with synthetic non-stationary data sets show strong aliasing at shorter wavelengths.

Source data

I used Sepkoski's compilations of fossil marine invertebrate families⁶ and genera⁷, with updates through 1997. Sepkoski aggregated some stratigraphic stages and subdivided others, making his stratigraphic intervals more uniform, and thus more suitable to spectral analysis, than the conventional stratigraphic timescale. I excluded the first few intervals (> 525 Myr ago), in which total diversity is so low that the per-taxon metrics are anomalously high. I also excluded all taxa that occur in only one stratigraphic interval to minimize Lagerstätten and monographic effects⁷. I assigned all originations in a given interval to the stratigraphic boundary that begins it, and all extinctions to the stratigraphic boundary that ends it; other possible assignments (for example, to the midpoint of each interval) give similar results.

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Table 2 Log-log slopes of fossil power spectra

Taxonomic level and metric	Power-law slope	
	Extinctions	Originations
Families		
per interval	0.04	0.73**
per Myr	-0.09	0.89***
% per interval	0.42*	1.15***
% per Myr	0.54*	1.37***
Genera		
per interval	0.30	0.94***
per Myr	0.27	0.93***
% per interval	0.35	0.94***
% per Myr	0.52*	1.08***

Statistical significance levels were estimated by repeating the same analysis on 10⁴ randomly reshuffled copies of each data set: *P < 0.05, **P < 0.01, ***P < 0.001.

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Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra

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Ecologists have long been intrigued by the ways co-occurring species divide limiting resources. Such resource partitioning, or niche differentiation, may promote species diversity by reducing competition^{1,2}. Although resource partitioning is an important determinant of species diversity and composition in animal communities³, its importance in structuring plant communities has been difficult to resolve⁴. This is due mainly to difficulties in studying how plants compete for belowground resources⁵. Here we provide evidence from a ¹⁵N-tracer field experiment showing that plant species in a nitrogen-limited, arctic tundra community were differentiated in timing, depth and chemical form of nitrogen uptake, and that species dominance was strongly correlated with uptake of the most available soil nitrogen forms. That is, the

most productive species used the most abundant nitrogen forms, and less productive species used less abundant forms. To our knowledge, this is the first documentation that the composition of a plant community is related to partitioning of differentially available forms of a single limiting resource.

Species-rich plant communities seemingly contradict the competitive exclusion principle, a fundamental tenet of ecology that predicts that species occupying the same niche cannot coexist, or that the number of species cannot exceed the number of limiting resources^{6,7}. Plants have nothing comparable to the 'food niche' of animals. At the global level the 300,000 terrestrial plant species may have only 20 different limiting resources (light, water, CO₂ and the same set of mineral nutrients), and field experiments indicate that at most three or four resources are limiting in any plant community². Consequently, some assert that resource partitioning is unimportant in maintaining species diversity in plant communities^{8,9}.

We studied tussock tundra in arctic Alaska where plant growth is primarily limited by soil nitrogen availability¹⁰. Despite this shared limitation, species with graminoid, deciduous shrub, evergreen shrub, cryptogam and forb growth forms typically co-occur in tussock tundra at scales of less than 0.1 m² (ref. 11). This 'paradox of diversity' could be resolved if variations in resource acquisition in space and time among plant species lead to resource partitioning¹², thereby allowing coexistence on a single limiting resource. There is abundant evidence that tundra plant species differ in rooting depth¹³, phenology¹⁴, and uptake preferences for different chemical forms of nitrogen (ammonium, nitrate and a variety of free amino acids)^{13,15}. Similar interspecific differences have been observed for many other plant communities^{12,16,17}. However, evidence that such differences contribute to resource partitioning within communities is limited¹⁸.

We used ¹⁵N-tracers in tussock tundra at Toolik Lake, Alaska (68° 38' N, 149° 34' W, elevation 760 m), to address two questions: how are species spatially, temporally and chemically differentiated in their use of soil nitrogen and are such niche differences consistent with community structure? We hypothesized that if niche differentiation reduces competition for soil nitrogen, its signature should be evident in patterns of species dominance (productivity). That is, dominant species should use the most available forms of soil nitrogen and subordinate species less available forms.

Soluble nitrogen fractions in tundra soils vary seasonally and are strongly dominated by organic forms, including free amino acids, with lower concentrations of ammonium and nitrate¹⁹. To trace how tundra species differ in uptake of different soil nitrogen sources, we injected three chemical forms (ammonium, nitrate and glycine) of ¹⁵N-labelled nitrogen at two soil depths (3 and 8 cm) twice (24 June and 7 August) in a growing season. Separate 1.5 m × 1.5 m plots were used for each of the 12 treatment combinations of chemical form, depth and time (3 × 2 × 2 factorial design). For each of the five most abundant vascular plant species (Table 1), we measured ¹⁵N tracers in aboveground tissues seven days after treatment for replicate plants (*n* = 3 to 6) in each plot. Uptake of the form of available nitrogen corresponding to the ¹⁵N label in each treatment

Table 1 Plant species analysed for uptake of ¹⁵N in tussock tundra at Toolik Lake, Alaska

Species*	Growth form	Peak aboveground biomass (% of community total)†	Aboveground net primary production (% of community total)‡
<i>Carex bigelowii</i>	Graminoid	1 ± 1	3 ± 1
<i>Eriophorum vaginatum</i>	Graminoid	19 ± 6	40 ± 14
<i>Vaccinium vitis-idaea</i>	Evergreen shrub	18 ± 3	10 ± 2
<i>Ledum palustre</i>	Evergreen shrub	32 ± 4	16 ± 2
<i>Betula nana</i>	Deciduous shrub	19 ± 5	16 ± 4

* The five species described here accounted for 89% of total community aboveground biomass and 84% of net primary production. Of the 15 vascular plant species we found in this community, these were the only species that occurred in all 12 treatments. There were an average of seven vascular species per quadrat within the 20 cm × 20 cm control quadrats used to measure biomass and productivity. On average, four out of the five species in Table 1 occurred in the same quadrats. Species' root systems were closely intertwined within the organic soil layer.

† Peak (August) total aboveground vascular plant biomass = 348 ± 30 g dry weight per m².

‡ Total aboveground vascular plant net primary production = 163 ± 21 g dry weight per m² per yr. Data are shown ± 1 standard error.