Reconciling taxon senescence with the Red Queen's Hypothesis

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In the fossil record, taxa exhibit a regular pattern of waxing and waning of occupancy, range or diversity between their origin and extinction. This hat-like pattern is well established for species, genera and higher taxa of terrestrial mammals[1,2,3], marine invertebrates[4,5,6], marine micro-organisms[7], and recently living Hawaiian clades of animals and plants[8]. This pattern appears to contradict the Law of Constant Extinction[9], which states that the probability of a taxon's extinction is independent of its age. Here we show that the apparent contradiction between stochastically constant extinction and the seemingly deterministic "hat" pattern disappears when we consider the peak of taxon's expansion rather than its final extinction. To a first approximation we find that biotic drivers of evolution pertain mainly to the peak, abiotic drivers mainly to the extinction of taxa. The Red Queen's Hypothesis[9], one of the most influential ideas in evolutionary biology since Darwin, was originally proposed as an explanation of the Law of Constant Extinction. Much effort has since been devoted to the question how this hypothesis, emphasizing biotic interactions, relates to the effects of environmental change. Often, biotic and abiotic processes have been thought to operate at different scales[10]. Our results suggest that a more informative focus is the phase of a taxon's history, from origination via peak occupancy to decline and extinction.

Leigh Van Valen discovered the Law of Constant Extinction[9] when he wanted to show that the probability of extinction increases with taxon age and found instead that it does not. Meanwhile, the discovery that taxa tend to have rising and falling occupancy, range or diversity trajectories, with typically a single peak between origination and extinction, seems to suggest that their probability of extinction does in fact depend on age, or at least that the time of extinction is somewhat deterministic. This pattern has by now been documented independently for multiple groups and taxonomic levels[1,2,3,4,5,6,7]. Superficially, this seems to suggest that the probability of taxon extinction both depends on age and is independent of it, which is absurd. And even if the dynamics of taxon's history are often more complex[11] than the formulation of the Law might suggest, there is still an urgent need to delve deeper in order to clarify this question at the heart of evolutionary biology and macroevolution.

This question is best approached by considering evolutionary success or failure as a process rather than as points in time. Extinction simply marks the end of the process: if "death and extinction are the extreme case of negative expansion, all of evolution can be considered as sustained differential expansion"[12] (p. 183). The Red Queen's hypothesis can thus be interpreted as a statement about competition for expansive energy – energy used for growth and reproduction[13].

Accumulating evidence shows that hat-like trajectories over the history of species or higher taxa, quantified as site occupancy[1,4,7], geographic range[5,6] or clade diversity[2], are, while not universal, persistently common at least in the fossil record of mammals[1,2,3], marine invertebrates[4,5,6], and marine plankton[7].

Random-like patterns are commonly observed in the fossil record[14,15,16,17,18] but explaining them has until recently not been perceived as fruitful and explanations remain few, as recent surveys show[17,18]. Pigot et al.[16] observed that a random walk model is able to generate the full spectrum of empirically observed age-area relationships, in other words, that a stochastic process is expected to produce patterns that are somewhat predictable with respect to taxon age and occupancy. We suggest that the patterns observed in the fossil record are difficult to distinguish from random walk because, as already suggested by the Red Queen's hypothesis in its original form, evolutionary processes actually do involve stochastic processes: "The probability of extinction of a taxon is then effectively independent of its age. This suggests a randomly acting process"[9] (p.17). Therefore, hat-like patterns are actually what we should expect to see in fossil record due to a stochastic process, such as the process described by the Law of Constant Extinction and the Red Queen's hypothesis.
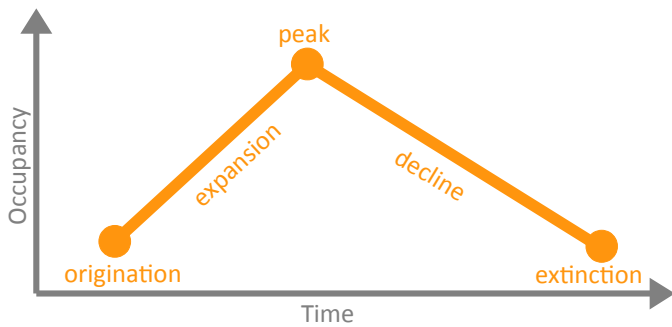
Figure 1: The "hat" pattern over a taxon's history in the fossil record. Conceptually, a taxon's history can be considered as containing five distinct phases: origination, expansion, peak, decline, and extinction. The observed trajectories are typically monotonic in expansion and decline with a clearly expressed peak.

A simple random walk model is likely to produce area-age trajectories with multiple peaks as depicted in Figure 2a, since at any point the chances for a taxon to expand or contract would not depend on the past trajectory. In reality, however, traits have history and they cannot be changed radically over a single time step. The concept of building upon already existing characteristics is known in evolutionary biology as phylogenetic inertia[19]. Regardless of whether such inertia is regarded as a result of constraints on adaptation or as an expected outcome of natural selection, it confers to the system a memory-like property. If we add memory to the random walk model, such a correlated random walk model will produce highly unimodal patterns, as illustrated in Figure 2b. By memory we mean that if a taxon expanded in the previous time step, it is more likely to expand in the next time step, as due to phylogenetic inertia under a similar environmental regime. Such correlated random walk models have been widely used for modelling animal dispersal[20] and could also explain how hat-like patterns of taxon's history can be produced by a stochastic-looking evolutionary process.

With a plain random walk, model taxa could potentially expand to infinity, because there are no limits on the available resources. In reality, if resources were unlimited, there would be no competition, and in turn no natural selection. If we add to the correlated random walk model a property that the probability of expanding or contracting depends on how many other taxa or individuals are already there, such a model would produce deterministic-looking patterns, mostly unimodal as in examples in Figure 2b,c.

In these random walk models, the intensity of competition under given environmental conditions modify the probabilities of expansion and contraction. Under environmental pressure (abiotic forcing), the population size trajectories of taxa are expected to synchronize with environmental changes in their expansions, peaks and declines, as shown in Figure 2d. Under competition pressure (biotic forcing), the trajectories are expected to synchronize with the intensity of competition. We may therefore ask an empirical question of the fossil record: to what extent does temporal clumping of the trajectories relate to competition, or environmental change, or both?

Ever since Darwin raised the issue in the Origin[21] it has been widely recognized that both biotic and abiotic factors have a role in shaping evolution[10,22,23,24,25,26,27], and that relative roles of biotic and abiotic factors may differ at speciation and extinction. Here we place both biotic and abiotic forces into the perspective of expansion as the main measure of a taxon's success, to analyse the respective roles of those forces over their history: origination, peak and extinction. For this three-point analysis the trajectories do not necessarily need to be unimodal, as unimodality is just the simplest arrangement of the phases of a taxon's existence, while points of origination, the last peak and extinction are omnipresent. In this context we analyse correlations of evolutionary rates with competition as a biotic factor and environmental change as an abiotic factor in the fossil record of large mammals. Our analysis covers North America and Europe at continental scales, as well as a region in Africa (the Turkana Basin).
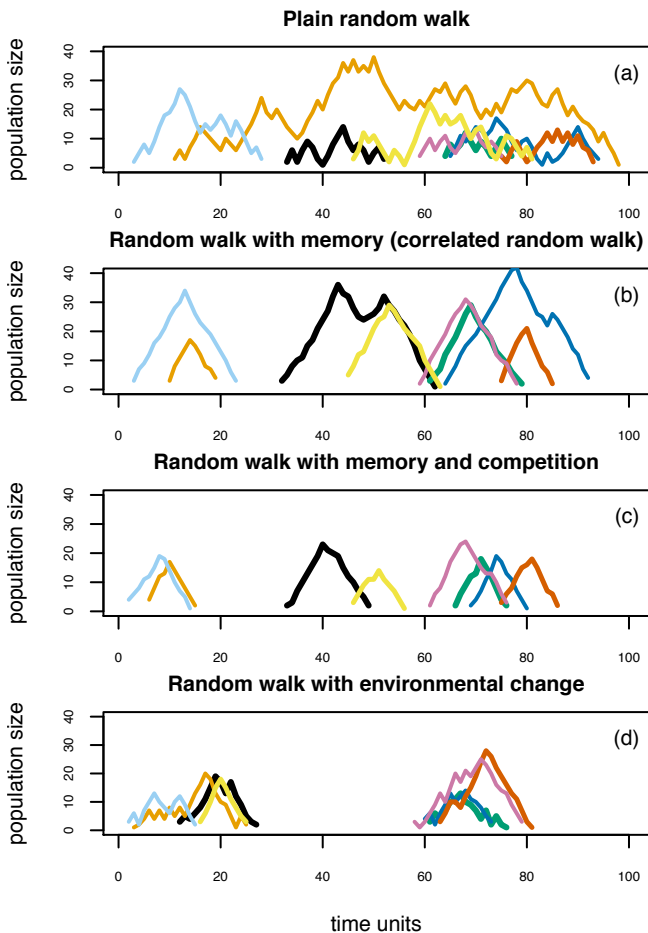
Figure 2. Variations in patterns of population size over time with different random walk models, examples of synthetically generated data: (a) plain random walk, (b) random walk with memory, (c) random walk with memory and competition, (d) random walk with environmental change. The protocols for each model are described in the Methods supplement. Each colour represents a different taxon. For each model we display eight randomly selected trajectories per panel, given that taxa go extinct within the observed time and the cumulative population size exceeds 80. Very short lived taxa are not shown.

We form the proxies for evolutionary rates, competition and environmental change from the fossil record in the following way. The extinction rate is defined as the number of last appearing genera over the total number of genera seen at a time unit. The origination rate is defined as the number of genera that first appear over the total number of genera seen at a time unit. The peak rate is defined as the number of genera at the peak of their site occupancy at all times divided by the total number of genera seen at a time unit. The occupancy is measured as the number of localities where a genus is found at a time unit over the total number of localities at this time unit. We measure the intensity of competition as the average number of genera per locality, following common reasoning[6,24], and environmental change via mean hypsodonty of co-occurring species as a proxy for net primary productivity[28,29]. These independently derived local proxies allow us to directly compare environmental changes at the localities in question.

For interpreting the analyses of the fossil record it would be helpful to compare with a baseline where biotic and abiotic forces do not operate, or operate independently of the faunal lists. A baseline without limiting forces would not be informative, because without limits on resources species would keep expanding and there would be no extinctions. A more informative baseline is a random walk model (like in Figure 2a), which is already an approximation of the fossil record, in line with the Red Queen's hypothesis and empirical tests[16]. In such a synthetically generated fossil record the limiting forces are unidentified.

Comparing to this baseline allows us to attribute forces found in the fossil record as biotic or abiotic. The baseline correlations are given in Table 1. Our proposition that the start of decline from the peak in the taxon's history should be competition-dominated, while the final extinction should be more due to environmental change, is well supported by observed correlations being far stronger than in the baseline, as presented in the table.

In the random walk model the relations of origination and extinction to competition are negative because the competition index grows, due to lack of pressure on the population size. This is what we would expect in the fossil record if resources were unlimited, under no competitive pressure. Extinction and environmental change are weakly correlated because when some taxa go extinct, mean hypsodonty of the affected locations changes slightly. Observing correlations above those modelled would indicate that taxa with particular traits in relation to the environment are more likely to go extinct, suggesting the operation of abiotic drivers. Because of the small number of time units sampled in the baseline model, there is weak residual correlation of the peak with competition.

Table 1. Correlations between rates of evolution, competition and environmental change proxies in the synthetic data and in the fossil data. Synthetic data shows the average over 10000 runs using a baseline random walk model, standard deviations are in brackets. In the fossil data the correlations that exceed the random walk model by more than one standard deviation are highlighted in bold. The columns corresponding to the main argument that the peak is more related to competition, while the end is more related to environmental change, are highlighted in grey.

	Competition-Origination	Environment-Origination	Competition-Peak	Environment-Peak	Competition-Extinction	Environment-Extinction
Synthetic data						
50 time units	-0.42 (0.13)	0.18 (0.15)	-0.07 (0.12)	0.05 (0.15)	-0.30 (0.13)	0.17 (0.15)
18 time units	-0.24 (0.23)	0.13 (0.24)	0.18 (0.20)	0.01 (0.24)	-0.14 (0.23)	0.12 (0.24)
13 time units	-0.21 (0.28)	0.12 (0.29)	0.23 (0.24)	0.01 (0.29)	-0.10 (0.28)	0.11 (0.29)
6 time units	-0.15 (0.43)	0.10 (0.44)	0.32 (0.39)	0.00 (0.45)	-0.02 (0.44)	0.09 (0.45)
Fossil data						
N. America (18)	-0.32	0.26	**0.48**	0.10	**0.11**	**0.55**
Europe (13)	-0.15	0.28	**0.86**	0.14	**0.47**	**0.63**
Turkana (6)	**0.32**	**0.62**	**0.87**	**0.90**	**0.78**	**0.65**

The results suggest that extinction primarily relates to environmental change, but a relation to competition is also strongly present. In all three datasets the relations to environmental changes are similar, whereas the relations to intensity of competition vary. The weakest competition is seen for North America, Europe is intermediate, while the strongest is seen for Turkana.

Across all the datasets the peak is competition-dominated and the relation to competition is at a similar level. The peak is the maximum point of a taxon's expansion and in extreme cases it may even coincide with origination or extinction. This result is consistent with the Law of Constant Extinction[9], where extinction is seen to be effectively independent of a taxon's age. The only condition is that it is the start of the decline rather than the extinction itself that shows this relationship.

Figure 3 conceptually summarizes the findings. The relations agree with those found in a study of Cenozoic plankton[25], showing that speciation is more strongly shaped by diversity dependence than by climate change, whereas the reverse is true for extinction. These findings are fully supported by a recent analysis of Hawaiian clades of animals and plants[8], which shows that when the islands reach maximum size the environment is no longer expanding, and thus competition increases in importance as species richness increases. Our findings are also in line with the analysis of large mammal extinctions[2], which shows that during growth there is an increasing pressure from competition. The time of peak genus richness is the time of maximum competition, when the diversity equals the carrying capacity. The role of the environment then increases as the carrying capacity continues to decay.
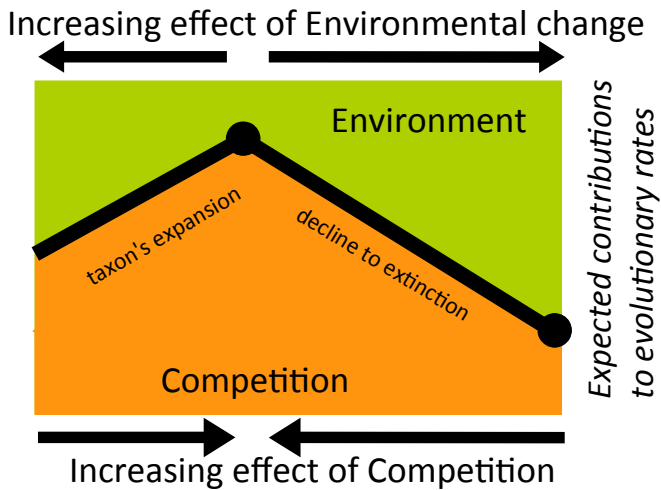
Figure 3. Conceptual representation of the relationship of taxon's history to evolutionary drivers. The success or failure of taxa in their prime is strongly competition-driven, at the end of their existence taxa are more exposed to environmental forcing. Both forces are shown equal at origin, reflecting uncertainty about their relative weight. Note that the axes are arbitrary and not intended to show precise proportions.

The correlations at origination indicate both competition and environmental change, although these relations are the least consistent across datasets and, at least in North America and Europe, appear quite close to the random baseline. It may well be that origination occurs more due to random circumstances (such as emergence of novel traits) than in relation to either biotic or abiotic factors. Answering this will require substantial further investigation.

Interestingly, Turkana shows an exceptionally strong positive relation of origination and extinction to environmental change. Turkana differs from the other datasets not only in covering less time but also in having the smallest spatial extent. Evolutionary trends have been shown to be driven by common species[30,31], and the average intensity of competition computed over all localities within a time unit is therefore expected mainly to reflect what forces the most common species are exposed to. We may therefore expect to see the closest relation between extinction and competition in Turkana, where localities are tightly packed and genus ranges typically cover the entire area. At smaller spatial scales extinction is also more likely to be a local population phenomenon and can therefore be faster and more related to competition than to the drawn-out process of full genus extinction.

Based on the modelling results and analysis of fossil data we propose that the Red Queen's hypothesis, emphasizing the role of competition in driving evolutionary rates, primarily relates to the peak in occupancy over the taxon's history. Since natural selection at any time maximizes the expected amount of expansive energy[12], evolutionary success is not so much to staying alive, but about expansion. In this view, traits are adapted to functional demands in a deterministic manner, but which particular taxon will next acquire a better-adapted trait will be largely random.

Expansion stops at the peak – the point where the species begins to fail and starts to decline towards extinction. The path to extinction ends with the extinction event, which occurs when the last individual disappears, or when the species becomes too rare to be detectable[32]. Small populations are more exposed and more vulnerable to environmental impact[33], and small geographic range of declining populations has been shown to be associated with a higher probability of extinction[34].

Emphasizing the peak of taxon's history makes good sense of the finding that major evolutionary trends are best captured by the subset of taxa that are common in each time interval[29,30] and strongly suggests that

competition is the main driver of such trends. It also illuminates the age-old question about biotic versus abiotic drivers of evolution. There may be no single correct, global answer to their relative weight. Rather, we find that it depends on context, especially on the phase (origin, peak, extinction) in the history of the taxon. The success or failure of taxa in their prime is strongly competition-driven, while taxa at the beginning and especially the end of their existence are more exposed to environmental forcing. At the end of its history, when a taxon is already rare, the final extinction is more at the mercy of environmental conditions. In this light, the Law of Constant Extinction might be usefully reformulated as the Law of Constant Peaking.

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Supplementary information Materials and methods are in the appendix.

Author Contributions I.Ž. and M.F. developed the theory. I.Ž. did the modelling and computational experiments. All the authors analysed the results. I.Ž. and M.F. wrote the initial text, all the authors contributed to the final text. N.C.S. initiated collaborative analysis to detect biotic and abiotic drivers in the fossil record, which inspired this spin-off paper.

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METHODS

Fossil data

We used fossil data from three continents, covering most of the North America, the western half of Europe, and a region in Africa (referred to as Turkana). We used genera as the unit of evolution. By choosing to look at relatively homogeneous geographic ranges and large herbivorous mammalian genera we may assume that the genera within a specific continent at a given time unit shared some overlapping resources, and in principle could have competed with each other.

North American data were downloaded from the NOW database (http://www.helsinki.fi/science/now/) on September 13, 2016. We used data from a square area covering most of the USA and parts of Mexico and Canada, ranging from 25 to 50 degrees latitude and to the left of -95 degrees longitude. (Figure S4 in Supplementary Information presents maps of site locations). Only those records within a single time unit, as recorded in the NOW database, were used. We selected localities from 40 million years old to the present time, and excluded time units that had fewer than five localities. We selected the following orders: Artiodactyla, Perissodactyla, Proboscidea, Primates, Hyracoidea, Carnivora, Creodonta, Tillodontia, Euprimates, Taeniodonta, Arctostylopida, Condylarthra, Creodonta, and Dinocerata. From within these orders we selected the genera that were annotated as herbivores in the database. We excluded unidentified genera and genera that were present in less than five localities. Table E1 in the Extended Data supplement summarizes the characteristics of the North American dataset.

European data were downloaded from the NOW database on March 19, 2016. We used data only from Western Europe, which included everything to the left of 20 degrees longitude (which passes through Poland). (Figure S5 in Supplementary Information presents maps of site locations). We only used records that were within single mammal Neogene (MN) time units (strict MN-equivalents defined as fitting entirely within the temporal boundaries on MN units)[35]. The data covered the time interval from 22 million years ago to the present time (MN2 to MQ19). We selected the following orders: Artiodactyla, Perissodactyla, Proboscidea, Primates, Hyracoidea, Carnivora, Creodonta, and from these we selected the genera that were annotated as herbivores in the NOW database. Multiple dietary assignments within a genus were resolved by assigning to the genus the label of the majority of species within this genus. We excluded unidentified genera and genera that were present in less than five localities. Table E2 in the Extended Data supplement summarizes the characteristics of the European dataset.

Turkana data were derived from the dataset published by Fortelius et al.[36] and covered the Turkana Basin from 7 to 1 million years ago. The original Turkana data recorded individual specimen found at localities, which we aggregated into occurrence of genera at localities. We further divided this time span into 11 time units of equal length (1.2 million years each). Four time units, including the oldest ones, had only one or a few localities but with high specimen counts. For these time units we split the localities randomly into subsets to construct at least five localities per time unit. We selected the following orders: Artiodactyla, Perissodactyla, Proboscidea and Primates, and considered them all to be herbivores. Table E3 in the Extended Data supplement presents the characteristics of the Turkana dataset.

Proxies

We work with genera as units of evolution, which at least in the fossil record of land mammals are more robust to noise of identification and potentially different granularity in defining distinct species across regions[37]. The Law of Constant Extinction was explicitly based on data at many hierarchical levels, and taxon unimodality has been demonstrated for genera as well as for species. Quental and Marshall[2] showed that the genus diversity of family-level clades is also unimodal, aligning this pattern directly with the level studied by Van Valen[9].

We form the proxies for evolutionary rates, competition and environmental change from the fossil record in the following way. The extinction rate is defined as the number of last appearing genera over the total number of genera seen at a time unit. The origination rate is defined as the number of genera that first appear over the total number of genera seen at a time unit. The peak rate (the turn-to-decline) is defined as the number of genera at maximum of their relative abundance (locality coverage) over the total number of genera seen at a time unit. The relative abundance is measured as the number of localities where a genus is found at a time unit over the total number of localities at this time unit. It is well documented in macroecology that abundance and occupancy have a strong positive relation[38].

Competition tends to be high if there is a high overlap in occupancy[6]. We measure the intensity of competition as the average number of genera per locality, assuming that the species in question more or less directly compete with each other[24], that is, they share an adaptive zone[39]. The large herbivorous mammals considered here can, as a rough approximation, be expected to compete directly with each other, making this a reasonable if rough proxy for competition, as good as can be obtained from occurrence data alone. Raia et al.[6] used geographic range overlap index, which is based on the same assumption – if species are in the same territory, they compete directly with each other.

The height (hypsdodonty) of the molar teeth of herbivorous mammals has a strong relation to environmental conditions. Mean hypsodonty is a well-established proxy for precipitation[40,41,36], and, more generally, for net primary productivity[42,43]. We measure environmental change via mean hypsodonty of occurring species, which allows us to relate environmental changes directly to the localities in question. We first compute mean hypsodonty for each locality, and then average it over all localities separately within each time unit. Environmental change is then defined as the absolute change in average hypsodonty over two neighbouring time units.

From the fossil record we tabulated during which time units and in how many locations each genus occurred. Origination and extinction times were therefore straightforward to identify, as we considered origination time to be the time unit in which a genus is first observed, and extinction time as the time unit in which a genus is last observed. We counted the genus to be alive from the time of origination to extinction even if there were time gaps within that period where the genus was not found in any location. Relative abundance at each time point over the history of the genus is calculated as the proportion of locations in which the genus X is present at time T:
Occupancy (at T for X) = no. localities X is present at T / total no. localities at T.

The peak in relative abundance was identified as the time point where the relative abundance for a given genus reached its maximum level, regardless of whether the trajectory was unimodal or not. If there were multiple time points where this occurred, the latest one was used. The peak is the maximum point of a taxon's expansion, and in extreme cases it may occur at origination or extinction.

The extinction rate was defined as the number of genera at their last appearance (which did not appear at (T+1) or later) over the total number of genera:
Extinction rate (at T) = no. genera last seen at T / no. genera alive at T.

The origination rate was defined as the number of genera that appear over the total number of genera:
Origination rate (at T) = no. genera first seen at (T + 1) / no. genera alive at (T +1). The origination rate was defined with respect to time (T + 1) in order to reflect the fact that the origination event happened sometime in between time T and (T + 1). The number of genera alive at (T + 1) includes the genera that just originated in order for the origination rate to be scalable (as a probability) between 0 and 1. When all genera originate in the following time unit the origination rate is 1.

We measure origination rate with respect to taxa that will originate in the next time step in order to be synchronized with the environmental change proxy. Environmental change proxy at time t describes

environmental change that happens from time t to time t+1. If we defined origination rate as the number of taxa first appearing at time t, then that would mean that these taxa actually originated at some time between t-1 and t, because at t they were already there. In such a case, it would not be synchronized with the environmental change proxy, which describes time between t and t + 1.

In order to align origination with the environmental change we need to consider taxa that was not available at time t and first appeared at t+1. Therefore, we count first appearing taxa at t+1 and report it at time t: Origination rate (at T) = no. genera first seen at (T + 1) / no. genera alive at (T +1).

The peak rate was defined as the number of genera at the maximum of their locality coverage over the total number of genera seen at a time unit. The locality coverage was measured as the number of localities where a genus is found at a time unit over the total number of localities where any genus is found at this time unit:
Peak rate (at T) = no. genera at locality coverage peak at T / no. genera alive at T.

The intensity of competition was defined as the average number of genera per locality:
Competition (at T) = no. observations (at T) / no. localities (at T).

Environmental change was quantified as the absolute change in mean hypsodonty. Hypsodonty is measured in the ordinal scale: 1 (brachydont), 2 (mesodont), and 3 (hypsodont). We computed the mean hypsodonty for each locality (over genera present that have assigned hypsodonty values). Next we computed the mean hypsodonty for each time unit as the mean over the localities belonging to that time unit.

For each time unit we computed expected environmental change as:
Environmental change (at T) = |mean hypsodonty (at T+1) – mean hypsodonty (at T)|.
The absolute value was taken because we were interested in the magnitude rather than the direction of the environmental change in this modelling.

We used raw proxies unadjusted for potentially unequal time units. As the proxies are different in nature, correcting them would have likely introduced extra bias. It is clear that the number of originations and extinctions could be expected to scale linearly with time, but it is questionable what would be the right way to scale the number of species alive, and how/whether to scale the change in hypsodonty if changes are not monotonic. We therefore considered it safer not to scale with respect to time, especially since the North American and European units were formed as homogeneously as possible and the Turkana time units were of equal length anyway. Therefore, for the purpose of analysis, we assumed that the time units are uniform in the middle and that changes in extinction and origination events are more likely to occur at the end of time units.

We computed all proxies over the fossil record, and took into consideration the potential circularity of reasoning when analysing the results. Even though the proxies originate from the same source, different known processes govern those proxies and there is different scientific reasoning behind each: mean hypsodonty is an ecometric proxy for a key environmental variable (productivity) while species density is an indicator of overlap in resource space and thus competition. Despite potential imperfections, this allows us to analyse the existing fossil record. For reassurance, we benchmarked our results against a null model.

Selected taxa were assumed to belong to the same adaptive zone, where they experience the same exposure to competition and environment. These assumptions facilitated an approach which allowed us to focus on the prime mechanisms behind evolutionary processes. The reality is undoubtedly more complex as there are many possible ways to form proxies, filter fossil data, and compute relative abundances. We have made these computational design choices in order to be able to analyse the theoretical arguments and the relatively scarce fossil record together.

The resulting proxies are given in Tables E4, E5, E6 in the Extended Data supplement. Raw occurrence datasets for each continent are given in Tables S9, S10, and S11 in the Supplementary Information.

Data analysis methods

The fossil data analysis consisted of two parts: generating a baseline model and correlation analysis.

The baseline model we used is not null in the sense that evolutionary forces are eliminated. In such a scenario extinctions would not occur (except for rare accidents), abundances would only increase, and therefore no fossil record would exist as such. This would be too far removed from the actual fossil record. Our goal with the baseline model was to have a baseline that would help to identify and discard artefacts that may have occurred due to small sample size and the way in which the proxies were formed. Therefore, our baseline model is a model where evolutionary downward pressure is present, but these forces are as independent as possible from the proxies being measured. It is a random walk model, which does not include competition forcing and environmental forcing. The baseline model differs from the fossil data in a way that it operates on abundances, while the fossil data represents relative abundances via localities. Since we cannot control the variable number of localities in the baseline model without introducing competition, we assumed that the number of localities was fixed and, as a result, the raw abundances generated by the baseline model could be compared to each other over time. Thus our model has no explicit dependence between competition and abundances, as desired. We used this model as a baseline to evaluate relations to competition and environmental forcing seen in the fossil data.

The baseline model was generated as follows with arbitrarily selected parameters, in order to resemble the fossil record. At any time the abundance of taxa can increase or decrease with ½ probability. The expansion or contraction in abundance at each step was drawn from the Gaussian distribution $N(3,1)$. At any given time a number of species to originate was drawn from the Gaussian distribution $N(7,7/3)$. Each taxon at origination was assigned a hypsodonty score (1, 2, or 3) at random. We assumed 20 localities at each time unit. The competition index was computed as the total abundance at a given time unit divided by the number of localities. The environmental change index was computed as the absolute change in the mean hypsodonty over all taxa alive. After computing indices we dropped the first and the last two time units to match the setting in the fossil data. We set a burn-in period to 30 time units to have taxa at various stages of their history when we start recording. After the burn-in we recorded the number of individuals over the taxon's history corresponding to the number of time units analysed in the North American (18), European (13) and Turkana (6) datasets. In addition, we recorded a longer time period of 50 time units in order to analyse the effects of the size of the datasets.

Table E7 reports the results of the baseline model. Some correlations of this random walk deviate from zero, which is not surprising given how the fossil record is formed. The relation of origination and extinction to competition is negative in the baseline model. This arises from the absence of a downward pressure in relation to abundance, causing the number of taxa and abundance to increase. This matches what we would expect if resources were unlimited, and is a desired property of the baseline model. Extinction and environmental change are correlated in the random walk model, because when taxa go extinct the distribution of hypsodonty in the localities changes. The presence of stronger correlations in the fossil record than those observed in the baseline model would indicate that taxa with particular traits in relation to the environment are more likely to go extinct, suggesting the influence of abiotic drivers. Competition is correlated with the peak in the baseline model primarily due to the small number of time units sampled, and with a larger number of time units (50 in our experiment) this correlation disappears. Observing correlations in the fossil record substantially above those present in the baseline model would indicate that a downward turn of taxa does not happen purely at random, but is related to the number of taxa already present, suggesting the operation of biotic drivers.

Correlation analysis uses simple linear correlation measures between evolutionary rates and competition and environmental proxies. For each experiment we generated 10000 datasets from the baseline model, and computed the mean and the standard deviation of the correlations. Then we calculated correlation coefficients for the fossil data, and benchmarked them against those of the baseline model. We used raw competition and environmental change indices to calculate the correlations.

Random walk models

The random walk examples shown in Figure 2 of the manuscript were generated using the following models. For each model we displayed eight trajectories per panel, which were selected randomly from the trajectories that finish by 100 time units and where the cumulative abundance (the total number of observations over all time units) exceeded 80.

Random walk. The basic random walk model is the same as the one used for benchmarking fossil data analysis results. At any given time the abundance of taxa can increase or decrease with ½ probability. The expansion or contraction in abundance at each step is drawn from the Gaussian distribution $N(3,1)$. At any given time a number of species to originate is drawn from the Gaussian distribution $N(7,7/3)$.

Random walk with memory (correlated random walk). This model is the same as the basic random walk model, but the probability at any given time for the abundance of taxa to increase or decrease depends on the previous direction. The probability to continue in the same direction is 0.9, and the probability to reverse direction is 0.1.

Random walk with memory and with competition. This model builds on the basic random walk model. At any point in time the probability of an increase in the abundance of taxa is ½ - k, where k is a correction factor computed as the mean abundance present in the previous time step. It is the average over a constant, large number of species that could be alive at all times. In other words, population size is divided by a constant. The constant is: the expected number of originations at a unit time, times the number of time units, times 3. In our experiments the denominator turns out to be 2100, which we consider a prudent estimate of the maximum number of species to ever originate during the experiment. Therefore, in practice k is less than one. The correction factor in this example is not a generic index of competition, but an arbitrary parameter created in order to synchronize with the mean number of originating taxa. Therefore, the mean is over a fixed number of species (2100). This number is the maximum number of species that could appear in this model. The averaging is over all species, not only species currently alive, which ensures comparability of the correction factors over time. In addition to the random walk with competition this model adds memory to the random walk, as described above.

Random walk with environment (no memory, no competition). In this model, the probability at any given time for the abundance of taxa to increase or decrease is influenced by a correction mechanism similar to the one for the model with memory. The probability of an increase is ½ + e, where e is the environmental condition. The environmental condition is defined recursively as e(at time T) = e(at time T-1) + x, where x is a random variable from the Gaussian distribution $N(0,0.1)$. For the simplicity of illustration, all taxa were defined as being affected by environmental changes in the same way.

Data availability statement

The authors declare that the data supporting the findings of this study are available within the extended data and supplementary information files.

The code used for experimental analysis and for generating examples of random trajectories in Figure 2 will be made available upon publication at https://github.com/zliobaite/RedQueen .

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EXTENDED DATA

Table E1. Characteristics of the North American dataset. HYP stands for hypsodonty. No. observed is the number of occurrence observations across all localities. No. genera is the number of distinct genera. No. alive includes genera that are not observed at the current time point, but are not yet extinct. No. first indicates the number of genera that will first appear in the next time unit. No. peak indicates the number of genera that have currently reached their peak of relative abundance. No. last indicates the number of genera that are last observed in the current time unit.

Time unit	Age	Mean HYP	No. localities	No. observed	No. taxa	No. alive	No. first	No. peak	No. last
Duchesnean	38.5	1.03	20	74	20	20	4	6	1
Chadronian-1	36.75	1.22	8	48	19	23	5	5	0
Chadronian-2	36.1	1.25	8	46	22	28	1	4	0
Chadronian-3	35.2	1.13	10	72	24	29	0	4	2
Chadronian-4	34.2	1.12	12	92	24	27	11	9	14
Arikareean-1	29.05	1.41	17	96	21	24	2	8	4
Arikareean-2	25.55	1.37	15	65	17	22	13	2	1
Arikareean-3	21.25	1.32	17	92	33	34	7	2	6
Arikareean-4	19.15	1.45	12	82	30	35	19	11	4
Hemingfordian-1	18.15	1.63	28	150	45	50	12	7	7
Hemingfordian-2	16.75	1.85	27	192	50	55	11	9	8
Barstovian-1	15.4	1.86	33	340	57	58	6	16	10
Barstovian-2	13.65	2.04	42	329	53	54	3	7	17
Clarendonian-1	12.3	2.53	5	38	28	40	4	8	2
Clarendonian-2	11.1	2.32	30	233	40	42	1	4	7
Clarendonian-3	9.55	2.31	17	85	29	36	7	2	9
Hemphillian-1	8.3	2.41	17	123	30	34	2	4	2
Hemphillian-2	7.2	2.44	15	122	32	34	0	11	4
Hemphillian-3	6.35	2.39	12	77	25	30	2	3	3
Hemphillian-4	5.4	2.53	16	85	27	29	5	3	10
Blancan-Early	3.7	2.34	47	206	24	24	0	4	9
Blancan-Late	2.2	2.43	34	147	15	15	0	6	15

Table E2. Characteristics of the European dataset.

Time unit	Age	Mean HYP	No. localities	No. observed	No. taxa	No. alive	No. first	No. peak	No. last
MN02	21.4	1.00	30	80	14	14	10	5	0
MN03	19	1.00	64	237	23	24	13	7	2
MN04	17.5	1.01	57	233	32	35	10	4	7
MN05	16.1	1.06	105	552	37	38	3	14	4
MN06	13.85	1.05	64	229	31	37	5	7	2
MN07	11.85	1.05	86	290	37	40	5	5	8
MN09	10.35	1.29	74	303	35	37	5	5	14
MN10	9.25	1.57	23	86	22	28	3	4	2
MN11	8.6	1.44	11	58	26	29	4	6	8
MN12	7.65	1.64	25	90	21	25	5	3	5
MN13	6.2	2.12	25	101	24	25	4	6	7
MN14	4.75	1.78	20	61	19	22	6	3	4
MN15	3.8	1.57	13	50	23	24	3	4	5
MN16	3	1.58	15	74	19	22	1	5	5
MN17	2.28	1.87	15	97	15	18	3	9	7
MQ18	1.54	2.27	5	16	11	14	8	4	2
MQ19	0.08	2.24	77	356	20	20	0	11	20

Table E3. Characteristics of the Turkana dataset.

Time unit	Age	Mean HYP	No. localities	No. observed	No. taxa	No. alive	No. first	No. peak	No. last
TU11	6.5	2.00	5	71	21	21	6	5	0
TU10	5.5	2.13	5	80	25	27	10	11	0
TU9	4	1.70	5	81	34	37	5	11	4
TU8	3.6	2.11	12	105	33	38	3	0	1
TU7	3.2	2.12	11	147	34	40	1	3	1
TU6	2.8	2.31	6	69	29	40	2	6	2
TU5	2.4	2.52	7	72	26	40	3	3	0
TU4	2	2.42	27	341	39	43	1	5	3
TU3	1.6	2.38	55	678	41	41	0	8	17
TU2	1.2	2.55	17	88	24	24	0	0	24

Table E4. The North American dataset.

Time unit	Age	Environmental change	Competition	Origination rate	Peak rate	Extinction rate
Chadronian-2	36.1	0.116	5.75	0.034	0.143	0
Chadronian-3	35.2	0.006	7.2	0	0.138	0.069
Chadronian-4	34.2	0.29	7.667	0.458	0.333	0.519
Arikareean-1	29.05	0.041	5.647	0.091	0.333	0.167
Arikareean-2	25.55	0.054	4.333	0.382	0.091	0.045
Arikareean-3	21.25	0.134	5.412	0.2	0.059	0.176
Arikareean-4	19.15	0.181	6.833	0.38	0.314	0.114
Hemingfordian-1	18.15	0.218	5.357	0.218	0.14	0.14
Hemingfordian-2	16.75	0.012	7.111	0.19	0.164	0.145
Barstovian-1	15.4	0.178	10.303	0.111	0.276	0.172
Barstovian-2	13.65	0.485	7.833	0.075	0.13	0.315
Clarendonian-1	12.3	0.204	7.6	0.095	0.2	0.05
Clarendonian-2	11.1	0.01	7.767	0.028	0.095	0.167
Clarendonian-3	9.55	0.093	5	0.206	0.056	0.25
Hemphillian-1	8.3	0.035	7.235	0.059	0.118	0.059
Hemphillian-2	7.2	0.051	8.133	0	0.324	0.118
Hemphillian-3	6.35	0.144	6.417	0.069	0.1	0.1
Hemphillian-4	5.4	0.195	5.312	0.208	0.103	0.345

Table E5. The European dataset.

Time unit	Age	Environmental change	Competition	Origination rate	Peak rate	Extinction rate
MN04	17.5	0.048	4.088	0.263	0.114	0.2
MN05	16.1	0.004	5.257	0.081	0.368	0.105
MN06	13.85	0	3.578	0.125	0.189	0.054
MN07	11.85	0.239	3.372	0.135	0.125	0.2
MN09	10.35	0.283	4.095	0.179	0.135	0.378
MN10	9.25	0.136	3.739	0.103	0.143	0.071
MN11	8.6	0.205	5.273	0.16	0.207	0.276
MN12	7.65	0.474	3.6	0.2	0.12	0.2
MN13	6.2	0.34	4.04	0.182	0.24	0.28
MN14	4.75	0.206	3.05	0.25	0.136	0.182
MN15	3.8	0.013	3.846	0.136	0.167	0.208
MN16	3	0.282	4.933	0.056	0.227	0.227
MN17	2.28	0.402	6.467	0.214	0.5	0.389

Table E6. The Turkana dataset.

Time unit	Age	Environmental change	Competition	Origination rate	Peak rate	Extinction rate
TU9	4	0.406	16.2	0.132	0.297	0.108
TU8	3.6	0.017	8.75	0.075	0	0.026
TU7	3.2	0.182	13.364	0.025	0.075	0.025
TU6	2.8	0.217	11.5	0.05	0.15	0.05
TU5	2.4	0.101	10.286	0.07	0.075	0
TU4	2	0.046	12.63	0.024	0.116	0.07

The Law of Constant Extinction or The Law of Constant Peaking?

The results of our analysis imply that the peak, rather than extinction, should be the phase in taxon's history most strongly related to evolutionary failure. The stochastically constant failure of taxa should then primarily relate to the peak. Figure S1 shows survivorship curves from our data used for analysis, similar to those on which the Law of Constant extinction was originally based[1]. The peaking lines appear consistently straight, implying that the probability of reaching the peak is by and large constant across taxon ages. A proposed reformulation of the Law of Constant Extinction to point to the of peak is then: the probability of stopping to expand is effectively independent of taxon's age.

The extinction lines appear slightly concave, implying slight dependence on age, with older taxa more likely to go extinct, whereas the peak lines are consistently more straight. This suggests that the probability of reaching the peak is the same for taxa at any age. This is at least partly due to our requirement of minimum presence, which weeds out short-lived genera, as analysed in the Sampling Effects section. Thus, the probability of reaching the peak does appear more constant across taxon age, suggesting a reformulation of the Law of Constant Extinction to point to the of peak: the probability of stopping to expand is effectively independent of taxon's age.
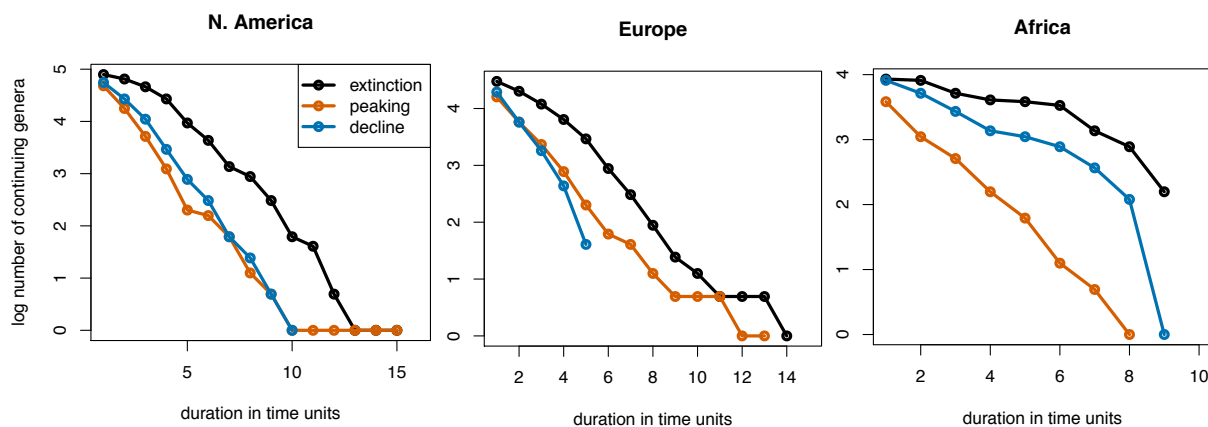
Figure S1. Illustration of the Law of Constant Extinction and Constant Peaking. We plot how many genera continue after a certain number of time units. "Extinction" means how many genera are not yet extinct from the beginning of their time, "Peaking" means how many genera have not yet reached the peak, "Decline" means how many genera are not yet extinct after their peak.

Figure S2 plots conditional probabilities of getting extinct or reaching the peak. The peaking (orange) line is flatter, suggesting a constant probability of reaching the peak with respect to age. There is a downward tendency of the probability of extinction (black) at the start, especially in the North American data. The downward tendency of the extinction is mostly due to the downward slope decline (blue), which is the most downward sloped among the three variables at all continents. Decline represents the phase from the peak to extinction, and is seems somewhat dependent on age – older genera are more likely to go extinct. The trend to a large extent disappears when we relax the requirement for genera to be present in at least five localities, which is illustrated in Figure S3.
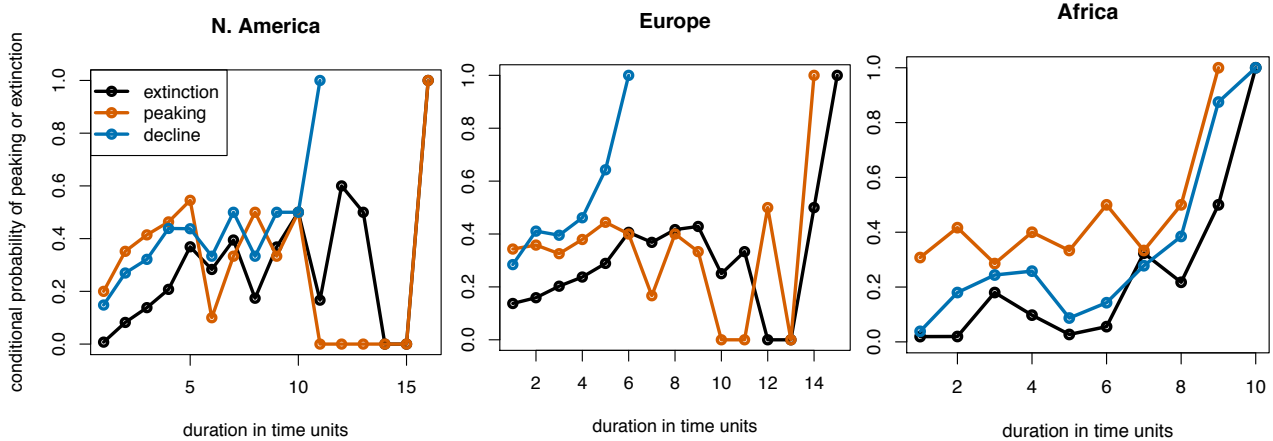
Figure S2. Conditional probabilities of peaking or extinction on the data used for our main analysis.
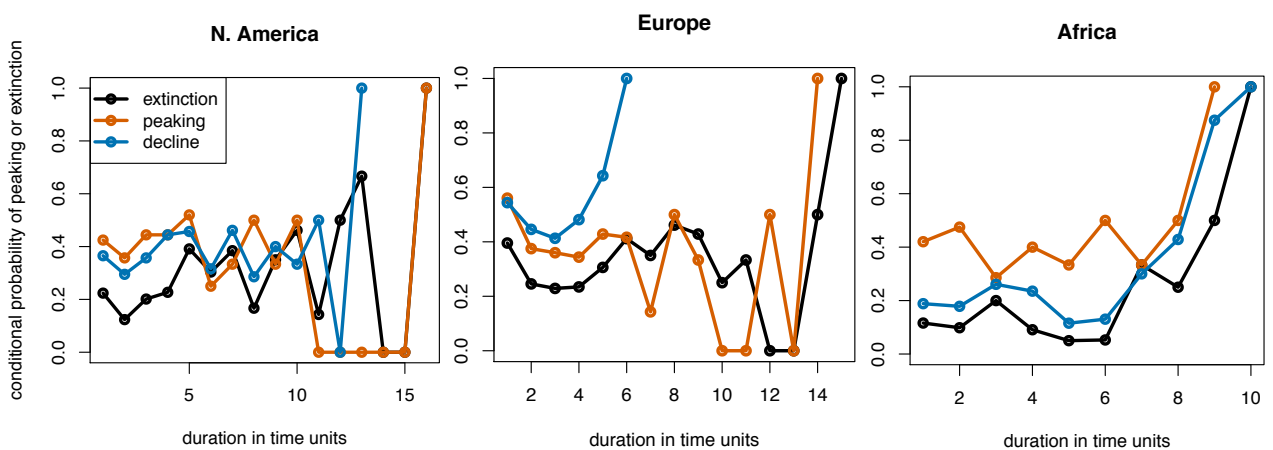
Figure S3. Conditional probabilities of peaking or extinction on more inclusive data, no requirement to be present in at least 5 localities.

The Law of Constant Extinction has been shown to work, but it certainly has exceptions[2,3], including some already highlighted in the original paper[1]. Universality of the Law is neither a prerequisite nor a precondition for the results of our analysis of biotic and abiotic factors to hold. We build upon a question to what extent the "hat" patterns are compatible with the Law, and we resolve this via reinterpretation of the Red Queen's hypothesis.

Analysis of sampling effects

The fossil record is inevitably biased, and biases may originate from different sources[4]. Preservation biases are always present, some habitats are more likely to produce fossils that others, and the habitats recorded in the fossil record may not be a uniform representation of the environments that were available at the time. For example, much of the terrestrial record is associated with fluvial and lacustrine environments, while forests, especially tropical forests, are poorly represented. Such general biases, while severe from some points of view, are not a major source of spurious difference between time units. Our study may be somewhat less prone to biases of this kind than macroevolutionary studies in general, since it focuses on common species (and by implication common habitats), so the major patterns are expected to be robust. Apart from preservation biases, there may be sampling biases, related to how fossils are found. Here we discuss potential sampling biases in the context of our study, run diagnostic tests, and consider what

potential effects this may or may not have to the outcomes of the analysis. There are two main angles to consider: unequal number of localities within each time unit and unequal length of the time units.

Unequal number of localities sampled over time makes the probability of observing rare taxa vary over time. Therefore, some of the indicators related to the taxon's history are expected to be correlated with the number of localities sampled, as indicated in Table S1; however, the ratios that we use for the analysis of biotic and abiotic drivers should not be significantly correlated with the number of localities, and, indeed, they are not, as it can be seen from Table S2.

Table S1. Linear correlations with the number of localities and gap statistics. Bold results highlight the relations with p-values less than 0.05 (two-tailed test). No. first denotes the number of first occurring taxa in the next time step (t+1), the same way as in the main analysis.

Continent	No. observed	No. taxa	No. alive	No. first	No. peak	No. last	Genus sampling probability	Mean proportion of sites occupied
N. America (18)	**0.94**	**0.86**	**0.78**	0.02	0.27	**0.67**	**0.66**	**-0.74**
Europe (13)	**0.95**	**0.91**	**0.89**	0.27	0.50	0.19	0.51	**-0.56**
Turkana (6)	**0.98**	0.76	0.77	-0.61	-0.24	0.19	0.53	-0.58

Table S2. Correlation between the number of sites and our proxies. There are no correlations for which p-values < 0.05 (two-tailed test).

Continent	Origination rate	Peak rate	Extinction rate	Environment change	Competition
N. America (18)	-0.13	-0.12	0.29	0.35	0.34
Europe (13)	-0.19	-0.03	-0.26	-0.38	-0.12
Turkana (6)	-0.60	-0.30	0.10	-0.60	-0.09

The correlations between the number of localities and the number of observed occurrences, the number of observed taxa, and the number of alive taxa are normally to be expected, and are present, as can be seen from Table S1. The more localities are sampled, the more occurrences are to be expected.

Genus sampling probability is correlated with the number of localities. This means that it is more likely to observe a genus that has already originated but is not yet extinct if more localities are sampled, which is consistent with a common intuition. When computing origination, peak and extinction ratios, we divide by the number of taxa alive (including unobserved taxa, which is not yet considered extinct, if it is to be observed at a later time unit) rather than the number of observed taxa, therefore, genus sampling probability does not directly concern our analysis of the peak. Mean proportion of sites occupied would be 1.0 if all the sites were occupied by all the species observed. Mean proportion of sites occupied is negatively correlated with the number of localities, as to be expected from the species-area relation in ecology. Our measure for competition may sound similar, but we intentionally do not divide by the number of species, instead we measure the mean number of occurrences per site, which then is not supposed to be significantly correlated with the number of localities, and, indeed, it is not, as can be seen from Table S9.

The number of last occurrences in North America is notably correlated with the number of localities, as can be seen from Table S1. Such correlation may be expected, since the more localities there are, the more taxa there are, and the more taxa there are, the more are prone to extinction. Number of last occurrences is not our proxy for the analysis, the ratio of last occurrences to the total number of taxa (probability of extinction) is. The ratio is not significantly correlate with the number of localities, as to be expected, and as can be seen from Table S2. Overall, neither of the proxies used in our analysis are significantly correlated with the number of localities, as can be seen from Table S2, therefore, sampling bias due to unequal number of localities over time does not pose any major concerns for the results of our analysis.

As an additional validation, we carry out a random downsampling analysis aiming at balancing the number of localities over time. We cap the number of localities per time unit to 15. The final number of localities at each iteration of random downsampling may be different, because our analysis protocol additionally prunes off the localities which end up having less than 5 genera. We do this analysis for North America and Europe only, because the Turkana dataset has only one time unit (out of six) that would be suitable for pruning, which restricts the amount of variability that we intend to induce.

Tables S3 and S4 show correlation analysis of competition and environmental change with the origination, peak and extinction rates of 10 runs of random downsampling. We would expect more noisy results than in the main analysis on the complete datasets reported in the main text in Table 2, yet we can see the patterns of competition having a stronger relation at the peak and environment having a stronger relation at extinction dominate quite persistently. In the North American dataset it holds at all times, in the European dataset the peak holds consistently, and the extinction becomes dominated by competition three times out of ten, out of which two times is by a low margin.

Table S3. Ten results of random downsampling, North America.

Competition-Origination	Environment-Origination	Competition-Peak	Environment-Peak	Competition-Extinction	Environment-Extinction	Number of time units
-0.35	0.26	0.5	0.39	0.15	0.39	18
-0.37	0.22	0.7	0.39	0.11	0.39	18
-0.37	0.56	0.82	-0.1	0.01	0.39	18
-0.08	0.32	0.7	0.32	0.32	0.55	18
-0.21	0.58	0.49	0.1	-0.11	0.25	17
-0.26	0.08	0.52	-0.18	-0.01	0.27	18
0	0.36	0.64	0.04	0.28	0.34	18
-0.47	0.61	0.46	0.02	-0.17	0.25	18
-0.26	0.38	0.47	0.27	0.1	0.41	18
-0.5	0.31	0.49	-0.18	-0.2	0.44	18

Table S4. Ten results of downsampling, Europe.

Competition-Origination	Environment-Origination	Competition-Peak	Environment-Peak	Competition-Extinction	Environment-Extinction	Number of time units
-0.86	-0.03	-0.12	-0.12	0.17	0.42	12
-0.43	-0.64	0.56	-0.37	0.59	0.62	13
-0.66	-0.31	0.77	-0.13	0.31	0.58	13
-0.33	-0.28	0.73	-0.08	0.65	0.46	12
-0.33	0.09	0.78	-0.14	0.28	0.53	12
-0.52	0.02	0.54	0.1	0.58	0.77	13
-0.75	0.35	0.85	0.14	0.46	0.54	13
-0.68	-0.12	0.57	0.16	0.79	0.23	13
-0.78	-0.4	0.49	0.26	0.58	0.57	12
-0.58	0.24	0.60	0.27	0.22	0.58	12

Tables S5 and S6 present aggregated results over 100 runs in each continent, these are different runs from the ones reported in Table S3 and S4. Mean results are very close to those on the complete dataset. As for stability, in North America the peak is dominated by environmental change in 1 out of 100 runs, and extinction is competition dominated in 9 out of 100 runs. In Europe the peak is never dominated by environmental change out of 100 runs, and extinction is competition dominated in 51 out of 100 runs. Extinction in Europe seems somewhat vulnerable, the dominant driver swaps about half of the times, most of the times by a low margin indicating that under low sampling the two drivers make a similar contribution to extinction. The pattern of the peak stays very stable. Overall, given that we apply quite a severe downsampling, which even sometimes cuts out compete time units out of the dataset, the main patterns hold very well.

Table S5. Aggregated downsampling results over 100 runs, North America.

	Competition-Origination	Environment-Origination	Competition-Peak	Environment-Peak	Competition-Extinction	Environment-Extinction
Original result	-0.32	0.26	0.48	0.10	0.11	0.55
Downsampled, mean	-0.32	0.33	0.58	0.08	0.04	0.38
Downsampled, st. deviation	(0.15)	(0.14)	(0.12)	(0.24)	(0.15)	(0.17)

Table S6. Aggregated downsampling results over 100 runs, Europe.

	Competition-Origination	Environment-Origination	Competition-Peak	Environment-Peak	Competition-Extinction	Environment-Extinction
Original result	-0.15	0.28	0.86	0.14	0.47	0.63
Downsampled, mean	-0.39	-0.17	0.71	0.09	0.46	0.47
Downsampled, st. deviation	(0.22)	(0.26)	(0.15)	(0.23)	(0.20)	(0.18)

Unequal time units refer to time units of analysis that differ in their duration. With the Turkana dataset we use time bins that are on purpose made to be of the same length (0.4 M years) and the issue of unequal time units does not apply. In the North American and European data time units are based on biostratigraphy and have unequal lengths. However, varying duration does not automatically imply sampling artefacts for the analysis. A desired property for the time units is to be relatively stable units in terms of their communities and environmental conditions. Biostratigraphy creates time units bounded by taxonomic turnover, implying that major environmental changes (if any) happen at the transitions between units. For example, MN5 is the longest unit in time, yet it shows the lowest extinction rate.

For better insights, Table S7 reports correlations between the duration of time units, count variables and our analysis proxies.

Table S7. Correlation between the size of a time unit between t and t+1 with other variables. Correlations for which p-values < 0.05 (two-tailed test) highlighted in bold. The Turkana dataset is not reported because time units of the analysed time bins are equal.

Continent	No localities	No. observed	No. taxa	No. alive	No. first	No. peak	No. last	Origination rate	Peak rate	Extinction rate	Environmental change	Competition
N. America (18)	-0.07	-0.12	-0.33	-0.39	0.33	0	0.23	**0.65**	0.28	**0.48**	0.10	-0.20
Europe (13)	**0.77**	**0.77**	**0.69**	**0.68**	0.28	0.54	-0.14	-0.11	0.04	-0.43	-0.34	-0.15

We can see that correlation patterns in North America and Europe look quite different, which is mainly due to high correlation between time duration and the number of localities in Europe but not the case in North America. To some extent this may reflect the fact that the European MN system is often disconnected from continuous rock sequences, whereas the stratigraphy in North America contains a strong lithostratigraphic basis. The more localities, the more occurrences or taxa are expected to be observed, thus the bold correlations in Europe are in line with expectations. If we were to adjust origination and extinction rates for any reason, we would have to adjust the remaining proxies as well for the analysis purposes. Yet the main object of analysis – the peak does not signal any substantial correlations with time duration, neither do the environmental change or competition proxies, therefore, we current analysis of North American data is the most representative given the data, and there are no signs of concern or reasons to adjust European or Turkana data with respect to time durations.

Peak statistics

Table S8 summarizes the patterns of taxon's history in the analysed datasets (including the first two and the last two time units). The dataset excludes genera that appear in less than 5 localities. Single peak accounts are computed on all deviations, no matter the size and including time units where a genus was not observed at all, and therefore is a conservative measure.

Table S8. Summary statistics of the peak patterns.

	N. America	Europe	Turkana
No. of genera	135	102	52
No. of genera peaking at the 1st time unit (%)	27 (20%)	35 (34%)	16 (31%)
No. of genera peaking at the last time unit (%)	20 (15%)	29 (28%)	9 (17%)
No. of genera with a strictly single peak (%)	62 (46%)	63 (62%)	22 (42%)
No. of genera peaking early (%)	50 (67%)	38 (37%)	32 (62%)
No of genera peaking in the middle (%)	23 (17%)	28 (27%)	9 (17%)
No of genera peaking late (%)	45 (33%)	36 (35%)	11 (21%)

Raw occurrence count data

Tables S9, S10, and S11 present raw occurrence counts for analysed genera.

Table S9. Locality occupancy over time in the North American dataset.

Duchesnean	Chadronian-1	Chadronian-2	Chadronian-3	Chadronian-4	Arikareean-1	Arikareean-2	Arikareean-3	Arikareean-4	Hemingfordian-1	Hemingfordian-2	Barstovian-1	Barstovian-2	Clarendonian-1	Clarendonian-2	Clarendonian-3	Hemphillian-1	Hemphillian-2	Hemphillian-3	Hemphillian-4	Blancan-Early	Blancan-Late	
0	0	0	0	0	10	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Sespia
0	0	0	0	0	13	10	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	Eporeodon
0	0	0	0	0	5	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Miotylopus
0	0	0	0	0	9	2	7	2	0	0	0	0	0	0	0	0	0	0	0	0	0	Nanotragulus
0	1	1	3	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Subhyracodon
0	0	1	0	3	6	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Hypertragulus
0	0	0	0	0	8	6	6	4	4	1	1	0	0	0	0	0	0	0	0	0	0	Diceratherium
0	0	0	0	0	1	0	4	3	0	0	1	0	0	0	0	0	0	0	0	0	0	Kalobatippus
0	0	0	0	0	0	0	5	8	15	12	9	13	2	17	11	1	1	1	0	0	0	Merychyus
0	0	0	0	0	0	2	6	4	1	2	0	0	0	0	0	0	0	0	0	0	0	Stenomylus
0	0	0	0	0	0	0	0	1	0	7	12	7	1	0	0	0	0	0	0	0	0	Miolabis
0	0	0	0	0	0	0	4	5	10	3	3	2	0	0	0	0	0	0	0	0	0	Parahippus
0	0	0	0	0	0	0	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	Tanymykter
0	0	0	0	0	0	0	1	3	5	0	0	0	0	0	0	0	0	0	0	0	0	Pseudoblastomeryx
0	0	0	0	0	0	0	1	1	7	6	8	5	0	0	0	0	0	0	0	0	0	Archaeohippus
0	0	0	0	0	0	0	0	0	4	9	17	20	2	4	0	0	0	0	0	0	0	Merychippus
0	0	0	0	0	0	0	1	0	7	5	0	0	0	0	0	0	0	0	0	0	0	Anchitherium
0	0	0	0	0	0	0	0	0	1	4	12	5	0	0	0	0	0	0	0	0	0	Ticholeptus
0	0	0	0	0	0	0	0	0	1	6	15	15	1	6	1	2	0	0	0	0	0	Aepycamelus
0	0	0	0	0	0	0	1	0	4	6	9	11	0	3	1	0	0	1	1	0	0	Merycodus
0	0	0	0	0	0	0	0	0	2	6	2	0	0	0	0	0	0	0	0	0	0	Parapliohippus
0	0	0	0	0	0	0	0	0	0	5	15	3	0	0	0	0	0	0	0	0	0	Acritohippus
0	0	0	0	0	0	0	0	0	0	9	16	4	0	0	0	0	0	0	0	0	0	Brachycrus
0	0	0	0	0	0	0	0	0	0	0	4	7	1	11	4	0	1	0	0	0	0	Cranioceras
0	0	0	0	0	0	0	0	0	1	3	18	12	1	6	3	0	0	0	0	0	0	Hypohippus
0	0	0	0	0	0	0	1	2	3	3	5	1	0	0	0	0	0	0	0	0	0	Hesperhys
0	0	0	0	0	0	0	0	0	4	7	7	13	1	9	1	0	0	0	0	0	0	Protolabis
0	0	0	0	0	0	0	0	0	0	3	10	1	0	0	0	0	0	0	0	0	0	Rakomeryx
0	0	0	0	0	0	0	0	0	1	6	8	3	0	0	0	0	0	0	0	0	0	Paramiolabis
0	0	0	0	0	0	0	0	0	0	0	1	11	0	9	4	2	2	2	2	0	0	Gomphotherium
0	0	0	0	0	0	0	0	0	0	0	2	9	1	4	0	0	0	0	0	0	0	Ramoceros
0	0	0	0	0	0	0	0	0	0	0	4	5	1	10	4	0	0	0	0	0	0	Cosoryx
0	0	0	0	0	0	0	0	0	0	0	3	9	2	5	1	0	0	0	0	0	0	Megahippus
0	0	0	0	0	0	0	0	0	0	0	2	8	3	16	6	6	7	5	2	0	0	Cormohipparion

																						Taxon
0	0	0	0	0	0	0	0	0	0	0	2	9	3	15	7	7	6	3	1	1	0	Pliohippus
0	0	0	0	0	0	0	0	0	0	0	0	1	1	7	4	13	10	6	5	7	2	Megatylopus
0	0	0	0	0	0	0	0	0	3	6	7	7	0	0	0	0	0	0	0	0	0	Bouromeryx
0	0	0	0	0	0	0	0	0	0	4	16	9	0	2	0	0	0	0	0	0	0	Dromomeryx
0	0	0	0	0	0	0	0	0	1	1	4	0	0	0	1	0	0	0	0	0	0	Hesperocamelus
0	0	0	0	0	0	0	0	0	0	0	6	4	0	0	0	0	0	0	0	0	0	Scaphohippus
0	0	0	0	0	0	0	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	Cynorca
0	0	0	0	0	0	0	1	3	4	7	5	7	0	4	0	1	0	0	0	0	0	Michenia
0	0	0	0	0	0	0	0	0	0	1	4	9	1	10	2	4	5	1	0	3	0	Procamelus
0	0	0	0	0	0	0	2	4	10	1	0	0	0	0	0	0	0	0	0	0	0	Menoceras
0	0	0	0	0	0	0	0	0	0	4	1	1	0	0	0	0	0	0	0	0	0	Sinclairomeryx
0	0	0	0	0	0	0	0	1	0	1	3	4	0	0	0	0	0	0	0	0	0	Pseudoparablastomeryx
0	0	0	0	0	0	0	0	0	1	2	9	15	1	6	1	0	0	0	0	0	0	Peraceras
0	0	0	0	0	0	0	0	0	1	5	11	13	1	11	5	10	9	8	9	5	0	Teleoceras
0	0	0	0	0	0	0	0	1	4	5	13	10	1	5	0	0	0	0	0	0	0	Blastomeryx
0	0	0	0	0	0	0	0	1	2	4	10	0	0	0	0	0	0	0	0	0	0	Desmatippus
0	0	0	0	0	0	0	0	0	1	3	12	14	1	9	3	8	8	5	3	2	0	Aphelops
0	0	0	0	0	0	0	0	0	0	0	1	1	0	7	7	3	3	1	1	0	0	Hipparion
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	4	0	0	Pediomeryx
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	4	0	3	0	0	Sphenophalos
0	0	0	0	0	0	0	0	0	0	0	0	1	0	5	5	8	9	6	8	0	0	Neohipparion
0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	2	2	1	4	15	13	Nannippus
0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2	7	9	7	10	4	0	Dinohippus
0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	1	1	1	1	3	4		Tapirus
0	0	0	0	0	0	0	0	0	2	5	11	6	2	2	1	0	0	0	0	0	0	Paracosoryx
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	5	0	0	0	0	Yumaceras
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	3	1	1	5	3	Mammut
0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	7	2	2	4	24	16	Hemiauchenia
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	3	2	2	0	Texoceros
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	3	4	4	Rhynchotherium
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	6	Odocoileus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	40	31	Equus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	14	14	Stegomastodon
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	17	Camelops
16	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Protoreodon
6	0	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Leptotragulus
4	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Simimeryx
0	0	0	1	7	7	5	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	Miohippus
0	0	0	0	0	8	6	7	5	2	0	0	0	0	0	0	0	0	0	0	0	0	Merycoides
2	1	0	1	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Eotylopus
0	0	0	0	0	2	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	Oreodontoides
0	0	0	0	0	0	0	0	0	1	10	1	0	0	0	0	0	0	0	0	0	0	Tylocephalonyx
1	2	4	1	0	6	4	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	Leptauchenia
0	0	1	2	4	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Hypisodus
0	0	0	0	0	3	12	7	6	6	1	0	0	0	0	0	0	0	0	0	0	0	Merycochoerus
2	2	3	7	4	1	2	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	Leptomeryx
0	0	0	0	0	0	1	4	5	2	0	0	0	0	0	0	0	0	0	0	0	0	Hypsiops
0	0	0	0	0	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Pseudolabis

0	0	0	0	0	0	0	3	4	5	1	0	0	0	0	0	0	0	0	0	0	0	Oxydactylus
0	0	0	0	0	0	0	2	4	2	1	7	0	0	0	0	0	0	0	0	0	0	Moropus
0	0	0	0	0	0	0	0	2	6	2	0	1	0	0	0	0	0	0	0	0	0	Barbouromeryx
0	0	0	0	0	0	0	1	2	4	1	0	0	0	0	0	0	0	0	0	0	0	Problastomeryx
0	0	0	0	0	0	0	0	0	5	2	0	0	0	0	0	0	0	0	0	0	0	Aletomeryx
0	0	0	0	0	1	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0	Arretotherium
0	0	0	0	0	0	0	0	0	1	3	4	2	1	0	0	0	0	0	0	0	0	Homocamelus
0	0	0	0	0	0	0	0	0	0	4	3	0	0	0	0	0	0	0	0	0	0	Subdromomeryx
0	0	0	0	0	0	0	0	0	1	2	2	3	0	0	0	0	0	0	0	0	0	Lambdoceras
0	0	0	0	0	0	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	Merriamoceros
0	0	0	0	0	0	0	0	0	3	1	4	0	1	0	0	0	0	0	0	0	0	Submeryceros
0	0	0	0	0	0	0	0	0	0	2	5	1	6	1	0	3	0	0	0	0	0	Protohippus
0	0	0	0	0	0	0	0	0	0	2	7	1	6	1	3	4	1	1	0	0	0	Calippus
1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	Tapiroidea
0	0	0	0	0	0	0	0	0	1	2	3	0	0	0	0	0	0	0	0	0	0	Zygolophodon
0	0	0	0	0	0	0	2	0	2	2	0	0	0	0	0	0	0	0	0	0	0	Floridatragulus
0	0	0	0	0	0	0	0	0	1	2	3	0	2	0	0	0	0	0	0	0	0	Nothotylopus
0	0	0	0	0	0	0	0	0	0	0	5	1	6	1	0	0	0	0	0	0	0	Longirostromeryx
0	0	0	0	0	0	0	0	0	0	2	4	9	0	1	0	0	0	0	0	0	0	Meryceros
0	0	0	0	0	0	0	0	0	0	0	4	3	8	2	0	0	0	3	1	0	0	Pseudohipparion
0	0	0	0	0	0	0	0	0	0	0	3	0	2	0	6	1	0	0	0	0	0	Plioceros
0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	2	0	1	0	0	0	Pseudoceras
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	2	1	Neotragocerus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	5	3	21	12	Platygonus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	4	2	3	2	0	Pleiolama
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5	3	0	0	0	Amebelodon
0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	4	3	1	0	0	0	Alforjas
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	10	Gigantocamelus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	10	Capromeryx
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	4	5	1	0	Astrohippus
5	5	0	5	5	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Agriochoerus
6	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Poabromylus
4	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Hendryomeryx
4	2	2	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Colodon
1	4	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Bathygenys
3	6	4	7	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Prodesmatochoerus
0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Pseudoprotoceras
0	0	2	5	7	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Poebrotherium
0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Parvitragulus
2	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Toxotherium
3	6	5	5	7	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Hyracodon
2	1	3	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Penetrigonias
1	2	1	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Oreonetes
3	5	4	7	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Mesohippus
0	1	1	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Megacerops
0	1	2	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Trigonias
0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0	0	Blickomylus
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Duchesneodus

1	0	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Aepinacodon
0	0	1	0	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	Paratylopus
0	0	0	0	0	0	0	0	1	3	0	1	1	0	0	0	0	0	0	0	0	0	Prosynthetoceras
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	3	0	0	Ilingoceros
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	4	Cuvieronius

Table S10. Locality occupancy over time in the European dataset.

MN02	MN03	MN04	MN05	MN06	MN07	MN09	MN10	MN11	MN12	MN13	MN14	MN15	MN16	MN17	MQ18	MQ19	
0	0	0	0	12	29	16	0	0	0	0	0	0	0	0	0	0	Listriodon
1	1	9	32	10	11	5	0	0	0	0	0	0	0	0	0	0	Brachypotherium
0	1	1	1	11	15	10	4	1	0	0	0	0	0	0	0	0	Alicornops
0	0	0	1	2	2	4	0	0	0	0	0	0	0	0	0	0	Dicerorhinus
0	13	22	50	16	14	4	0	0	0	0	0	0	0	0	0	0	Anchitherium
0	0	17	46	9	7	9	2	3	0	0	0	0	0	0	0	0	Dorcatherium
0	5	17	32	14	14	6	0	0	0	0	0	0	0	0	0	0	Palaeomeryx
0	0	2	11	23	21	10	8	3	0	0	0	0	0	0	0	0	Micromeryx
0	0	1	7	12	3	1	0	0	0	0	0	0	0	0	0	0	Heteroprox
0	0	0	3	5	24	16	2	2	1	0	0	0	0	0	0	0	Euprox
1	3	25	44	11	22	8	0	0	0	0	0	0	0	0	0	0	Gomphotherium
3	2	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	Metaschizotherium
0	0	0	4	6	2	4	0	0	0	0	0	0	0	0	0	0	Hoploaceratherium
0	0	4	13	7	11	5	0	0	0	0	0	0	0	0	0	0	Lartetotherium
0	0	0	8	12	4	4	0	0	0	0	0	0	0	0	0	0	Pliopithecus
0	0	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	Plesiopliopithecus
0	0	1	14	5	6	6	3	1	0	0	0	0	0	0	0	0	Anisodon
0	0	1	22	10	4	2	0	0	0	0	0	0	0	0	0	0	Dicrocerus
0	0	3	3	2	1	0	0	0	0	0	0	0	0	0	0	0	Archaeobelodon
0	0	2	16	10	8	6	0	0	4	4	0	0	0	0	0	0	Zygolophodon
0	0	2	1	5	27	25	6	5	5	0	0	0	0	0	0	0	Deinotherium
0	0	9	17	5	7	0	0	0	0	0	0	0	0	0	0	0	Eotragus
0	1	9	29	6	4	5	0	0	0	0	0	0	0	0	0	0	Prodeinotherium
0	0	0	0	0	9	5	0	0	0	0	0	0	0	0	0	0	Dryopithecus
0	0	0	0	0	12	6	0	0	0	0	0	0	0	0	0	0	Protragocerus
0	0	0	11	7	3	0	0	0	0	0	0	0	0	0	0	0	Tethytragus
0	8	16	30	7	2	0	0	1	0	0	0	0	0	0	0	0	Lagomeryx
0	17	28	34	0	0	0	0	0	0	0	0	0	0	0	0	0	Procervulus
0	1	7	24	4	0	0	0	0	0	0	0	0	0	0	0	0	Amphimoschus
1	9	14	22	3	0	0	0	0	0	0	0	0	0	0	0	0	Plesiaceratherium
0	2	10	24	2	1	0	0	0	0	0	0	0	0	0	0	0	Prosantorhinus
11	27	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Protaceratherium
1	35	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Brachyodus
9	22	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Diaceratherium
12	14	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	Amphitragulus
0	0	0	3	0	0	1	0	1	0	0	0	0	0	0	0	0	Orygotherium
1	3	0	1	0	0	10	1	1	0	1	2	3	4	1	0	0	Tapirus
0	0	8	16	0	0	0	0	0	0	0	0	0	0	0	0	0	Hispanotherium
0	0	0	8	2	2	0	0	0	0	0	0	0	0	0	0	0	Stehlinoceros
0	0	0	2	0	5	20	4	5	10	5	0	1	0	0	0	0	Miotragocerus
0	0	3	2	1	3	18	9	3	4	1	0	0	0	0	0	0	Aceratherium
0	0	0	0	0	0	10	9	4	6	5	2	0	0	0	0	0	Dihoplus
0	0	0	0	0	1	29	11	6	4	8	0	0	0	0	0	0	Hippotherium
0	0	3	6	0	1	11	1	1	1	0	0	0	0	0	0	0	Chalicotherium
0	0	0	0	0	0	8	0	1	0	0	0	0	0	0	0	0	Amphiprox
0	0	0	0	0	3	19	8	4	6	3	0	0	0	0	0	0	Tetralophodon
0	0	0	0	0	2	7	2	0	0	0	0	0	0	0	0	0	Hispanopithecus
0	0	0	0	0	0	5	6	3	12	15	3	3	0	1	0	0	Hipparion
0	0	0	0	0	0	5	1	0	0	0	0	0	0	0	0	0	Decennatherium
0	0	0	0	6	5	2	1	1	0	0	0	0	0	0	0	0	Hispanomeryx
0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	Triceromeryx
0	0	0	0	0	0	0	2	1	1	6	1	0	0	0	0	0	Tragoportax
0	0	0	0	0	0	0	1	1	6	3	4	4	6	7	0	0	Gazella
0	0	0	0	0	0	0	2	2	0	11	0	0	0	0	0	0	Cremohipparion
0	0	0	0	0	0	0	0	3	2	1	0	0	0	0	0	0	Birgerbohlinia
0	0	0	0	0	0	0	2	0	0	2	1	0	0	0	0	0	Pliohyrax
0	0	0	0	0	0	0	0	0	5	3	0	1	0	0	0	0	Hispanodorcas
0	0	0	0	0	0	1	0	2	3	2	1	1	3	0	0	1	Procapreolus
0	0	0	0	0	0	0	0	1	3	2	9	3	7	6	0	0	Anancus
0	0	0	0	0	0	0	0	0	0	1	4	2	6	9	1	0	Croizetoceros
0	0	0	0	0	0	0	0	0	0	8	2	0	0	0	0	0	Hexaprotodon
0	0	0	0	0	0	0	0	0	0	5	5	0	2	0	0	0	Parabos
0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	Pliocervus
0	0	0	0	0	0	0	0	1	1	4	1	3	2	0	0	0	Mesopithecus

0	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	0	Tragoreas
0	0	0	0	0	0	0	1	1	1	0	4	1	0	0	0	0	Protoryx
0	0	0	1	0	0	0	0	0	0	3	6	8	10	11	2	23	Stephanorhinus
0	0	0	0	0	0	0	0	0	0	0	4	1	3	0	0	0	Plesiohipparion
0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0	Alephis
0	0	0	0	0	0	0	0	0	0	0	5	3	7	9	1	44	Cervus
0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	Maremmia
0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	Oreopithecus
0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	Dolichopithecus
0	0	0	0	0	0	0	0	0	1	1	0	3	5	0	0	0	Mammut
0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	18	Capreolus
0	0	0	0	0	0	0	0	0	0	0	0	1	2	5	2	30	Mammuthus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	Gallogoral
0	0	0	0	0	0	0	0	0	0	0	0	1	2	9	0	0	Gazellospira
0	0	0	0	0	0	0	0	0	0	0	0	0	3	11	1	1	Eucladoceros
0	0	0	0	0	0	0	0	0	0	0	0	0	4	8	3	54	Equus
0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	4	Hemitragus
0	0	0	0	0	0	0	0	0	0	0	0	1	3	11	1	0	Leptobos
0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0	0	Paradolichopithecus
4	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Oriomeryx
7	23	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Andegameryx
0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	6	Alces
11	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	Dremotherium
11	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Pomelomeryx
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	Bison
0	18	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Ligeromeryx
0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Acteocemas
7	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	Paratapirus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	Rangifer
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	Bos
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	Dama
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	10	Hippopotamus
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	19	Megaloceros
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	Coelodonta
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	Ovibos
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	10	Capra
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	Rupicapra
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	Palaeoloxodon

Table S11. Locality occupancy over time in the Turkana dataset.

TU11	TU10	TU9	TU8	TU7	TU6	TU5	TU4	TU3	TU2	
0	0	2	3	4	0	0	6	3	0	Cercopithecoides
1	0	0	3	3	0	1	6	15	1	Sivatherium
5	5	2	10	5	5	6	14	27	2	Aepyceros
4	5	2	3	6	3	6	18	35	7	Kobus
0	1	5	10	8	2	2	15	33	4	Tragelaphus
0	0	3	4	7	1	3	12	24	3	Giraffa
0	0	0	2	0	0	1	8	12	1	Connochaetes
0	0	3	2	5	0	0	0	0	0	Simatherium
0	0	1	1	3	2	0	0	3	0	Parmularius
5	5	5	4	3	2	1	3	2	0	Parapapio
0	0	1	5	8	6	3	17	37	3	Theropithecus
0	0	5	3	8	5	3	6	24	8	Hippopotamus
0	2	2	5	3	3	3	17	16	7	Gazella
0	0	0	2	6	2	0	15	19	6	Megalotragus
0	0	3	7	9	6	6	18	6	0	Notochoerus
5	5	5	7	6	1	0	0	0	0	Nyanzachoerus
5	4	1	5	7	5	4	13	25	3	Hipparion
1	1	3	4	7	2	3	9	7	1	Deinotherium
0	0	0	1	1	0	0	17	38	8	Equus
0	0	0	1	5	0	5	19	38	7	Kolpochoerus
0	0	0	1	1	1	4	19	42	10	Metridiochoerus
1	0	1	2	0	0	0	0	3	0	Raphicerus
5	5	3	1	0	0	0	5	5	0	Eurygnathohippus
0	0	4	1	3	2	0	3	19	0	Australopithecus
0	3	3	1	0	0	0	0	0	0	Damalacra
3	3	1	1	1	0	0	3	3	1	Hippotragus
0	0	3	4	5	1	0	4	2	0	Loxodonta
0	2	3	2	6	4	6	14	17	1	Elephas
5	5	2	4	1	0	0	8	36	3	Hexaprotodon
2	3	2	2	3	2	1	6	18	2	Ceratotherium
2	1	0	1	3	2	0	0	1	0	Potamochoerus
0	0	1	2	2	2	0	6	1	0	Rhinocolobus
2	5	2	0	3	1	2	4	29	0	Damaliscus
2	2	1	1	5	0	2	16	19	2	Menelikia
0	0	0	0	0	0	0	2	8	1	Beatragus
0	0	0	0	0	0	0	8	18	2	Homo
0	0	0	0	0	0	1	7	37	4	Pelorovis
0	0	0	0	0	0	0	0	11	0	Cercocebus
0	0	0	0	0	0	0	1	5	0	Colobus
0	0	0	0	0	0	2	1	3	0	Paranthropus
0	0	0	0	0	1	1	3	6	0	Oryx
0	0	0	0	4	1	2	11	19	0	Antidorcas
0	4	3	0	2	2	1	2	9	1	Diceros
0	2	1	0	0	1	0	0	3	0	Madoqua
0	0	0	0	2	1	1	3	0	0	Paracolobus
1	2	3	0	0	0	0	1	0	0	Anancus
5	1	1	0	0	0	0	0	0	0	Miotragocerus
4	2	1	0	0	0	0	0	0	0	Stegotetrabelodon
5	5	2	0	0	0	0	0	0	0	Brachypotherium
5	4	1	0	0	0	0	0	0	0	Palaeotragus
3	3	0	0	0	1	0	0	0	0	Tragoportax
0	0	0	0	2	2	2	1	0	0	Ugandax

Geographic location of sites

Figures S4, S5 present geographic location of sites of the North American and European data, sites on these continents are geographically spread out. Some sites overlap in their location, therefore, the number of points at each time unit may be smaller than the reported number of localities. Overall, we see reasonably even distribution over space and time, which does not raise any concerns that location related biases could have any misleading impacts on the results of the analysis.
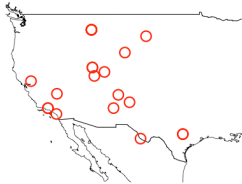
Duchesnean age 38.5   Chadronian-1 age 36.75   Chadronian-2 age 36.1   Chadronian-3 age 35.2
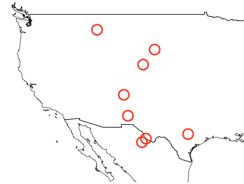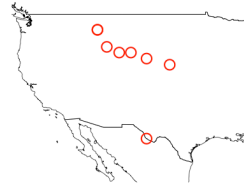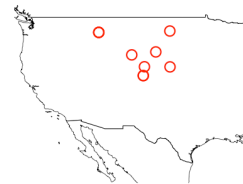
Chadronian-4 age 34.2   Arikareean-1 age 29.05   Arikareean-2 age 25.55   Arikareean-3 age 21.25
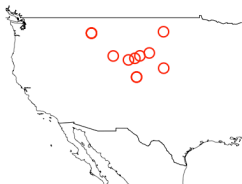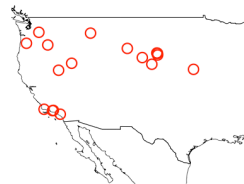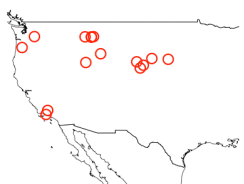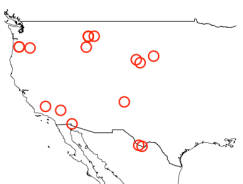
Arikareean-4 age 19.15   Hemingfordian-1 age 18.15   Hemingfordian-2 age 16.75   Barstovian-1 age 15.4
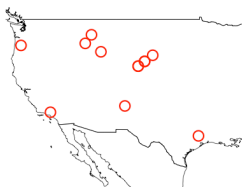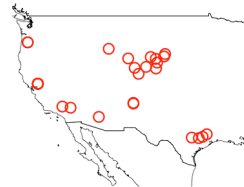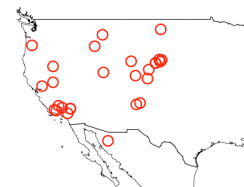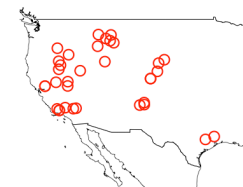
Barstovian-2 age 13.65   Clarendonian-1 age 12.3   Clarendonian-2 age 11.1   Clarendonian-3 age 9.55
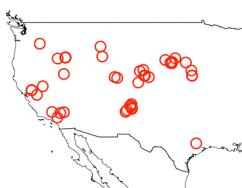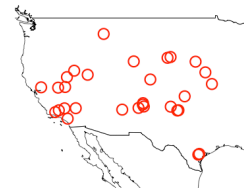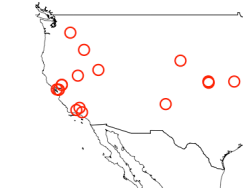
Hemphillian-1 age 8.3
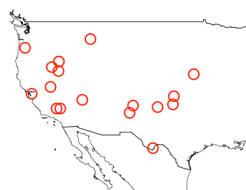
Hemphillian-2 age 7.2
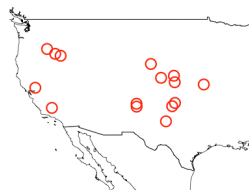
Hemphillian-3 age 6.35
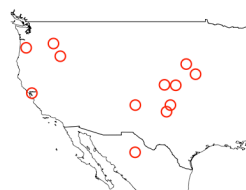
Hemphillian-4 age 5.4
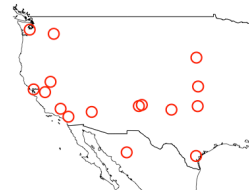
Blancan-Early age 3.7
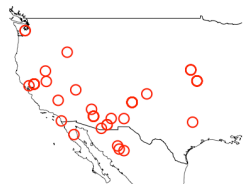
Blancan-Late age 2.2
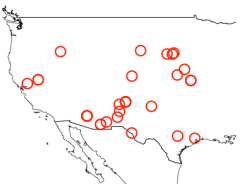
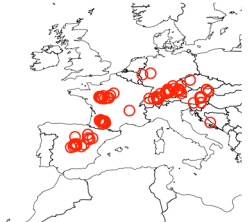**Figure S4. Site locations in the North American data.**

MN02 age 21.4

MN03 age 19
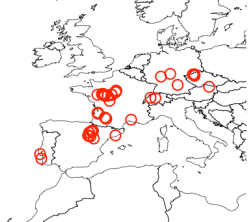
MN04 age 17.5

MN05 age 16.1

MN06 age 13.85

MN07 age 11.85

MN09 age 10.35
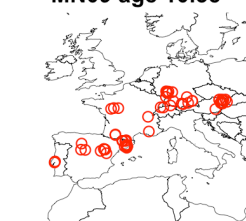
MN10 age 9.25
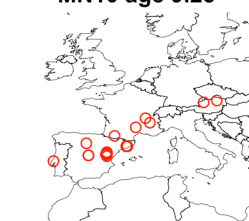
MN11 age 8.6

MN12 age 7.65

MN13 age 6.2

MN14 age 4.75

MN15 age 3.8

MN16 age 3

MN17 age 2.28

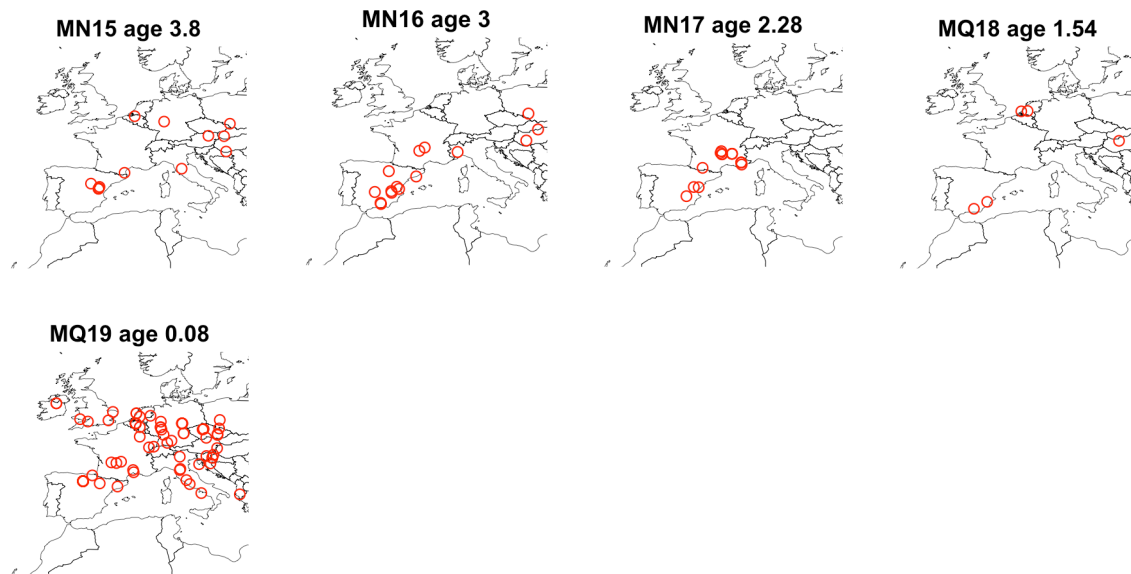**MQ18 age 1.54**

MQ19 age 0.08
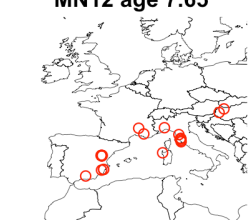
Figure S5. Site locations in the European data.

References for Supplementary Information

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