Current Biology

Contrasting "Fish" Diversity Dynamics between Marine and Freshwater Environments

Highlights

- Phylogenetic diversities of fish groups are compared with models of diversity dynamics

- Marine diversity fits an equilibrium model, while freshwater diversity is in expansion

- Greater freshwater competition, isolation, and perturbations account for this pattern

- Fish diversity dynamics confirm previous models designed for the entire biosphere

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In Brief

Guinot and Cavin demonstrate that deep-time phylogenetic "fish" diversity dynamics fit an equilibrium model in marine environments and an expansion model in freshwater environments. "Fish" diversity dynamics support former empiric models designed for the whole biosphere, with a maximum carrying capacity in marine environments.

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Contrasting "Fish" Diversity Dynamics between Marine and Freshwater Environments

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SUMMARY

Two theoretical models have been proposed to describe long-term dynamics of diversification: the equilibrium model considers the Earth as a closed system with a fixed maximum biological carrying capacity, whereas the expansion model hypothesizes a continuously increasing diversification of life. Based on the analysis of the fossil record of all organisms, Benton [1] suggested contrasting models of diversity dynamics between marine and continental realms. Diversity in marine environments is characterized by phases of rapid diversification followed by plateaux, i.e., an equilibrium model [2–4] directly derived from insular biogeography theories [5, 6], whereas diversity in continental environments is characterized by exponential growth. Previous studies that aimed at testing these models with empirical data were based on datasets extracted directly from the reading of the vagaries of the raw fossil record, without correcting for common fossil record biases (preservation and sampling). Although correction of datasets for the incompleteness of the fossil record is now commonly performed for addressing long-term biodiversity variations [7, 8], only a few attempts [9] have been made to produce diversity curves corrected by phylogenetic data from extant and extinct taxa. Here we show that phylogenetically corrected diversity curves for "fish" (actinopterygians and elasmobranchs) during the last 200 million years fit an equilibrium model in the marine realm and an expansion model in the freshwater realm. These findings demonstrate that the rate of diversification has decreased for marine fish over the Cenozoic but is in sharp expansion for freshwater fish.

RESULTS AND DISCUSSION

Here we test the fit between mathematical models and corrected diversity curves for two aquatic vertebrate groups (elasmobranchs and ray-finned fishes) based on phylogenetic diversities including both fossil and living taxa. Corrected diversity curves were computed by adding to observed temporal ranges of taxa (read directly from the fossil record) the ghost lineages to accommodate first appearance age of taxa with their corresponding phylogenetic relationships. Both fish clades together account for more than half of total vertebrate diversity and constitute about 10% (9.7%) of aquatic animal diversity as well as almost 83% of aquatic vertebrate diversity (Table 1). In addition, the evolutionary history of ray-finned fishes encompasses three of the largest diversifications among jawed vertebrates [15], including the biggest (percomorphs). In view of these characteristics, we consider that the diversity trajectories of these groups are good proxies for assessing global diversity patterns in the marine and freshwater realms.

Fish diversities considered here span the Late Triassic to Recent interval for elasmobranchs and the Late Jurassic to Recent interval for actinopterygians, at family level. In a previous study [16], we provided a range of computed diversity values according to the various phylogenies considered and their corresponding congruence with the fossil record, indicating that genuine diversity values should lie within this range. Consequently, the median diversity value was selected here for each time bin in order to sum up all hypotheses in one curve. The total actinopterygian dataset is divided into three subsets: fully marine, fully freshwater, and mixed-environment taxa (see Data S1). The latter subset encompasses clades that include either taxa from both freshwater and marine environments or euryhaline taxa (salt-tolerant and diadromous fishes). The marine actinopterygian subset and elasmobranch data were merged in order to provide a "total marine fish" dataset. Observed and computed data were compared with mathematical models that are commonly proposed to represent the main theoretical diversification dynamics of biological organisms. These include the additive, expansionist, and equilibrium models, represented mathematically by the linear, exponential, and logistic functions, respectively. In addition, the quadratic polynomial function (e.g., polynomial of degree 2) was included as an alternative representation (in the case of a negative discriminant) of the expansionist theoretical model of diversification. Model selection was performed using the Akaike information criterion with correction for finite/small sample sizes (AIC_c) (see Supplemental Experimental Procedures).

Fits of the various models of diversity dynamics to the main "fish" (here, actinopterygians and elasmobranchs) diversity datasets considered here are provided in Table 2 (see Table S1 for detailed results). With the exception of the freshwater

Table 1. Species Richness for All Extant Animals, Vertebrates, and "Fish" in the Marine and Freshwater Realms

	Freshwater	Marine	Total
Animals	125,530 (10.1%)	171,082 (9.3%)	296,612 (9.7%)
Vertebrates	18,235 (69.9%)	16,354[a] (97.1%)	34,589 (82.8%)
"Fish"	12,740	15,886	28,626

Percentages in parentheses indicate the contribution of elasmobranchs and ray-finned fishes to corresponding diversity. Data are from Balian et al. [10] (freshwater data), Mora et al. [11] (marine animals), Kaschner et al. [12] (115 cetacean species), Croxall et al. [13] (346 seabirds), and Carrete Vega and Wiens [14] (14,736 marine ray-finned fishes), plus 7 species of sea turtles and 1,150 elasmobranchii.
[a]"Fish" plus air-breathing marine megafauna (sea mammals, sea birds, and sea turtles)

actinopterygian dataset, the results indicate a better fit of computed phylogenetic diversity patterns to a logistic model than to any other candidate models (Figure 1), with strong support from AIC$_c$ weights (wAIC$_c$). Some of these datasets (marine actinopterygians, total marine "fishes") show a better fit to the exponential model when raw (i.e., "uncorrected") diversity values are considered, although this fit is weakly supported by wAIC$_c$. The latter result illustrates how the inclusion of phylogenetically corrected diversity estimates impacts curve shapes. The raw diversity pattern for the freshwater actinopterygian data best fits the exponential model, but the quadratic model is preferred when "corrected" phylogenetic diversity is considered. One could argue that values corresponding to today's diversity may influence the observed patterns because extant diversity is not affected by preservation biases, but comparable results were obtained once extant diversities were removed from the data (Tables 2 and S1). Similarly, both observed and corrected genus-level elasmobranch diversity curves better fit logistic models than any other competing models, with strong support from wAIC$_c$, regardless of the inclusion or exclusion of modern diversity points (Table S2).

Our results clearly indicate that diversity dynamics of freshwater fish echo those of continental organisms by fitting an expansionist model [17]. Another consequence of our results is that a given biological group (here, ray-finned fishes) can show different diversity dynamics depending on whether diversifications occur on continents (expansion) or in the sea (equilibrium).

Our results should be weighed in the light of biases that affect the fossil record and its study. Among taxonomic ranks, only species corresponds approximately to a biological reality, whereas higher taxonomic ranks—such as genera and families, used here—are artificial, and their counting through time may not reflect true biodiversity. However, extant and extinct lower-level taxa may not represent comparable biological definitions, and working at a supra-specific level prevents this problem as well as issues related to synonymy for both extant [11] and extinct [18] taxa. In addition, it has been proven that family rank is a good proxy for estimating extant [11] and past [19] species diversity. Using the family taxonomic level as a starting point, our results indicate that different marine "fish" groups show the same equilibrium diversification pattern. Empirical comparisons of raw diversity curves at different taxonomic ranks [1, 20, 21] have proposed that logistic diversity curves prevail for higher taxonomic

ranks and then gradually change toward an exponential distribution when lower levels are considered. The commonly proposed reason for this pattern is that the number of lower taxonomic ranks (genera, species) must increase faster and/or later than the diversity of higher-level taxa (families, orders) during diversifications [22]. According to this point of view, families can be regarded as groups gathering taxa that share key morphological or physiological characters, especially since rates of diversification and morphological evolution seem correlated [23]. Hence, although the family-level marine actinopterygian diversity curve fits an equilibrium model, new intra-familial specializations and habitat colonizations can occur, leading to an expansionist pattern at lower taxonomic scales as demonstrated for coral-reef-associated fish clades [24, 25]. Alternatively, the familial marine ray-finned diversity pattern may reflect similar dynamics at lower taxonomic levels as in various living and extinct groups [11, 19], suggesting that the equilibrium is reached. Our elasmobranch data agree with the latter hypothesis, as diversity dynamics follow a logistic model at ordinal [26] as well as familial and generic levels (this study) for this group. Hence, it appears more likely that diversification dynamics in the marine realm follow a logistic distribution at any taxonomic level, at least in some clades, which implies that some marine ecospaces may be limited by a global carrying capacity. This is not inconsistent with the fact that clades can reach higher diversities after a diversity plateau, as in the three evolutionary faunas of Sepkoski [27], provided that carrying capacity changed through time. This can be done either by wiping out competitive groups (mass extinctions), in the case of a biological carrying capacity, or by increasing ecological niches (e.g., plate tectonics), in the case of a physical carrying capacity. Consequently, the difference in curve shape is just a matter of how distant from the initial diversification we stand, or in other words, how far a clade is from its equilibrium.

At the present day, oceans cover 71% of Earth's surface. Freshwater environments represent only a tiny proportion (less than 0.01%) of the total water volume on Earth, whereas ocean waters encompass about 96% of this volume [28]. This would intuitively lead to the expectation that marine carrying capacity is higher than on continents. However, life in the sea is much less diverse than on land [29, 30], which may indicate that the former ecosystem has a carrying capacity but the latter does not, or that carrying capacity on land has not yet been reached. In fact, today's diversity in the marine realm is limited to a relatively restricted portion of the oceanic volume (especially for vertebrates), mostly in coastal waters of the intertropical regions [31] and mainly within the photic zone [32]. In addition, the freshwater realm (and to a greater extent the whole continental realm) differs from marine ecosystems in that it possesses more numerous and effective barriers to dispersal across small spatial scales, which produces more isolation and speciation [30, 33]. This leads to numerous specialized low-density populations with intense individual selection, which contributes to the attainment and maintenance of high taxic richness on continents [32] at both high and lower taxonomic levels. Restricted freshwater niches and populations correlate with intense competition (for space and resources) and predation. Although competition may be regarded as a limit to diversity [34], it is often considered a driver of diversifications [32]. As specialization reduces direct competition by subdividing ecospaces, competition may favor

Table 2. Fit of the Main Diversity Datasets Considered Here to Four Theoretical Models of Diversification Dynamics

		AIC_c	ΔAIC_c	$wAIC_c$	AIC_c	ΔAIC_c	$wAIC_c$
		Actinopts (Marine)			Actinopts (Freshwater)		
Computed diversity							
	Logis	283.361342*	0*	0.99901813*	207.484827	2.42569613	0.22860857
	Lin	308.718322	25.3569801	3.11E-06	263.4475	58.3883689	1.61E-13
	Exp	312.657251	29.295909	4.35E-07	216.461369	11.4022381	0.00256957
	Poly	297.218726	13.8573841	0.00097832	205.059131*	0*	0.76882186*
Observed diversity							
	Logis	300.429075	0.93632753	0.29147752	300.429075	53.3475126	2.58E-12
	Lin	327.83653	28.3437824	3.26E-07	278.313583	31.2320203	1.63E-07
	Exp	299.492747*	0*	0.46550677*	247.081562*	0*	0.98950169*
	Poly	300.792751	1.30000369	0.24301539	256.173567	9.09200461	0.01049815
Computed diversity (−Extant)							
	Logis	276.338581*	0*	0.99911924*	201.527692	1.57690232	0.31186408
	Lin	301.032585	24.6940042	4.34E-06	255.541678	55.5908886	5.82E-13
	Exp	305.316907	28.9783257	5.09E-07	211.587697	11.6369075	0.00203921
	Poly	290.417307	14.0787261	0.00087591	199.950789*	0*	0.68609671*
Observed diversity (−Extant)							
	Logis	267.213925*	0*	0.67485126*	267.213925	125.166335	6.61E-28
	Lin	303.871443	36.657518	7.40E-09	236.027747	93.9801569	3.91E-21
	Exp	272.440322	5.22639739	0.0494664	142.04759*	0*	0.99999931*
	Poly	269.004411	1.79048619	0.27568233	170.416982	28.3693923	6.91E-07
		Elasmobranchs			Marine Fishes (Total)		
Computed diversity							
	Logis	261.530624*	0*	0.9999996*	294.020388*	0*	0.91529199*
	Lin	341.035762	79.5051376	5.44E-18	301.852361	7.83197254	0.01823343
	Exp	360.507481	98.9768567	3.22E-22	309.614686	15.5942979	0.0003761
	Poly	290.990009	29.4593844	4.01E-07	299.276583	5.25619464	0.06609848
Observed diversity							
	Logis	241.340576*	0*	0.99999459*	310.033004	1.74612112	0.23582153
	Lin	266.154914	24.8143382	4.09E-06	327.628401	19.3415187	3.56E-05
	Exp	312.782559	71.4419836	3.07E-16	308.286883*	0*	0.56461035*
	Poly	268.420984	27.0804081	1.32E-06	310.3672	2.0803175	0.19953249
Computed diversity (−Extant)							
	Logis	257.471507*	0*	0.99999946*	286.987617*	0*	0.91535052*
	Lin	334.588417	77.1169098	1.80E-17	294.454072	7.46645531	0.02189108
	Exp	353.921398	96.449891	1.14E-21	302.39062	15.4030033	0.00041387
	Poly	286.324856	28.8533491	5.43E-07	292.360879	5.3732624	0.06234453
Observed diversity (−Extant)							
	Logis	233.100919*	0*	0.99999895*	280.588007*	0*	0.45638935*
	Lin	261.189801	28.0888826	7.95E-07	301.834977	21.2469693	1.11E-05
	Exp	307.647164	74.5462449	6.49E-17	282.291156	1.70314902	0.19476073
	Poly	263.434419	30.3335005	2.59E-07	281.12548	0.53747263	0.34883881

See Table S1 for results on complete datasets. Scores indicating best model fit (lowest AIC_c, ΔAIC_c = 0) are indicated with asterisks (*). Logis, logistic; Lin, linear; Exp, exponential; Poly, second-degree polynomial (quadratic polynomial). "−Extant" indicates that the value corresponding to today's diversity was removed.

increasing adaptive evolution and speciation [35], particularly in restricted or isolated environments. In addition to exhibiting greater isolation, specialization, and competition, freshwater fish groups appear less affected by extinction events at the family level in comparison with marine clades [16], which may explain parts of the differential diversity dynamics observed. This might relate to the different structure of these ecosystems, with the marine biota from the photic zone being based on
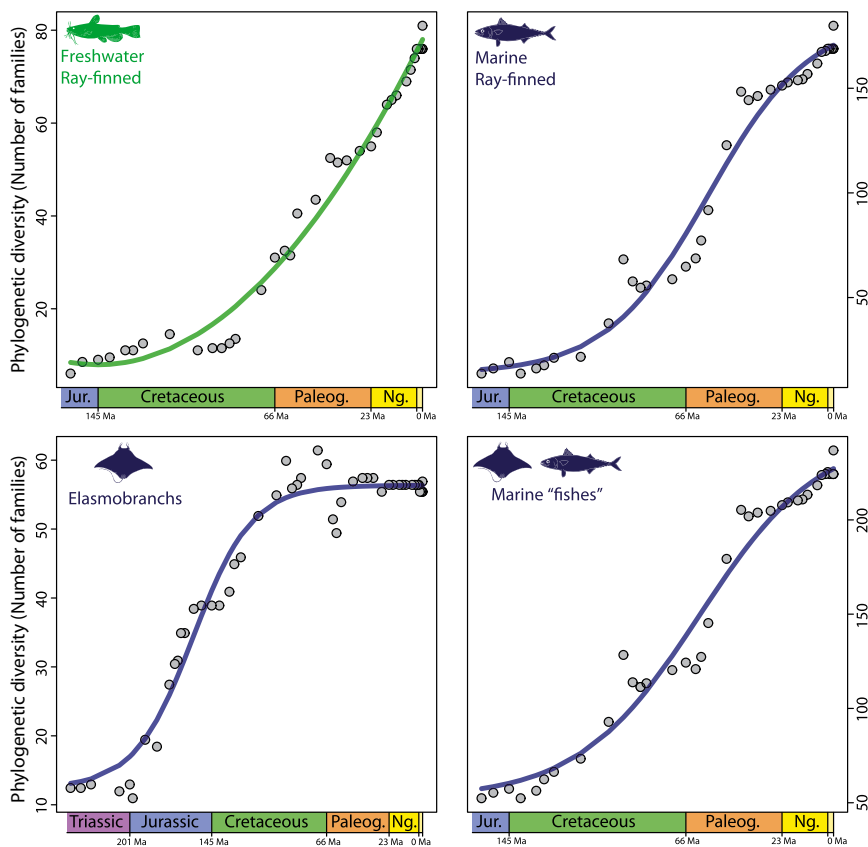
Figure 1. Curves of Best-Fitting Models Plotted over Phylogenetic Family-Level Diversity through Geological Times

Gray dots represent values of corrected diversity (phylogenetic diversity) per geological stage. All marine datasets (blue) fit a logistic model (representing the equilibrium model of evolution), whereas the freshwater ray-finned data fit a quadratic polynomial function (representing the expansion model of evolution). Curves are scaled to zero for graphical purpose. Jur., Jurassic; Paleog., Paleogene; Ng., Neogene.

primary producers and zooplankton whereas freshwater ecosystems also largely rely on detrital food webs. Hence, marine diversity depends on the fluctuations of phyto- and zooplankton, which are themselves linked with environmental forcing and therefore more prone to extinctions through time, whereas continental food webs sustain less perturbation. Tectonics, and to a greater extent the evolution of Earth's geographical and environmental configuration, are another factor that may explain the contrasting deep-time evolution of the freshwater and marine "fish" diversities. The Mesozoic-Cenozoic interval is characterized mainly by the breakup of Pangaea, which provided increasing ecological niches in both marine and continental ecosystems [16]. In the marine realm, it has been shown that periods of high sea levels coupled with warm global temperatures (Upper Cretaceous, Paleocene-Eocene) are linked with major diversification events within "fishes" [16] and more broadly vertebrates [15], along with habitat complexification related to the settlement of modern reef ecosystems (Paleocene-Eocene). Similarly, diversity in continental "fish" faunas seems to have been positively affected by high temperatures and sea level variations, but also by periods of heterogeneous global heat distribution, including monsoonal activities in the Lower Cretaceous [16]. Although post-Eocene marine geography and eustasy have undergone relatively few important perturbations until the present day (in comparison with pre-Oligocene times), this period encompasses marked climatic fluctuations (glaciations, temperature gradients) and major orogenesis and rifting events in the continental realm that deeply modified regional climatic settings and river net-

works. These still-ongoing processes shaped new continental hydrographic systems, increased the complexity of continental aquatic environments and atmospheric circulations, and are possible factors in the higher carrying capacity (if any) of freshwater ecosystems in comparison to the marine realm.

Our survey of "fish" diversity dynamics covers a short portion of the complete history of the metazoan evolution, but it covers most of the Modern Fauna time interval as defined by Sepkoski [27], which is characterized by the expansion of chondrichthyan and osteichthyan "fishes," among others. Based on this ascertainment and the large proportion of aquatic vertebrate diversity represented by "fish," the distinctions found here between the models for marine and freshwater realms are regarded as reflecting global features associated with these peculiar environments, which impact how life diversifies.

SUPPLEMENTAL INFORMATION

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1. Supplemental Tables

Supplemental Table S1. Fit of the family-level diversity datasets considered here to four theoretical models of diversification.

		Actinopts (Total)			Actinopts (Marine)			Actinopts (Freshwater)		
		AIC_c	ΔAIC_c	$wAIC_c$	AIC_c	ΔAIC_c	$wAIC_c$	AIC_c	ΔAIC_c	$wAIC_c$
Computed diversity										
	Logis	329.884769*	0*	0.99990222*	283.361342*	0*	0.99901813*	207.484827	2.42569613	0.22860857
	Lin	368.723437	38.8386678	3.68E-09	308.718322	25.3569801	3.11E-06	263.4475	58.3883689	1.61E-13
	Exp	362.350913	32.4661437	8.91E-08	312.657251	29.295909	4.35E-07	216.461369	11.4022381	0.00256957
	Poly	348.351963	18.4671934	9.77E-05	297.218726	13.8573841	0.00097832	205.059131	0	0.76882186
Observed diversity										
	Logis	345.84371*	0*	0.38589056*	300.429075	0.93632753	0.29147752	300.429075	53.3475126	2.58E-12
	Lin	382.316461	36.4727506	4.64E-09	327.83653	28.3437824	3.26E-07	278.313583	31.2320203	1.63E-07
	Exp	346.540605	0.69689433	0.27235508	299.492747*	0*	0.46550677*	247.081562*	0*	0.98950169*
	Poly	346.086633	0.24292319	0.34175435	300.792751	1.30000369	0.24301539	256.173567	9.09200461	0.01049815
Computed diversity (-Extant)										
	Logis	321.62855*	0*	0.99990625*	276.338581*	0*	0.99911924*	201.527692	1.57690232	0.31186408
	Lin	359.401293	37.7727437	6.28E-09	301.032585	24.6940042	4.34E-06	255.541678	55.5908886	5.82E-13
	Exp	353.633022	32.0044721	1.12E-07	305.316907	28.9783257	5.09E-07	211.587697	11.6369075	0.00203921
	Poly	340.180681	18.5521308	9.36E-05	290.417307	14.0787261	0.00087591	199.950789*	0*	0.68609671*
Observed diversity (-Extant)										
	Logis	300.120451*	0*	0.91541768*	267.213925*	0*	0.67485126*	267.213925	125.166335	6.61E-28
	Lin	357.057896	56.9374444	3.96E-13	303.871443	36.657518	7.40E-09	236.027747	93.9801569	3.91E-21
	Exp	314.114071	13.9936198	0.00083742	272.440322	5.22639739	0.0494664	142.04759*	0*	0.99999931*
	Poly	304.903662	4.78321025	0.0837449	269.004411	1.79048619	0.27568233	170.416982	28.3693923	6.91E-07

		Actinopts (Mixed-Envir.)			Elasmobranchs			Marine Fishes (Total)		
		AIC$_c$	ΔAIC$_c$	wAIC$_c$	AIC$_c$	ΔAIC$_c$	wAIC$_c$	AIC$_c$	ΔAIC$_c$	wAIC$_c$
Computed diversity										
	Logis	272.249859*	0*	0.99993535*	261.530624*	0*	0.9999996*	294.020388*	0*	0.91529199*
	Lin	301.505282	29.2554221	4.44E-07	341.035762	79.5051376	5.44E-18	301.852361	7.83197254	0.01823343
	Exp	299.534724	27.2848646	1.19E-06	360.507481	98.9768567	3.22E-22	309.614686	15.5942979	0.0003761
	Poly	291.593903	19.3440431	6.30E-05	290.990009	29.4593844	4.01E-07	299.276583	5.25619464	0.06609848
Observed diversity										
	Logis	248.596129*	0*	0.99866024*	241.340576*	0*	0.99999459*	310.033004	1.74612112	0.23582153
	Lin	302.039667	53.4435383	2.48E-12	266.154914	24.8143382	4.09E-06	327.628401	19.3415187	3.56E-05
	Exp	272.054711	23.4585817	8.04E-06	312.782559	71.4419836	3.07E-16	308.286883*	0*	0.56461035*
	Poly	261.836022	13.2398934	0.00133172	268.420984	27.0804081	1.32E-06	310.3672	2.0803175	0.19953249
Computed diversity (-Extant)										
	Logis	266.119742*	0*	0.99990613*	257.471507*	0*	0.99999946*	286.987617*	0*	0.91535052*
	Lin	294.489965	28.3702222	6.91E-07	334.588417	77.1169098	1.80E-17	294.454072	7.46645531	0.02189108
	Exp	292.265155	26.1454129	2.10E-06	353.921398	96.449891	1.14E-21	302.39062	15.4030033	0.00041387
	Poly	284.727125	18.6073822	9.11E-05	286.324856	28.8533491	5.43E-07	292.360879	5.3732624	0.06234453
Observed diversity (-Extant)										
	Logis	228.707545*	0*	0.99998767*	233.100919*	0*	0.99999895*	280.588007*	0*	0.45638935*
	Lin	290.473403	61.7658582	3.87E-14	261.189801	28.0888826	7.95E-07	301.834977	21.2469693	1.11E-05
	Exp	263.317039	34.6094938	3.05E-08	307.647164	74.5462449	6.49E-17	282.291156	1.70314902	0.19476073
	Poly	251.319562	22.6120174	1.23E-05	263.434419	30.3335005	2.59E-07	281.12548	0.53747263	0.34883881

Scores indicating best model fit (lowest AICc, Δ AICc = 0) are indicated with asterisks (*). Logis, logistic; Lin, linnear; Exp, exponential; Poly, second-degree polynomial (quadratic polynomial). "− Extant" indicates that the value corresponding to today's diversity was removed.

Supplemental Table S2. Fit of the genus-level diversity dataset for elasmobranchs to four theoretical models of diversification.

		Elasmobranchs (genera)		
		AIC$_c$	ΔAIC$_c$	wAIC$_c$
Computed diversity				
	Logis	471.537337*	0*	0.99809739*
	Lin	516.1433	44.6059626	2.06E-10
	Exp	527.707368	56.1700309	6.34E-13
	Poly	484.062582	12.5252445	0.00190261
Observed diversity				
	Logis	435.372023*	0*	0.80975498*
	Lin	438.867331	3.49530749	0.14104485
	Exp	448.83328	13.461257	0.00096667
	Poly	441.013379	5.64135596	0.0482335
Computed diversity (-Extant)				
	Logis	463.127132*	0*	0.99701072*
	Lin	506.902861	43.7757296	3.11E-10
	Exp	518.264684	55.137552	1.06E-12
	Poly	474.746588	11.6194563	0.00298928
Observed diversity (-Extant)				
	Logis	382.591979*	0*	0.99981523*
	Lin	400.444799	17.8528196	0.00013281
	Exp	420.982944	38.3909648	4.61E-09
	Poly	402.322009	19.7300295	5.20E-05

See Supplemental Table S1 for details.

2. Supplemental experimental procedures

2.1. Data sets

The 'fish' diversity data used here were taken from a recent study [1] that provided elasmobranch and actinopterygian supertrees including both extant and extinct families along with the fossil record (ages of first and last occurrence) of corresponding terminal taxa. For both groups, four competing tree topologies representing alternative phylogenetic hypotheses were plotted against the fossil record of terminal taxa. This resulted in the addition of artificial stratigraphic range (ghost range) to the observed fossil record of a taxon to fit the first appearance date of its sister

taxon (two sister taxa must have the same age of first occurrence). Comparing stratigraphic ranges of taxa and corresponding phylogenetic relationships requires dealing with uncertainties related to each datasets, namely the range age of first occurrence (stratigraphy) and polytomies (phylogeny). Consequently, the method used in Guinot & Cavin [1] followed that of Boyd *et al.* [2] for measuring congruence scores of the fit of stratigraphic data to phylogenies. This resolves polytomies in two ways: one *Chronological* where the original polytomous clade is resolved in a pectinate arrangement, placing taxa with the oldest age of first occurrence at the base of the clade and one *Reverse Chronological* polytomy resolution where taxa with the youngest age of first occurrence are placed at the base of the resolved clade. Uncertainties with the age of first occurrence were considered in randomly picking an age within the age range of first occurrence of each taxon, using 1 000 000 replicates. Hence, for each of the four phylogenetic hypotheses considered, range values of computed first appearance ages are provided for the Chronological method and Reverse Chronological method. Guinot & Cavin [1] finally selected four 'phylogenetically corrected' diversity values that correspond to the most and least congruent data for each of the two methods of polytomy resolution (Supplemental Data Set S1). Taken separately, none of these phylogenetic diversity estimates represent the genuine diversity variations though time as 'true' diversity values lie within the range values of computed phylogenetic, for each time bin. In the present paper, we consequently selected the median diversity value for each time bin in order to sum up all four hypotheses in one curve and to avoid giving more weight to any of the phylogenetic diversity estimates.

Diversity values span the Late Triassic to Recent interval for elasmobranchs (sharks, skates, rays and the extinct hybodonts) and the Late Jurassic to Recent interval for actinopterygians, at family level. The total actinopterygian dataset is split into three subsets including fully marine, fully freshwater and mixed-environment taxa based on the environmental distributions of taxa provided in Guinot & Cavin [1]. The 'mixed environment' subset encompasses clades that either include taxa from both freshwater and marine environments as well as euryhaline taxa (salt-tolerant and

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diadromous fishes). The marine actinopterygian subset and elasmobranch data were merged in order to provide a 'total marine fish' dataset restricted to the Late Jurassic to Recent interval. The genus level data on observed and phylogenetically corrected elasmobranch diversities are also from Guinot & Cavin [1].

2.2. Model fitting

Observed and computed data were compared with mathematical models that are commonly proposed to represent the main theoretical diversification dynamics of biological organisms. These include the additive, expansion and equilibrium models represented mathematically by the linear, exponential and logistic functions, respectively. In addition, the quadratic polynomial function (e.g. polynomial of degree 2) was included as an alternative representation (in the case of a negative discriminant) of the expansion theoretical model of diversification.

Model fitting was made in R [3] using the package *stats.* The *nls* function was used for fitting the data to logistic and exponential models and the *lm* function was used for linear and quadratic polynomial models.

Model selection was performed using the Akaike Information Criterion with the correction for finite/small sample sizes (AIC_c). Among the four candidate models, the favoured model is the one with the lowest AIC_c score. Differences in AIC scores between a given candidate model and the one with the best fit (ΔAIC_c) allow comparison between models' fit and computation of Akaike weights (AIC_c w). The latter provide probabilities that a model is the best one given the observed data and considering the set of candidate models. An important point to be aware of when using model selection in ecology is that none of the theoretical models tested completely represent the real mechanisms underlying the distribution of data. Model selection is rather based on the identification of the best approximation of true distributions given the set of candidate models considered.

3. Supplemental references

S1.   Guinot, G., and Cavin, L. (2015). "Fish" (Actinopterygii and Elasmobranchii) diversification patterns through deep time. Biol. Rev. DOI: 10.1111/brv.12203

S2.   Boyd, C. A., Cleland, T. P., Marrero, N. L., and Clarke, J. A. (2011). Exploring the effects of phylogenetic uncertainty and consensus trees on stratigraphic consistency scores: a new program and a standardized method. Cladistics *27*, 52–60.

S3.   R Development Core Team (2010). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria).