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# Contemporary and Phanerozoic Patterns of Global Biodiversity

By

Attila Kalmar

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# Abstract

*Contemporary and Phanerozoic Patterns of Global Biodiversity* is a global study testing theories explaining variation in taxic richness, and drawing parallels between contemporary- and paleodiversity. The unifying idea of the thesis is that most of the variation in contemporary and past richness depends on analogous factors: (1) sampling effects, (2) richness-energy relationships, and (3) geometric considerations pertaining to isolation and fragmentation. We present a predictive model of global island biogeography, uniting classic ideas of the Equilibrium Theory of Island Biogeography (ETIB) with the Species-Energy Theory (Chapter 1). We quantify insular isolation and propose an equation to measure the isolation reducing effects of neighboring islands. In Chapter 2 we extend our model to continental parcels of land. We show that area-climate interactions are strong both on continents and on islands. Notwithstanding, species-area slopes do not depend either on distance-based or on historical isolation, in apparent contradiction with some predictions of the ETIB. Thus, broad-scale patterns of diversity on islands and continents are commensurable. In Chapter 3 we evaluate the completeness of the global Phanerozoic record of continental (terrestrial and freshwater) metazoans, aiming to use these data in subsequent chapters. Results of this analysis suggest the relative completeness of the continental fossil record is not markedly inferior to that of the marine fossil record at the taxonomic level of the family and at the stratigraphic level of the stage. The exponential diversification curve of suprageneric continental taxa is unlikely to be the result of rock bias.

## *Abstract*

Chapter 4 adopts a multivariate approach to model variation in fossil diversity. Our main finding is that turnovers of metazoan families are strongly correlated with the number of magnetic polarity reversal records per stratigraphic stage over the Phanerozoic. This suggests that either variation in fossil richness and reversal intensity are both strongly influenced by preservation bias, or that extinction and origination rates have a strong and quantifiable perturbation regime. In Chapter 5 we classify stratigraphic stages into alternating extinction and origination cycles to test for supercyclicity. Paleomagnetic and fossil data both support this hypothesis over the Lower Paleozoic, the Upper Paleozoic and the Mesozoic.

# Résumé

*Patrons globaux de biodiversité au Phanérozoïque et au temps présent* est une étude globale qui teste des théories reliées à la diversité taxonomique, tout en rapprochant les domaines de l'écologie contemporaine avec la paléodiversité. L'idée unifiante de la thèse veut que la variation en diversité contemporaine, comme celle du passé, dépende des facteurs analogues: (1) effets d'échantillonnage, (2) climat et énergie, et finalement (3) des considérations géométriques, y compris l'isolement et la fragmentation. Nous présentons un modèle prédictif de la biogéographie insulaire qui unifie des idées classiques de la théorie de biogéographie insulaire avec la théorie espèces-énergie. Nous quantifions l'effet de l'isolement insulaire, y compris l'effet atténuant des îles avoisinantes. Chapitre Deux est une extension de l'étude insulaire aux échantillons d'aires continentaux. Nous démontrons que l'interaction entre l'aire et le climat s'avère forte dans les régions continentales, tout comme dans les espaces insulaires. Au contraire, la pente de la relation aire-espèces ne dépend apparemment ni de l'isolement basé sur la distance ni de l'isolement historique, c'est qui est en contradiction avec certaines prédictions de la théorie de biogéographie insulaire. En conséquence, les modèles de diversité à large échelle sont pratiquement identiques entre les milieux continentaux et insulaires. Chapitre Trois évalue l'intégrité du record global des métazoaires terrestre et d'eau douce du Phanérozoïque entier, en vue de l'inclure dans les analyses qui suivent. Notre étude suggère que, au niveau taxonomique de la famille et au niveau stratigraphique de l'étage, l'intégrité relative

## *Résumé*

du record continental n'est guère inférieur à celui du record marin. Il est donc peu probable que la courbe de diversification exponentielle des taxa continentaux supra-génériques soit un artefact de préservation. Chapitre Quatre adopte une approche multivariée à la quantification de la variation de la diversité des métazoaires fossiles. Nous avons trouvé que les taux de turnover des familles métazoaires sont fortement corrélés avec le nombre de records de renversements magnétiques par étage au cours du Phanérozoïque entier. Cela suggère que les taux de variation de richesse des fossils et les taux d'intensité des renversements magnétiques sont tous les deux fortement influencés par les biais taphonomiques, ou bien les taux d'extinction et d'origination dépendent d'un régime de perturbation quantifiable. Dans Chapitre 5 nous classifions des étages stratigraphiques en cycles d'extinction et d'origination alternantes en vue de tester pour supercyclicité. Les registres paléomagnétique et fossile supportent cette hypothèse pour le Paléozoïque inférieur, le Paléozoïque supérieur et le Mésozoïque.

# Introduction

"Contemporary and Phanerozoic Patterns of Global Biodiversity" is a study aimed to test and develop theories explaining spatial and temporal variation in biodiversity. Since both contemporary and past patterns of diversity have been related to a set of analogous factors, describing sampling effects, climate, geometric considerations and perturbation, we adopt a general multiple-regression approach to explain variation in contemporary and past patterns of diversity. In the following pages, we will present a general overview of the theories and methods related to our work, and the rationale which lead us to the gradual extension of the original island geography paper. We will also mention some of our analyses and results which have been important in the making of the thesis, even though they are not part of the final articles or manuscripts.

## The equilibrium theory of island biogeography and the species-energy theory

Our island biogeography study (Chapter 1) combines two schools of thought in contemporary ecology which played prominent roles in diversity studies over the second half of the twentieth century. These are the Equilibrium Theory of Island Biogeography (ETIB) and the species-energy theory. According to the ETIB the number of species on an island represents an equilibrium between opposing rates of extinction and colonization (MacArthur and Wilson 1963, 1967). Thus, in essence, this theory emphasizes the effects of area and isolation on insular richness. On the other hand, the species-energy theory (Hutchinson 1959; Wright

## *Introduction*

1983) postulates that richness on a given parcel of land increases as a function of area and available energy. Thus, islands or continental parcels of land with a defined area can be regarded as energy collectors. The species-energy theory have been widely applied in large-scale continental studies, where climate varies considerably among samples. In contrast, the ETIB is used primarily to explain patterns of richness at the regional scale. For example, species-area slopes are often calculated for individual archipelagos, where climate varies little among islands.

Since both climate and isolation impact on richness, these two theories appear to be complementary to one another in explaining patterns of richness. Nevertheless, until now no unified model has been presented incorporating the ETIB and the species-energy theory into a globally consistent, predictive relationship. Although patterns of richness have been related to a bewildering variety of factors describing scale effects, topography, isolation, habitat diversity, historical effects, dispersal ability, etc., the mechanisms behind the species-area, species-energy and species-isolation relationships are still debated (e.g. Hawkins et al. 2003; Wiens and Donoghue 2004). One possible explanation for this is that the answers to these questions are, to some extent, taxon specific.

We choose birds as the taxonomic group for this study because bird species ranges are the best documented globally. Since bird watching associations are present in virtually every country in the world, we were able to obtain reliable checklists and distribution maps for practically every part of the globe. Some may say that birds are not a representative group to study the effects

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of isolation because of their high dispersal ability. Nevertheless, a large portion of the classic literature on island biogeography has used bird data in support of the theories we are testing.

Can most of the variance in insular bird diversity be explained by a tractably small set of variables on the global scale? To test this hypothesis, we assembled a data set, representing virtually all types of islands on our planet, from tropical atolls to Antarctic islands under permanent ice cover. We collected data from the driest, rainiest, hottest, flattest, etc. islands in the world, to simultaneously maximize the variance in all predictor variables. This study demonstrated that most of the variance in global patterns of avian richness can be statistically related about equally strongly to area, isolation and climate. Thus, the species-energy theory and the ETIB are complementary to one another, i.e. the effects of energy and isolation on richness are linearly additive.

### Equilibrium vs. non-equilibrium theories

Aside from a predictive global model of avian richness, the island study produced two notable results. First, we found no interaction between area and distance-based isolation, i.e. although insular bird richness depends strongly both on the size of an island and its distance from the mainland, the effects of area and distance-based isolation were additive. Second, we found very strong area-climate interactions, and demonstrated that  $z$  values (the slope of the richness-area relationship) depend consistently on temperature and precipitation (Chapter 1, Fig. 7). The first of these discoveries is at odds with much of the

## *Introduction*

current and classic literature, and may constitute the first step toward a new paradigm in the field of island biogeography. As Whittaker (2006) pointed out in a commentary on our paper (Kalmar and Currie, 2006), remote oceanic islands show very little turnover of species, despite frequent arrivals of non-resident birds (Lack 1969). Therefore, impoverished island faunas may reflect the paucity of local resources, rather than extinction-immigration dynamics.

The controversial yet unequivocal results of the island study required a more in depth analysis of the species-area relationship (SAR). Do species-area slopes differ between islands and continental parcels of land? Do SAR slopes vary with historical isolation among continents, landbridge islands and oceanic islands? To answer these and other questions, we assembled a data set consisting of continental parcels of land, comparable to our island data set (Chapter 2, Table 1).

While many would agree that species-area slopes depend on isolation, there are different opinions as to how and why? According to MacArthur and Wilson's equilibrium model (1967) SAR slopes are increasing with isolation. Therefore, the steepest SAR slopes can be expected from remote oceanic archipelagoes. However, according to Lawlor's (1986) non-equilibrium model SAR slopes are the steepest on land bridge islands because on oceanic islands richness is limited by low immigration rates. Finally, according to our island study, SAR slopes do not vary with distance based isolations significantly (Fig. 1).

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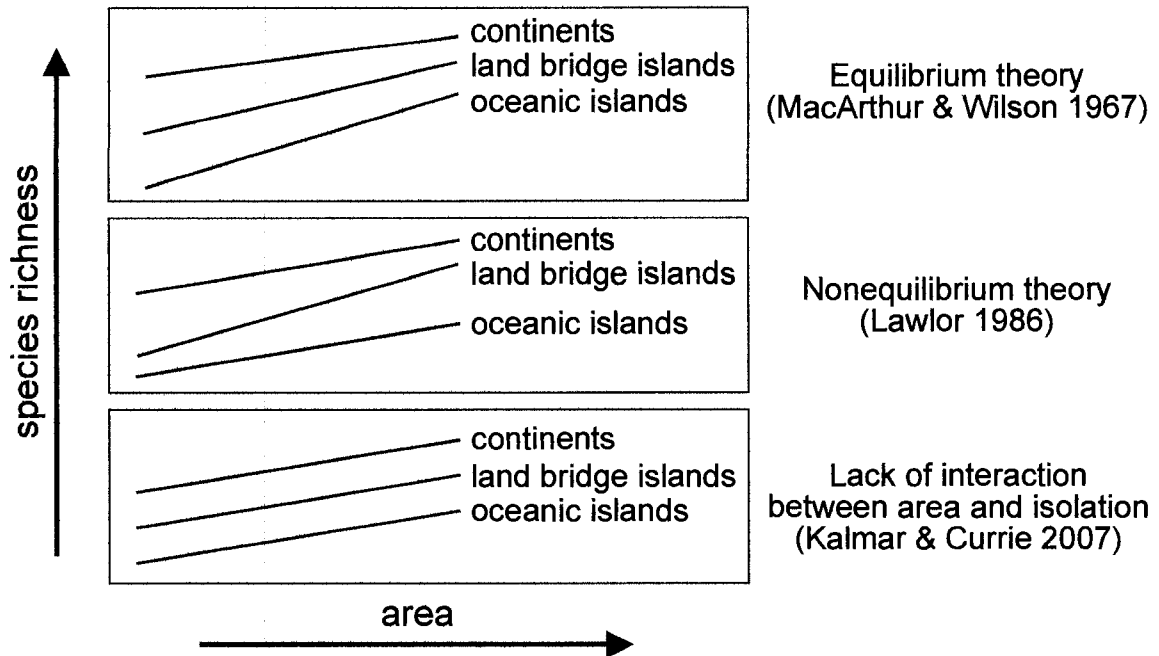


Figure 1. Models explaining variation in species-area slopes among oceanic islands, land bridge islands and continental parcels of land.

Until now, no predictive global model has been presented to explain patterns of richness both on islands and on continents. One of the main reasons for this is that species-area slopes are thought to be steeper on islands than on continents (e.g. Preston 1962). Our second study of avian richness demonstrated not only that SARs are essentially the same on islands and continents, but also that area-climate and temperature-precipitation interactions are so as well. Consequently, avian richness on islands and on continents is commensurable and can be modelled in a single global relationship (Chapter 2, Fig. 6a).

Quantifying the effects of isolation

The greatest challenge of the island study was the quantification of insular isolation. While "distance to continent" has long been regarded as a practical index of insular isolation, there is no generally accepted way to quantify the isolation-reducing effects of neighboring islands. We spent considerable time trying to find out how close and how big neighboring islands have to be to represent a primary source or species pool of potential colonizers for oceanic islands located far from the continental mainland. Finally, our efforts boiled down to a single formula taking into account the number of neighbors, their size and their distances from a target island (Chapter 1, equation 2).

Although few would question that patterns of richness in continental parcels of land depend to some degree on isolation, the quantification of this effect has attracted little attention in the literature. We attempted to quantify spatial gradients of elevation, temperature and precipitation on continents. Since there are no general guidelines on how to proceed on this field, we experimented with various arbitrary operational criteria. Overall, we found that while area and climate variables can explain about 60% of the variation in insular bird richness, they can explain 72% of the variation in continental bird richness. Since measurement error is unlikely to be higher on islands than on continents, this difference may be interpreted as a quantitative measure of the lesser importance of isolation on continents, relative to islands.

Originally, we also addressed the question of peninsular impoverishment. We found that the degree to which a peninsula is surrounded by the sea tends to

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be negatively correlated with elevation, temperature and precipitation. Thus, our results suggest that apparent peninsular impoverishment is equally attributable to climate. Since these results are in line with earlier findings (Brown 1987, Means and Simberloff 1987, Brown and Opler 1990), and some reviewers have suggested that the topic deserves a paper of its own, we finally decided not to include the peninsular effect in Chapter 2.

### Log vs. power transformation

In chapters 1 and 2 our approach to the problem of normalization of error distributions was quite standard statistically, but apparently revolutionary in diversity studies. Until now, in nearly all diversity studies, species numbers have been either log-transformed or untransformed for biology-theoretic reasons. However, these solutions generally yield under- or over-transformed dependent variables. The compromise between the two is a power transformation, the exponent of which should be identified for every data set. The use of different power transformations would practically mean that species-area slopes (z values) would no longer be comparable among various studies. However, we are not convinced that they are truly comparable even using the classic logarithmic transformation because, as Lomolino (2000) pointed out, the theories interpreting z values have never been coupled with an understanding of c, the other fitted constant of the species-area equation ( $S=cA^z$ ).

Since we used a power transformation of bird richness (Chapter 1: exponent 0.2; Chapter 2: exponent 0.3), reviewers have raised the question that

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some of our findings might be artifacts of the transformations we used. In our view, it is odd to argue that artifacts arise from using statistically defensible methods rather than methods that violate the assumptions of the statistics, even if the former appears to be more convenient from a mathematical point of view. We hope that our two papers (Kalmar and Currie 2006, 2007; corresponding to chapters 1 and 2 respectively) will stimulate researchers to adopt a more critical attitude toward the current practice of log-transforming richness.

We emphasize that the inappropriate use of log-transformation may produce artifactual SAR patterns. This is because overtransformed richness yields steeper SAR slopes for smaller sample areas. This is a problem in most island studies because island area and isolation are correlated, i.e. more isolated islands are usually smaller.

### From species richness to paleodiversity

Our global model of avian richness was applied to samples varying in size by about eight orders of magnitude (Chapter 2, Table 1). Even an area of continental size such as Australia would fall nicely in the observed vs. estimate relationship (Chapter 2, Fig. 6a). This observation prompted the idea that the Earth itself could be considered as a single isolate where (global) diversity fluctuates as a function of climate over geologic time. This hypothesis was the original reason why we embarked in our study of paleodiversity.

Studies of paleodiversity have often used Sepkoski's (1992) genus-level marine database. While recognizing the potential advantages of a finer taxonomic

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resolution, we opted to use Benton's (1993) family-level global compendium, *The Fossil Record 2*, which covers both continental and marine organisms. Benton suggests that the Phanerozoic rock record may provide uniformly good data only at the taxonomic level of family and the stratigraphic level of the stage (Benton et al. 2000).

Unlike earlier paleodiversity studies, our study presents multivariate analyses to explain variation in various metrics of marine and continental fossil richness at the taxonomic level of the family (Table 1). This multivariate approach in chapters 3 and 4 emphasizes the analogy between factors controlling contemporary diversity and paleodiversity.

Table 1. Comparison between the two parts of the thesis "Contemporary and Phanerozoic Patterns of Global Biodiversity".

	Contemporary diversity study	Paleodiversity study
scope of study	global	global
organisms studied	birds	marine and continental metazoans
taxonomic level	species	family
samples	islands and continental parcels	stratigraphic stages
predictor variables	area	rock volume
	temperature and precipitation	RCO <sub>2</sub> *
	isolation	provinciality **
perturbation	not considered	polarity reversals, bolide impact

\* past/present ratio of atmospheric carbon dioxide

\*\* not formerly assessed (see thesis conclusion)

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Fossil richness strongly depends on sampling effects, just as contemporary richness patterns depend on the area sampled (Connor and McCoy 1979, Connor et al. 1983). For example, marine fossil richness has long been related to variation in underwater continental shelf area (Sepkoski 1976). Based on their Miocene Mammal Mapping Project, Barnosky et al. (2005) found a species-area effect, comparable to those in contemporary diversity counts. Also, fossil diversity depends on the available amount of rock for sampling (e.g. Raup 1976) and on the number of sedimentary formations (e.g. Peters and Foote 2002), probably reflecting an area and/or habitat diversity effect.

Energy availability and/or climate seem likely to have influenced past diversity (Bambach 1985, 1993) as they do today (e.g. Hawkins et al. 2003). For example, Cornette et al. (2002) found a strong correlation between fractional origination rates of marine animals and atmospheric CO<sub>2</sub> levels for the past 545 million years. RCO<sub>2</sub> levels reflect, to some extent, global estimates of solar radiation and surface temperatures at sea and land (Berner and Kothavala 2001).

Global paleodiversity increases also with provinciality, i.e. the number of distinct paleo-faunal regions (Valentine et al. 1978). Changing provinciality is often invoked to explain the decline or radiation of taxa on the global scale. For example, Adrain et al. (2000) relates the decline in global richness of Ordovician-Silurian trilobites to a decrease in provinciality caused by the approaching of the historically separated landmasses of Avalonia and Baltica to Laurentia. Thus, provinciality can be regarded as a global index of isolation and fragmentation, factors that play an important role in contemporary island biogeography theory (e.g., Whittaker

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1998, chap. 7, 9).

In summary, both contemporary and past patterns of diversity seem to be related to four types of abiotic factors: (1) Area and sampling effects. (2) Climate and energy. (3) Isolation and fragmentation. (4) Perturbation. Based on these analogies and on the assumption that patterns of extinctions and originations are consistent with multiple causal mechanisms (Plotnick and Sepkoski 2001), we extended our multiple regression approach to the second part of this thesis, related to paleodiversity. Unfortunately, quantitative climate data were available only for the Cenozoic and the Cretaceous. Therefore, our attention turned toward the general question of what controls variation in fossil richness (and paleodiversity) over the Phanerozoic?

We gathered data on various geological, astronomical and environmental phenomena, related to fossil richness and variation in fossil richness in earlier studies. These include magnetic polarity reversals, bolide impacts, rock volumes associated with geologic time periods, atmospheric CO<sub>2</sub> ratios, stage duration, etc. We also examined the effect of sea-level change, but this section was later omitted because we found no simple way to quantify per stage sea level change. This is a methodological problem similar to quantifying isolation on continents. Also, the resolution of the available data (Vail et al. 1977) is not constant over time. Higher resolution data on sea-level change has recently become available and may be analyzed at a later time (Haq and Al-Qahtani, 2005).

The quality of the continental fossil record

Continental families make up nearly 40% of all metazoan families with a fossil record. However, in general, paleodiversity studies are limited to the study of marine organisms (e.g. Jablonsky 1999; Foote 2000; Lu et al. 2006). The inclusion of continental taxa into the study of Phanerozoic diversification patterns may be important because an inverse relationship seems to exist between continental and marine diversity (Chapter 4, Fig. 3). Thus, a true picture of global diversity is likely to be a composite of marine and continental patterns. But, is the quality of the continental fossil record adequate to justify its inclusion in global diversity studies?

The completeness of the continental fossil record, as a whole, has not been the subject of quantitative analysis yet. Nevertheless, some recent studies of various continental taxa (reviewed by Benton 2001) seem to challenge the traditional view about the generally poor quality of the continental fossil record (e.g. Padian and Clemens, 1985). Although continental organisms show exponential diversification over the Phanerozoic, as opposed to the logistic curves of marine organisms, this is not necessarily an indication of a poor fossil record (Benton 1997).

Our goal in Chapter 3 is to assess the completeness of the global continental fossil record via quantitative comparisons with marine fossil richness and present day patterns of continental diversity. Our results suggest that, at the family-level, the continental fossil record is not severely less complete than the marine record. We conclude that the continental record is probably adequate and representative to be included in global diversity studies at the suprageneric level.

Magnetic polarity reversals and extinction-origination dynamics

Rates of extinctions and originations exhibit alternating highs and lows throughout the Phanerozoic (Fig. 2). There seems to be little temporal trend as to the magnitude of these alternating see-saw patterns. While origination events are often viewed as biotic rebounds following extinction events, the causes of extinction events are still not well understood (Walliser 1996).

We adopt, once again, a multivariate approach to model variation in fossil richness as a function of abiotic predictors (Chapter 4). Aside of geologic time and stage duration, we assess the predictive values of several factors previously related to variation in fossil diversity (e.g. magnetic polarity reversals: Uffen 1963, Raup 1985; bolide impact cratering: Rampino and Stothers 1984, Becker et al. 2001; paleolevels of atmospheric CO<sub>2</sub>: Cornette et al. 2002).

Raup (1985) proposed a global scale correlation between magnetic polarity reversal activity and extinction events, with a ca. 30 million years stationary periodicity over the past 165 million years. His arguments remained largely unconvincing, possibly because of the low resolution of the magnetic data at hand. To our knowledge, the study we present is the first to use Pisarevsky's (2005) Global Paleomagnetic Database to quantify magnetic polarity reversal intensity and use it to predict variation in fossil richness.

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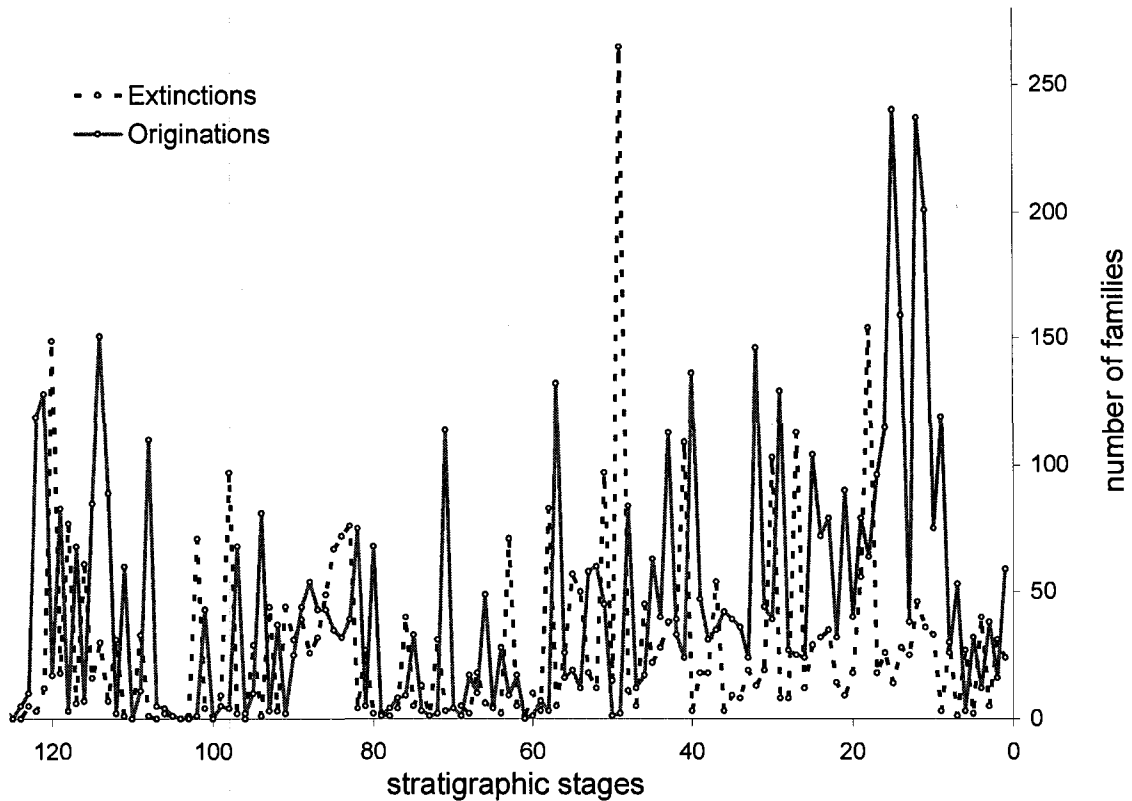


Figure 2. Per stage extinction and origination rates of metazoan families over the Phanerozoic. Time scale is from youngest (Pleistocene=2) to oldest (Tommotian=123). Note the general pattern that stage to stage fluctuations are drastic and peaks tend to be alternating. Data from Benton (1993).

Among all the variables we examined, we found magnetic polarity reversal intensity to be the strongest predictor of variation in fossil family richness. This result is compatible with two explanations. The correlation between the magnetic and fossil data is either the result of strong preservation bias in both, or alternatively, some factor of perturbation may be the link between them. We suspect, however, that mass death and high rates of sedimentation are fairly strongly correlated in Phanerozoic times, making the separation between true diversity trends and sampling bias difficult.

We also found that rates of extinctions and originations, as well as magnetic

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reversal intensity and cratering, all appear to show strong negative autocorrelation at lag+1 stage (Chapter 4, Fig. 2). This suggests that consolidating the correspondence between bio- and geoevents and chronostratigraphic units may improve our ability to detect cyclic and periodic phenomena.

### The Phanerozoic Time Synchronization Chart

Despite frequent revisions, the geologic time scale shows little sign of gradual refining (Table 2). Although the vertical ordering of (sub)stages and their positions within systems are well established, stage durations are still not known accurately (Newman and Palmer 1999, p.4). There are also considerable differences in opinion regarding the number of stages, especially in the Lower Paleozoic and the Carboniferous (Chapter 5: Fig. 10). These uncertainties make the detection of cyclic and periodic phenomena difficult with conventional time series analyses.

To solve this problem, we propose a modified Phanerozoic time scale, designed to study cyclic and periodic phenomena over the Phanerozoic (Chapter 5: pp. 211-212). We have classified Phanerozoic stages into alternating extinction and origination intervals, thus allowing the dynamics of bioevents to define a new chronostratigraphic unit, we call "half-cycle". We propose that an origination half-cycle and an extinction half-cycle make up a complete origination-extinction cycle, and that Phanerozoic history is a series of such cycles. Some evidence suggests that half-cycles are also related to eustatic cycles (Hallam 1996: Fig. 2).

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Table 2. Estimated durations of Phanerozoic periods [Myr], according to nine versions of the geologic time scale, published between 1937 and 2004.

	1937	1948	1958	1961	1973	1982	1990	1995	2004
Cenozoic	70	58	60	63	65	65	65	66.4	65
Cretaceous	38	69	70	72	71	65	80.6	77.6	81
Jurassic	37	25	25	46	59	74	62.4	64	54
Triassic	48	30	30	49	30	41	37	37	51
Permian	34	21	25	50	55	45	45	41	48
Pennsylvanian			25	30		30	32.8	34	19.1
Mississippian	{ 48	{ 52	30	35	{ 65	40	39.7	40	41.1
Devonian	38	58	52.5	60	50	40	46	48	56.8
Silurian	18	37	40	20	50	18	30.5	30	27.7
Ordovician	61	80	80	75	55	77	71	67	44.6
Cambrian	78	80	80	100	70	35	60	65	53.7

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The PTSC enabled us to demonstrate a strong supercyclic pattern repeating itself over three large segments of the geologic column: the Lower Paleozoic, the Upper Paleozoic and the Mesozoic. We found that patterns of extinctions, originations, total metazoan family richness and magnetic polarity reversal intensity all exhibit this previously undocumented supercyclic pattern (Chapter 5: Fig. 3, 6a, 8, 9). Further, cratering intensity and magnetic polarity reversal intensity both appear to peak at the end of extinction half-cycles. Since it is unlikely that cratering, an astronomical phenomena, is influenced by endogenous earth processes, these observation prompted us to develop a general mechanistic model, according to which the ultimate drivers of variation in paleodiversity are astronomical phenomena.

### The Distant Solar Companion Theory

A series of articles published in 1984 generated substantial debate about periodic patterns in mass extinctions and potential astronomical explanations for them (Davis and Muller 1984; Rampino and Stothers 1984; Schwartz and James 1984; Whitmire and Jackson 1984). Raup and Sepkoski's (1984) original paper drew a flood of criticism (Hallam 1984; Kitchell and Pena 1984; Hoffman 1985; Lutz 1986; Stigler and Wagner 1987; Patterson and Smith 1987, 1989; Benton 1995). During the 1990s the debate subsided, with proponents and opponents of periodicity unable to convince each other (Raup and Sepkoski 1986; 1988; Sepkoski 1987, 1990).

Several of the above mentioned studies suggested that an astronomical

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driving force can explain long term periodicity in the fossil record. The theory of a distant solar companion was proposed (Whitmire and Jackson 1984; Raup 1999, Muller 2002), but this remains unconvincing because the companion star would require a highly eccentric and unstable orbit to explain the proposed ca. 26-32 million years periodicity in extinction events (e.g. Raup 1985, Tiwari and Rao 1999). The oscillation of the Solar System around the galactic mid-plane has also been suggested (Rampino and Stothers, 1984). This scenario remains untestable, because the distant past and future trajectory of the Solar system can not be determined accurately.

In Chapter 6 we present a radically new version of the distant solar companion theory. This model has two main characteristics: (1) In contrast to earlier binary models, we propose relatively short orbital periods for the Sun and the hypothetical distant solar companion. (2) We propose that three distinct astronomical phenomena are the ultimate driving forces behind cyclic bio- and geo-events. This general model relates astronomical phenomena to geomagnetic, geotectonic, eustatic and bio-events, with the goal to illustrate the importance of developing mechanistic, multidisciplinary models, capable to connect the findings of various fields of research.

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## Chapter 1

# A global model of island biogeography

## *A global model of island biogeography*

### Abstract

The goal of our study was to build a global model of island biogeography explaining bird species richness that combines MacArthur and Wilson's area-isolation theory (1967) with the species-energy theory (Hutchinson, 1959; Brown, 1981; Wright 1983). We assembled a global data set of 346 islands representing virtually all types of climate, topography and degree of isolation on our planet, ranging in size from 10 hectares to 800 000 km<sup>2</sup>. We found that about 85-90 % of the global variance in insular bird species richness can be explained by simple, contemporary abiotic factors. On a global scale, the three major predictors - area, average annual temperature and the distance separating the islands from the nearest continent - all have constraining (i.e., triangular rather than linear) relationships with insular bird species richness. We found that the slope of the species-area curve depends on both average annual temperature and total annual precipitation. Range in elevation - a surrogate for diversity of habitat - showed a positive correlation with bird diversity in warmer regions of the world, while its effect was negative in colder regions. Insular isolation depends not only on the distance of an island from the continent, but also on the presence or absence of other neighbouring islands. We also propose a global statistical model to quantify the isolation-reducing effect of neighbouring islands. In summary, the variation in avian richness among islands worldwide can be statistically explained by contemporary environmental variables. The Equilibrium Theory of Island Biogeography and the species-energy theory are complementary to each other in explaining patterns of spatial variation in diversity: on the global scale avian

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richness depends about equally upon area, climate, and isolation. Finally, the slope of the richness-area curve depends upon climate, but not on isolation, in contrast to MacArthur and Wilson's theory.

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Variation in species richness among islands gave rise to one of the most fruitful areas of ecology. The simple hypotheses proposed in MacArthur and Wilson's (1967) *The theory of island biogeography* spawned an enormous literature with both theoretical and conservation implications (Gilbert, 1980; Rosenzweig, 1995; Whittaker, 1998) that are discussed in most contemporary ecological textbooks. Yet, the literature that addresses the factors that determine species richness on islands contains a very curious gap.

MacArthur and Wilson (1963, 1967) proposed that species richness on islands is the result of immigration (sometimes reinforced by speciation) and extinction. They hypothesized that larger islands have lower extinction rates than smaller ones, and that islands farther from the mainland have lower immigration rates than coastal islands. Their hypothesis predicts that species richness should covary positively with island area in a set of similarly isolated islands. Further, richness should covary negatively with distance from the source of colonists in a set of islands of similar size. The classic tests of the mechanisms involved in the equilibrium model of island biogeography examined these predictions mainly at local to regional scales (Table 1). Thus, the data implicitly excluded the effects of factors that vary over larger spatial scales (e.g., climate or evolutionary history).

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In contrast, many other studies of biodiversity gradients have focused on habitat variables that might somehow limit diversity. Hutchinson (1959), for example, hypothesized that species richness is limited by the partitioning of available energy among the species present in any locality (Hutchinson, 1959; Brown, 1981). Gradients of richness would thus arise where energy availability differs among regions. Similarly, areas with more diverse habitats may have more species (e.g. Kerr and Packer, 1997; Ricklefs and Lovette, 1999). Latham and Ricklefs (1993) suggest that regional differences in evolutionary history largely determine spatial variation in species richness. Tests of these ideas have typically examined species richness over very large spatial extents (Adams and Woodward, 1989; Francis and Currie, 2003).

Wright (1983) attempted to refine MacArthur and Wilson's theory using the species-energy hypothesis (Hutchinson, 1959; Brown, 1981). He proposed that islands are essentially energy collectors. The amount of energy collected by an island varies with primary productivity per unit area, and it increases in proportion to island area. Islands that are warm and wet (i.e., high actual evapotranspiration, AET) are more productive, and therefore more speciose than islands with low AET. To test this idea, Wright (1983) related land and freshwater bird species richness on 28 islands around the world to the product of island area and per-unit-area net primary productivity. Wright's regression models statistically explained nearly 80% of non-marine bird species richness by total net primary productivity per island. Yet, Wright did not address the question of isolation, which figures prominently in works deriving from MacArthur and Wilson. Since almost all the islands in Wright's

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data were on continental shelves (i.e. isolation varied little among his samples), it is not surprising that area and climate explained most of the variance in insular bird richness among his samples. Therefore, just as MacArthur and Wilson excluded the effects of variables such as climate by focusing on individual archipelagos, so too Wright excluded the effects of isolation by considering islands located at relatively small distances from the nearest continent (median = 171.5 km, n=36; cf. Table 1).

More generally, research in the past three decades on island species richness has concentrated on the study of particular archipelagos, which represent very limited subsets of the set of islands that exist globally. These studies often examined different sets of independent variables. Consequently, the predictor variables most strongly related to species richness often differed not only among taxa but also among archipelagos. One interpretation of these results is that the factors that determine richness on islands are local and idiosyncratic (e.g., Slud, 1976). Another possible explanation is that regional differences in evolutionary history have strongly affected diversity (e.g., Ricklefs, 2004). In addition, the importance of predictor variables in various studies depends strongly on scale (i.e., the range of variation in area, isolation, elevation, etc.) and on the mobility of the taxa studied (Martin, 1981; Rosenzweig, 1995; Whittaker, 1998, 2000). In the present paper we show that it is possible to construct a global area-isolation-climate model, encompassing virtually the full scale of variability in all the predictor variables used (Table 1).

Acknowledging that many factors *can* be related to patterns of richness

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under particular circumstances, we propose to test simultaneously the disparate set of hypotheses discussed above by examining bird species richness on islands covering a full range of area, elevation, isolation and climate. In particular, we examine how much of the global variation in species richness is related to climate (temperature and precipitation), island area, isolation, topography (e.g., Ricklefs and Lovette, 1999), and biogeographic region.

### Methods

We examined the relationship between bird species richness and island characteristics based on published records from islands worldwide. We collected data describing 346 islands ranging in area from less than 0.1 km<sup>2</sup> to more than 800 000 km<sup>2</sup>, located in all major geographic and climatic regions on Earth (Fig. 1). The data include the full range of island types, from isolated tropical atolls to Antarctic islands embedded in permanent ice. Although most of our data were included non-systematically (i.e., we included data as we encountered them), we did actively seek to maximize the range of variability in predictor variables and to minimize collinearity by finding islands with particular characteristics (e.g., large islands with low elevation, small coastal islands, small satellite islands, etc.).

Islands in this study are nearly always single landmasses. About two dozen are atolls (these may have separate islets within their lagoon) and half a dozen are fragmented islands (highly compact groups forming a single ensemble e.g., Andros in the Bahamas, or Aru near New Guinea). We did not include recently formed volcanic islands, tidal islands, islands located in freshwater bodies, nor

data pooled over groups of islands (e.g., the Philippines as a single unit: Wright, 1983)

The number of breeding bird species on each island was determined from annotated checklists and distribution tables in international field guides and ornithological journals. We also used range descriptions and range maps in cases where this could be done unambiguously (i.e., not in cases where a species could be absent from an island even though its geographic range overlaps the island). For New Caledonia and three islands in the Lesser Sundas (Flores, Sumba and Timor) we used the number of breeding land and freshwater bird species indicated in Wright's study (1983).

We only included species described as breeding, or probably breeding, on a given island. Thus, migratory birds were counted only in their breeding range. We did not try to include all recorded species from each island because "complete" checklists tend to include varying numbers of vagrant species, depending on sampling intensity. There were rarely sufficient data to distinguish among non-breeding winter visitors, migrants, regular vagrants, irregular vagrants, etc.

In addition to extant and recently extinct species, we included species extirpated within the past 400 years, using information from Walters (1980), Fuller (1987), Ripley (1977) and Greenway (1958). We also included species that are likely to have independently – i.e., without direct human intervention - colonized islands. By including both recent natural colonists and extirpated species, we may have over-estimated instantaneous species richness. We did this because it was rarely possible to pinpoint times of extinction or colonization. However, since

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cases of observed natural colonization are rare (an order of magnitude less frequent than extinctions), their effect on our analyses is probably minimal. Fossil species, introduced species, and established populations of domesticated birds were excluded from our analysis.

We also excluded marine species from our study because their distribution patterns are likely governed by factors other than those affecting terrestrial birds. These are the Spheniscidae (penguins), Procellariiformes (albatrosses, shearwaters, storm petrels, etc.), Phaethontidae (tropic birds), Sulidae (boobies and gannets), Fregatidae (frigate birds), Stercorariidae (skuas), and Alcidae (auks). Marine species or local marine populations of species in the following taxa were also excluded: Pelecanidae (pelicans), Phalacrocoracidae (cormorants), Anatidae (ducks and geese), Laridae (gulls and terns), and Rynchopidae (skimmers).

We used average annual temperature and total annual precipitation - the two readily obtainable components of actual evapotranspiration - as our descriptors of climate. For islands having weather stations, we calculated the island's mean temperature and precipitation from local weather station records (Wernstedt, 1972; Walter and Lieth, 1967). For islands without any weather station, temperature and precipitation were inferred from measurements at the nearest weather stations and from maps showing temperature and precipitation gradients. We would have liked to examine relationships between richness and potential evapotranspiration (Currie, 1991) and/or net primary production (Adams and Woodward, 1989). However these data proved to be unavailable for many

small islands.

To examine isolation effects, we considered three factors: (1) distance from each island to the nearest continent, (2) distances to other neighbouring islands, and (3) the area of these neighbours. We hypothesized that the effect of neighbouring islands on the richness of a target island is additive, and that richness could, in principle, depend on all islands closer than the continent. We postulated that the importance of a neighbour as a potential source of colonization is proportional to its area ( $A$ , km<sup>2</sup>), and inversely proportional to the distance ( $D$ , km) that separates it from the target island. A general formula for the neighbour effect ( $N$ ) can therefore be written as:

$$N = \sum \frac{A^a}{(D+1)^b}$$

eq. 1

where the exponents  $a$  and  $b$  are empirical constants, estimated iteratively by modifying them to maximize the correlation with species richness. Theoretically the summation includes all islands closer than the continent. But, for practicality we omitted neighbours that would contribute only negligibly to the summation because they are too small and/or too distant. Thus, the 346 islands of our data set each have, on average, 8.5 neighbours (SD=7.9). For 19 islands we found no sizeable neighbour closer than the continent. So that these would not be missing cases in the analyses, we assigned a hypothetical neighbour half the size of the smallest neighbour in our data set, located at half the distance to the continent (the midpoint of the possible range). This is analogous to adding a value of 0.5 to data before log transformation so that values of 0 do not become undefined. Distance

to the neighbour (km) was increased by 1 in eq. 1 to prevent very close neighbours from having inordinate influence on  $N$ .

Isolation was measured as the linear distance over open sea. For island chains, the distances between islands were summed, excluding the distances over the land areas of the "stepping stones". Neighbouring islands having no land birds at all were excluded from our neighbour index. (It would be biologically meaningless, for example to consider a large Antarctic island as a potential source of colonization for a smaller island nearby, if the larger island does not support land bird species at all. For the same reason, Antarctica was not considered as a continent or a neighbour).

Species richness ( $S$ ) values were transformed as  $S' = (S + 0.5)^{0.2}$  in order to stabilize residual variance in statistical analyses. In practice, this transformation is close to the logarithmic transformation that has been used more commonly in earlier literature. The fifth root transformation yields residuals that conform more closely to a normal distribution in the present data set. The results presented below are qualitatively identical when the logarithmic transformation is used.

Independent variables in our analyses were transformed before analysis such that their distributions would be approximately symmetric. Thus, we related species richness to the following environmental variables: (1) logarithm of the total land area of an island in  $\text{km}^2$ ; (2) range in elevation on the island, i.e., the difference in metres between sea level and the highest point, raised to the power of 0.4; (3) mean annual temperature in  $^{\circ}\text{C}$ , untransformed; (4) total annual precipitation in mm, raised to the power of 0.4; (5) distance to the continent

measured as the shortest distance over open sea to the nearest continental coast in km, raised to the power of 0.2; (6) logarithm of the neighbour index (defined by equation 2). (7) We also included faunal region in our analyses: a categorical variable with seven levels: Palearctic, Oriental, Ethiopian, Australasian, Nearctic, Neotropical and Antarctic/Sub-Antarctic (Sclater, 1858). The Oriental-Australasian boundary follows Weber's line (Weber, 1902).

## Results

Collinearity among predictor variables in our data set is reasonably low (Table 2). Three cases deserve special attention. Mean annual temperature and precipitation are collinear, reflecting the low absolute humidity of cold air. In general, islands in polar regions cannot have as much annual precipitation as tropical islands. Further, as a consequence of convection and Hadley cell circulation, there are few dry islands in temperate regions. Second, maximum elevation is related to island size: very small islands cannot be as high as large islands. Third, as distance from the continental shore increases, the abundance of large islands decreases, thus island area is negatively correlated with the distance to the continent. Note that the strongest of these three collinearities is  $r=0.58$ .

Islands tend to have a clustered distribution over the globe (Fig. 1). To estimate the extent of autocorrelation in our data, we randomly selected 2000 pairs of islands, and we generated a semivariogram (i.e., the squared difference in number of species as a function of the distance between the pairs of islands, both fifth-root transformed). The correlation between semivariance and distance in our

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data set was very weak ( $r^2=0.035$ ). We concluded that spatial autocorrelation is not pronounced, and it is unlikely to influence significance tests to any great degree in the models presented below. Nonetheless, to remain conservative we only interpret relationships stronger than  $p<0.001$  (except where noted).

On the global scale, relationships between richness and most environmental variables we examined are restrictive (triangular), rather than simple functions (e.g., Fig. 2). It appears that area, temperature, precipitation and distance to the nearest continent can all potentially set an upper limit to richness, but richness falls below this maximum on many islands due to one or more of the other potential limiting factors. Consequently, in data that include islands globally, richness is significantly related to area, isolation and climate, but no individual correlation dominates (Table 3).

Richness is often more strongly related to interactions among environmental variables than to individual variables (Table 3). Consider, for example, the richness-area relationship (the “species-area curve”). As a function of temperature, the slope of the richness-area relationship (Fig. 3a) increases progressively from 0.04 at  $-20^{\circ}\text{C}$  to 0.41 at  $+30^{\circ}\text{C}$  (the slope of log-log species-area relationships increase from -0.005 to 0.44). Area, temperature, and their interaction can statistically account for 64 % of the global variation in insular bird species richness (Table 4, model 1).

Richness depends similarly upon an interaction between area and precipitation (Fig. 3b). Among dry islands, richness is nearly independent of island area, but the richness-area slope increases progressively with precipitation (Fig.

3b). Note that the area - precipitation interaction term alone explains more variance in richness than area and temperature or area and precipitation additively (Table 3).

In our worldwide data, richness is only weakly correlated with elevation range (Table 3), a variable thought to be a surrogate for habitat diversity (e.g., Ricklefs and Lovette, 1999). The simple richness-elevation correlation is so strongly collinear with area (Pearson,  $r=0.58$ ) that, when both variables are included in a model, elevation range becomes non-significant (Table 4, model 4). However, the effect of elevation range has an important interaction with temperature (Fig. 3c). When elevation range and an elevation range – temperature interaction are included together in a multiple regression, they are both significant (Table 5). Cumulatively, temperature, elevation range and their interaction can explain 29% of insular bird diversity (cf. Table 4, model 1).

Richness also relates to an interaction between temperature and precipitation (Fig. 3d). Among very cold islands, richness is either unrelated to precipitation or weakly negatively related. In temperate regions, richness is a moderately peaked function of precipitation, and the peak increases with temperature. In hot regions, richness increases with precipitation. From another perspective, richness is a plateauing function of temperature on dry islands, but on wet islands, richness continues to increase with increasing temperature. The residual variation explained by the temperature – precipitation interaction in multiple regression models is small (Table 5) because it is strongly collinear with other climate descriptors. The simple correlation between richness and this

interaction is  $r^2=0.18$ .

Several statistically indistinguishable multiple regression models (ex. Table 4, model 3) can be constructed that include area, quadratic functions of temperature and precipitation, and interactions among these variables, all with  $R^2=0.69$  to  $0.70$ . Their common elements are that all three variables remain in the models, usually involving interaction terms. Area and temperature effects predominate.

Richness on islands is also very clearly related to isolation (Table 3 and Table 4, models 6 and 7). The strongest single correlate of richness is the distance to the nearest continent, although the relationship is again approximately triangular (Fig. 4). Richness is also positively related to the presence of neighbouring islands, but much less strongly than to the proximity of a continent (Table 3). By iteratively varying the exponents of neighbour area and distance to neighbour (eq. 1), we found that the correlation between richness and the neighbour index is maximal when the coefficients  $a$  and  $b$  in eq. 1 are approximately 1 and 2, respectively. In other words, the effect of neighbouring islands is proportional to their area, and inversely proportional to the square of their distance. Thus, equation 1 can be rewritten as:

$$N = \sum \frac{A}{(D+1)^2} \quad \text{eq. 2}$$

In multiple regressions, the neighbour index is significant only by its interaction with distance to the continent. This is probably because the effect of neighbours is diminished when the continent is close. Cumulatively, our two isolation metrics can statistically explain 48.5% of the variance in insular bird species richness

(Table 4, model 6). The neighbour index is not correlated with distance to the continent (Table 2); its statistical significance indicates that insular isolation is diminished by the presence of neighbouring islands (Table 4, models 6-7). Interestingly, we found no significant interaction between area and isolation metrics, suggesting that the slope of the richness-area curve does not depend on isolation.

A multiple regression model (Table 5) incorporating the effects described above can statistically explain 86.6% of the variance in bird species richness among the world's marine islands, yielding a relationship that is no longer triangular (Fig. 5). Note that the main factors are the area-precipitation interaction, distance to the continent and temperature. These three terms can explain 82.6% of the variance in insular bird species richness.

To test if there are significant differences in insular species richness among biogeographic regions we included the categorical variable Faunal Region in forward- and backward-stepwise models including the variables listed in Table 5. In the forward selection regression, Faunal Region was the only term eliminated as non-significant. Using backward elimination, Faunal Region was significant ( $p < 10^{-7}$ ) and the temperature-precipitation interaction is not selected. The effect of Faunal Region is mainly due to lower than expected diversity in the Sub-Antarctic/Antarctic region. Post hoc tests showed that there are no significant differences among the Palaearctic, the Oriental, the Australasian, the Nearctic and the Neotropical regions (Figure 6; Tukey  $p \geq 0.2$  with the exception of Palaearctic-Nearctic comparison, where  $p = 0.044$ ).

## Discussion

Variation in non-marine bird species richness among oceanic islands worldwide can be related to environmental conditions. Variables describing island size, climate and isolation account for >87% of the global variation (Table 5). This result is very similar to studies of broad-scale variation in continental species richness (Francis and Currie, 1993; Hawkins *et al.* , 2003). Since this model is applicable to virtually all types of marine islands, there is no evidence to suggest that insular bird diversity is idiosyncratic as has been suggested (cf., Slud, 1976).

As several earlier studies have observed, only very small differences in species richness among faunal regions remain after accounting for contemporary environmental variables (Adams and Woodward, 1989; Francis and Currie, 2003; Hawkins *et al.* , 2003). Although we found diversity to be somewhat lower than expected in the Ethiopian and especially in the Sub-Antarctic/Antarctic regions, we found virtually no differences between faunal regions with outstandingly different history, such as the Australasian, the Palaearctic or the Neotropical regions. The lower than expected diversity in the Ethiopian region may be due to an observer effect (poorer data than elsewhere). In the Antarctic/Sub-Antarctic region diversity may be lower than expected because Antarctica ceased to be a source of potential colonisers long ago.

Our results show that care must be taken in interpreting the slope of species-area relationships. The species-area relationship is usually described as approximately log-linear (e.g., Arrhenius, 1921; MacArthur and Wilson, 1963, 1967; Schoener, 1976; Triantis *et al.*, 2003). Authors often point out that, for

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islands, the exponent  $z$  of the classic species-area equation (Arrhenius, 1921) is generally  $0.15 < z < 0.35$ . Differences in  $z$  have been attributed to a number of biotic and abiotic factors such as the mobility and range size of species, feeding behaviour (predator vs, prey), range of areas sampled, type of area (islands, habitat islands, mainland), habitat fragmentation, etc. However,  $z$  also clearly varies with climate. This was also noted by Malyshev (1975, cited by Venevskaja and Venevsky, 2002). Malyshev's plant study suggests that  $z$  varies from 0.07 (deserts and tundra) to 0.36 (tropics). Also, Venevsky and Venevskaja (2003) incorporate an area-climate interaction into their model of plant species richness. These results are compatible with our finding that  $z$  varies systematically with precipitation (Fig. 7).

Although Wright (1983) did not include isolation in his global model of richness on islands, we found that isolation is very important contributor to the global variation in insular species richness. Our findings on insular isolation can be summarized as follows. (1) Richness depends strongly on the distance between islands and the nearest continental shores (Table 3, Fig. 4), which presumably reflects an effect of isolation. (2) Isolation can be reduced by the presence of neighbouring islands (Table 4, models 6-7). (3) The isolation-reducing effect of a neighbouring island is proportional to the size of the neighbour and inversely proportional to the square of the distance which separates it from the target island (equation 2). (4) This neighbour effect is additive and theoretically it depends on all islands that are closer to island A than the nearest continent, although in practice the effect of small and faraway islands is negligible (equation 2).

(5) The importance of neighbours increases with the distance of the target island from the continent. These relationships are largely consistent with the current understanding of the effect of isolation on species richness (MacArthur and Wilson, 1967, p. 22; Rosenzweig, 1995, p. 236 ff.).

Our results are also consistent with a small effect of habitat diversity on species richness. Our choice to approximate habitat diversity by elevation range rather than a measure of habitat types or vegetation cover was dictated by data availability rather than by theoretical considerations. It is possible that the significance of this term in our regression models underestimate the importance of habitat diversity. Nonetheless, we found that richness is significantly positively related to elevation range in warm areas, and negatively so in polar and sub-polar regions (Fig. 3c). The negative relationship in cold areas is probably because high altitude zones are too cold to support many species. Note that the variation in slope of the richness-elevation relationship varies continuously with temperature; we observe no threshold as suggested by Kerr and Packer (1997).

These results beg the question of what mechanisms produced patterns of richness on islands. Insular bird richness depends upon island area and isolation in a manner that is largely consistent with the mechanisms proposed by MacArthur and Wilson (1963, 1967): colonization, speciation, and extinction. In contrast to MacArthur and Wilson, however, we found that the effects of area and isolation are merely additive. Instead of area-isolation interaction we found strong area-climate interactions (Figures 3a-b). On the global scale, the species-area relationship is not linear, but restrictive just like species-climate or species-isolation relationships

(Figures 2, 4, 7).

We have shown that, using classic log-transformed richness as a dependent variable,  $z$  values increase progressively with precipitation (Fig. 7). We found a similar relationship between  $z$  values and temperature as well (not illustrated). These results are compatible with the notion of higher beta-diversity in tropical regions. In general, bird richness increases with available energy in a globally consistent manner, as Francis and Currie (2003) observed for angiosperms. The mechanism(s) that underlie these patterns are still hotly debated (cf. Hawkins *et al.*, 2003; Ricklefs, 2004; Wiens and Donoghue, 2004). This study was not designed to distinguish among them (but see Currie *et al.*, 2004).

Finally, our observed relationship between richness and elevation suggests that habitat heterogeneity can increase richness by adding habitats in warm areas, and reducing available habitat in cold places. In contrast, our statistical evidence suggests either that regional/historical effects have minor impact on species richness, or that those effects must be very strongly collinear with contemporary climate (cf. Francis and Currie, 2003; Qian and Ricklefs, 2004; Currie and Francis, 2004).

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Tables and figures

Table 1. Dependent and independent variables used in our regression models explaining non marine bird species richness. N=346

variable	minimum	maximum	median
number of species	0	547	29
island area (km <sup>2</sup> )	0.085	820033	625.0
highest elevation (m)	3	5030	710.5
mean annual temperature (°C)	-26	30	20.3
total annual precipitation (mm)	25	5470	1077.5
distance to continent (km)	0.23	6178	364.0
neighbour index *	2.7e-07	1823	0.012

\* no units (based on eq. 2)

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Table 2. Pearson correlation matrix of predictor variables used in our multiple regression models to explain variation in insular bird species richness. For  $n = 346$ , correlations at  $|r| \geq 0.105$  are significant at  $p = 0.05$  (\*), and at  $|r| \geq 0.175$  they are significant at  $p = 0.001$  (\*\*).

	log(area)	elevation <sup>0.4</sup>	temperature	precipit. <sup>0.4</sup>	distance to continent <sup>0.2</sup>
log(area)	1.000				
elevation <sup>0.4</sup>	0.580**	1.000			
temperature	-0.272**	-0.046	1.000		
precipitation <sup>0.4</sup>	-0.049	0.130*	0.564**	1.000	
(distance to cont.) <sup>0.2</sup>	-0.373**	0.053	0.164*	0.231**	1.000
log(neighbour index)	0.441**	0.231**	-0.085	0.029	-0.261**

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Table 3. Correlations between avian richness (fifth root transformed) and various environmental variables and two-way interaction terms. N = 346.

term	r <sup>2</sup>	p
log(area)	0.29	<10 <sup>-15</sup>
temperature	0.12	<10 <sup>-10</sup>
precipitation <sup>0.4</sup>	0.08	<10 <sup>-7</sup>
log(area) x temperature	0.37	<10 <sup>-15</sup>
log(area) x precipitation <sup>0.4</sup>	0.45	<10 <sup>-15</sup>
distance to continent <sup>0.2</sup>	0.39	<10 <sup>-15</sup>
log(neighbour index)	0.18	<10 <sup>-15</sup>
dist. to continent <sup>0.2</sup> x log(neighbour index)	0.41	<10 <sup>-15</sup>
elevation <sup>0.4</sup>	0.07	<10 <sup>-5</sup>
elevation <sup>0.4</sup> x temperature	0.09	<10 <sup>-8</sup>
elevation <sup>0.4</sup> x log(area)	0.19	<10 <sup>-15</sup>

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Table 4. Multiple regression models predicting bird species richness (fifth root transformed) on islands worldwide. Model 1 accounts for the combined effects of area and temperature, and model 2, for area and precipitation. Model 3 is a general species-energy model. Model 4 shows that elevation range has little effect per se (cf. Table 3). Model 5 is a climate model without area (cf. model 3). Models 6 and 7 show the effects of our two isolation metrics. N = 346.

model	Predictors used in GLMs	p	model R <sup>2</sup>
1	log(area)	0.001	0.64
	temperature	<10 <sup>-7</sup>	
	temperature x temperature	<10 <sup>-7</sup>	
	log(area) x temperature	<10 <sup>-4</sup>	
2	log(area)	0.035	0.48
	precipitation <sup>0.4</sup>	0.697	
	precipitation <sup>0.4</sup> x precipitation <sup>0.4</sup>	0.017	
	log(area) x precipitation <sup>0.4</sup>	<10 <sup>-12</sup>	
3	temperature	<10 <sup>-15</sup>	0.70
	temperature x temperature	<10 <sup>-15</sup>	
	precipitation <sup>0.4</sup>	<10 <sup>-15</sup>	
	log(area) x precipitation <sup>0.4</sup>	<10 <sup>-15</sup>	
	temperature x precipitation <sup>0.4</sup>	<10 <sup>-15</sup>	
4	log(area)	<10 <sup>-4</sup>	0.29
	elevation <sup>0.4</sup>	0.150	
5	temperature	<10 <sup>-3</sup>	0.26
	temperature x temperature	<10 <sup>-3</sup>	
	precipitation <sup>0.4</sup>	0.001	
	precipitation <sup>0.4</sup> x precipitation <sup>0.4</sup>	0.027	
	temperature x precipitation <sup>0.4</sup>	0.001	
6	dist. to continent <sup>0.2</sup>	<10 <sup>-11</sup>	0.48
	dist. to cont. <sup>0.2</sup> x log(neighbour index)	<10 <sup>-13</sup>	
7	dist. to continent <sup>0.2</sup>	<10 <sup>-10</sup>	0.54
	dist. to cont. <sup>0.2</sup> x log(neighbour index)	<10 <sup>-9</sup>	
	log(area)	<10 <sup>-6</sup>	

*A global model of island biogeography*

Table 5. A global model of insular bird species richness (fifth root transformed) on environmental variables. Variables are listed in order of inclusion by forward selection (beginning with the variables listed in Table 3), with the cumulative proportion of explained variance. The proportion of the variance explained by the variable when added last and the AIC value of the cumulative model are also shown. N=346.

term	cumulative R <sup>2</sup>	increase in R <sup>2</sup> if added last	AIC
log(area)×precipitation <sup>0.4</sup>	0.452	0.084	-638
distance to continent <sup>0.2</sup>	0.728	0.092	-879
temperature *	0.827	-	-1032
dist. to cont <sup>0.2</sup> x log(neighbour index)	0.847	0.013	-1072
precipitation <sup>0.4</sup> x precipitation <sup>0.4</sup>	0.858	0.010	-1094
temperature x precipitation <sup>0.4</sup>	0.860	0.003**	-1097
elevation range <sup>0.4</sup> ***	0.877	0.017	-1138
elevation range <sup>0.4</sup> x temperature ***			

\* Temperature – selected by forward selection - becomes non-significant (p=0.51) after the inclusion of elevation range and the elevation range-temperature interaction.

\*\* Not significant in backward elimination.

\*\*\* Elevation range and its interaction with temperature are only significant if they are both included in the regression.

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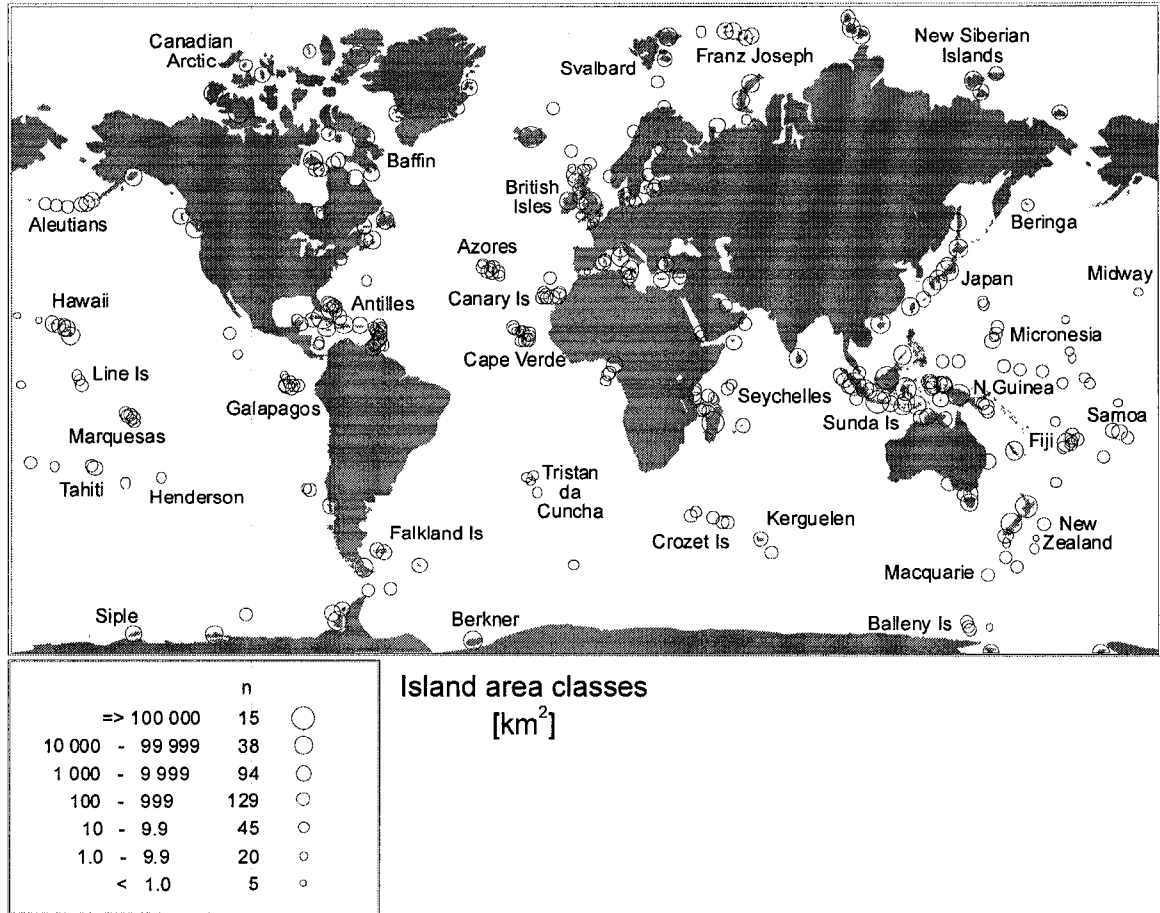


Figure 1 Spatial distribution of the 346 islands included in this study.

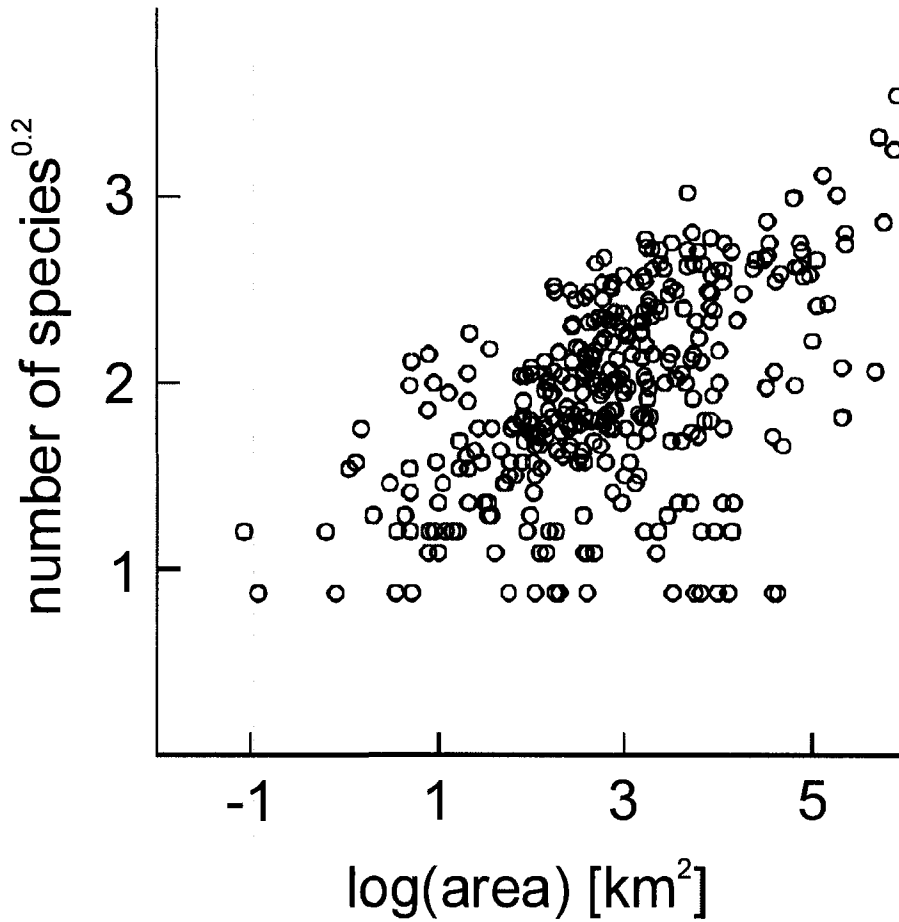


Figure 2 Relationship between bird species richness<sup>0.2</sup> (plus 0.5) and island area. Similar restrictive (i.e., triangular) relationships are observed when the predictor variable is temperature or precipitation. N = 346.

*A global model of island biogeography*

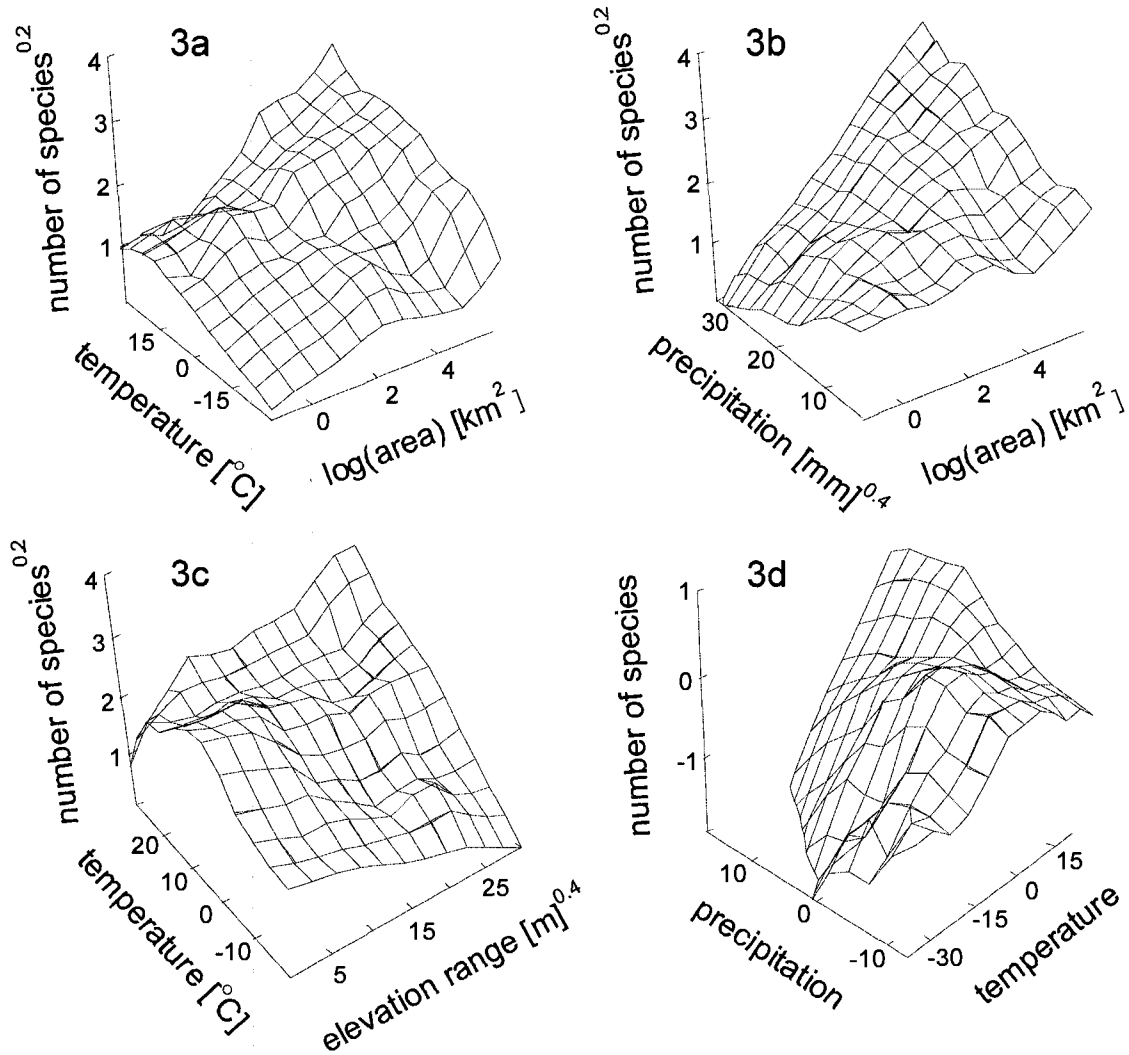


Figure 3 Relationship between bird species richness and island area, mean annual temperature, total annual precipitation and elevation range on islands.

Smoother method: distance weighted least square (DWLS), tension 0.7, N = 346.

Panel 3d shows residuals after controlling for area.

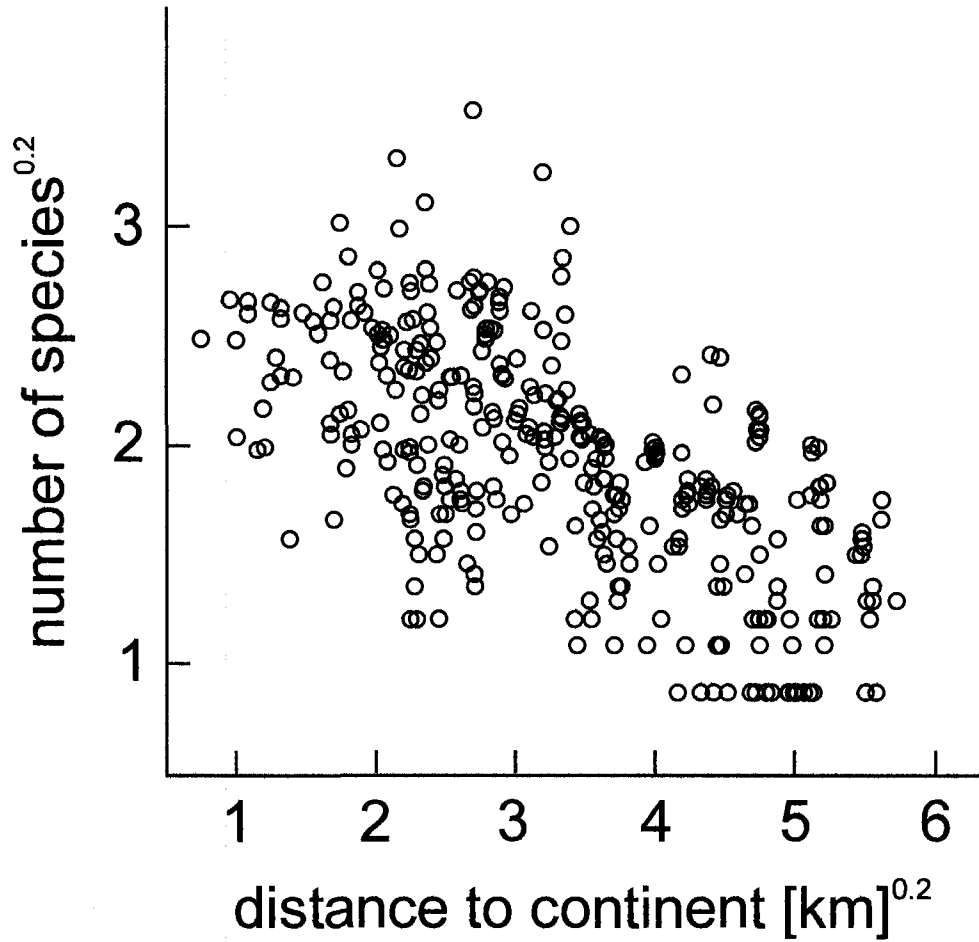


Figure 4 Relationship between species richness and insular isolation (distance to continent = shortest distance over open sea from an island to the nearest continental shore). Note that this relationship is restrictive, approximately triangular (cf. Fig. 2). N = 346.

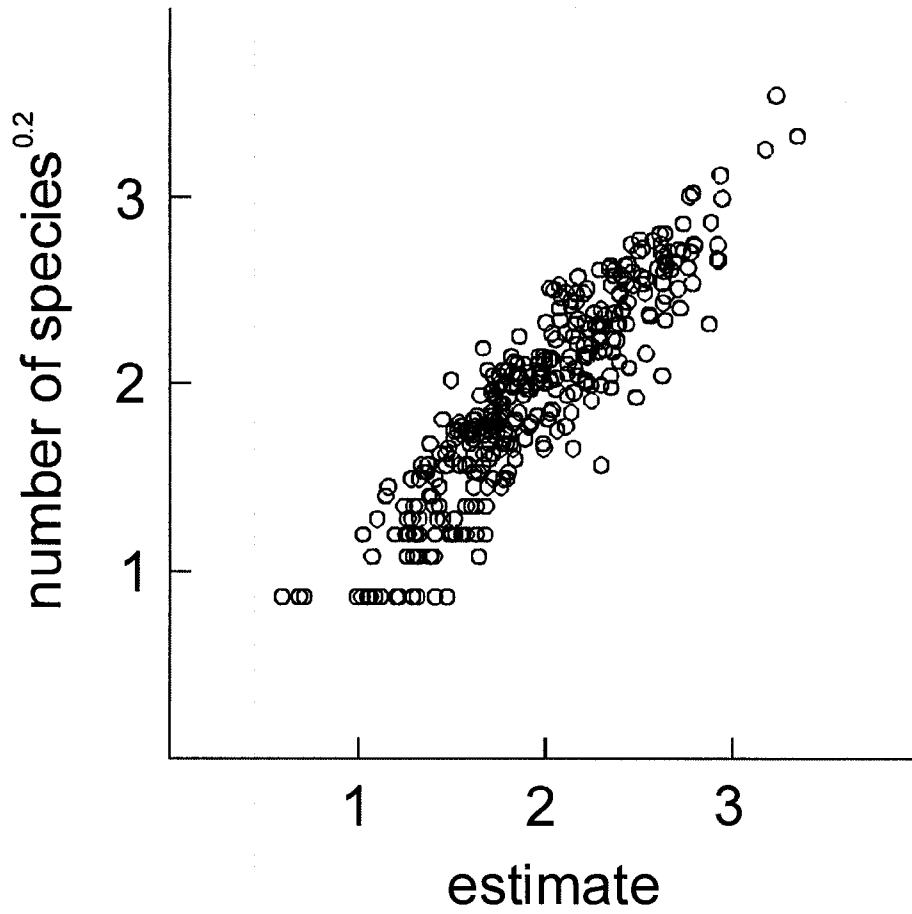


Figure 5 Bird species richness and the estimate of a multiple regression model using 3 of the predictor variables presented in Table 5: Area-precipitation interaction, distance to continent and temperature. N = 346.

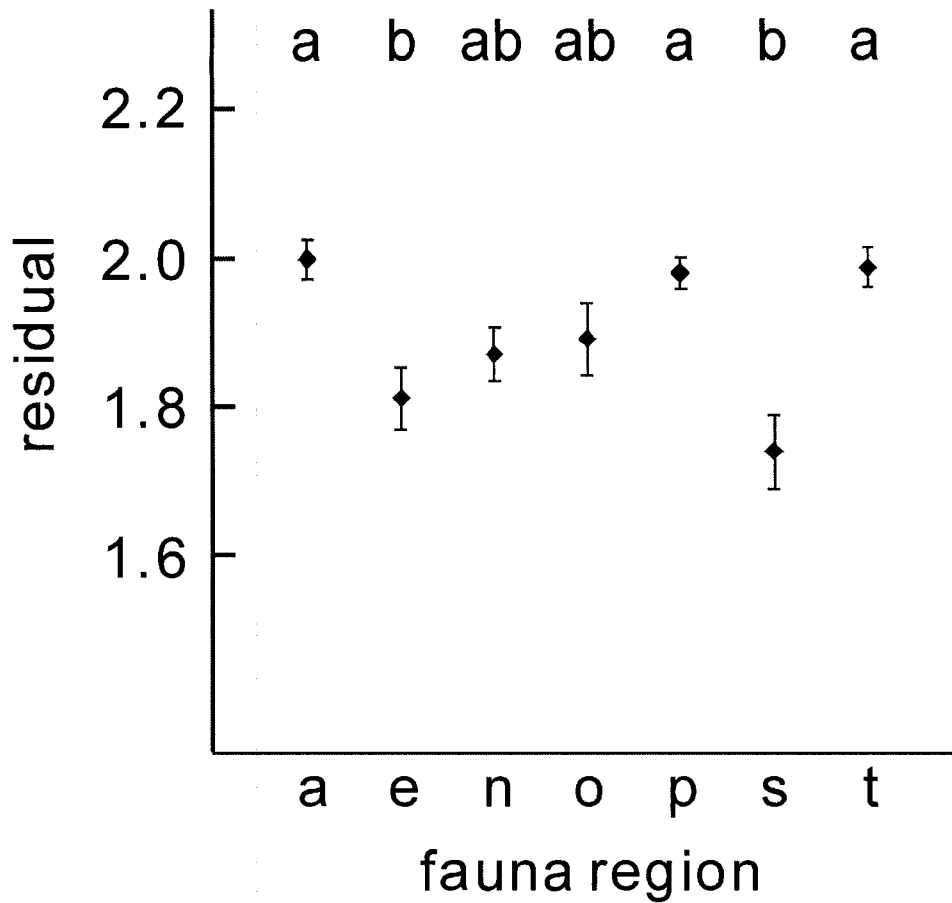


Figure 6 Regional differences of insular bird species richness after accounting for environmental variables describing area, climate and isolation as listed in Table 5 (backward elimination model). Note that results are very similar if we account only for 3 of these i.e. area-precipitation, temperature and distance to continent. Abbreviations: a – Australasian, e – Ethiopian, n – Nearctic, o – Oriental, p – Palearctic, s – Sub-Antarctic/Antarctic, t – Neotropical. N = 346.

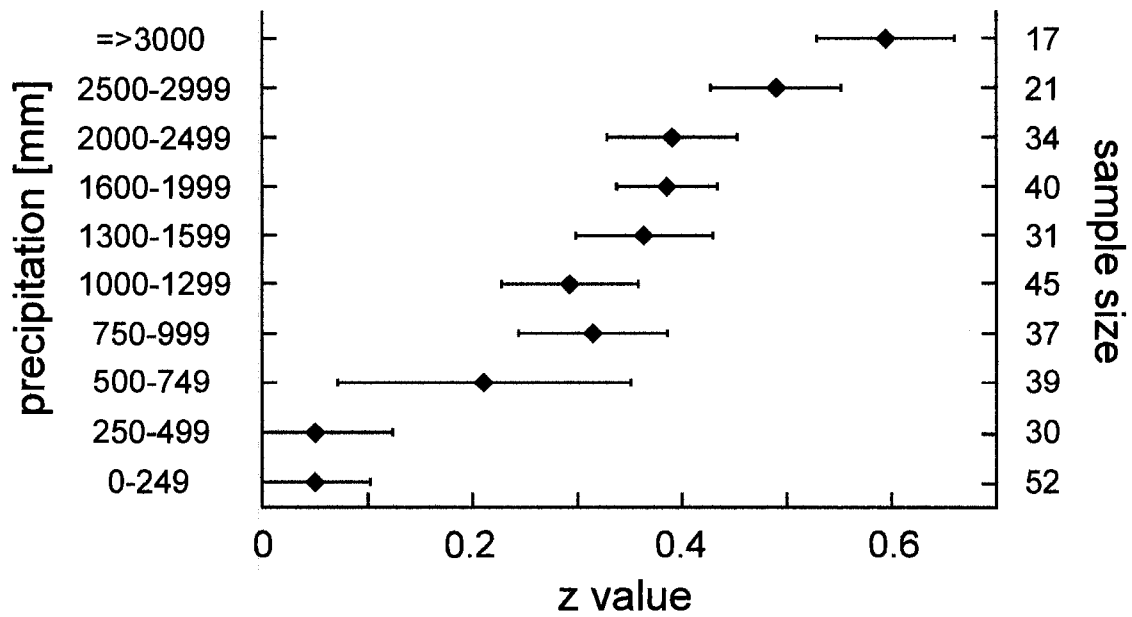


Figure 7 Increase of z slope values of the classic log species log area relationship with precipitation. Mean z values and SE are based on single linear regressions for 10 subsets of our island data, based on ranges of precipitation.

Appendix I

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## Chapter 2

**A unified model of avian species richness**

**on islands and continents**

Abstract

How many species in a given taxon should be found in a delimited area in a specified place in the world? Some recent literature suggests that the answer to this question depends strongly on the geographical, evolutionary and ecological context. For example, current theory suggests that species accumulate as a function of area differently on continents and islands. Richness-climate relationships have been examined separately on continents and on islands.

This study tests the hypotheses that (1) the functional relationship between richness and climate is different on continents and islands; (2) the richness-area slope varies with distance-based isolation; (3) richness-area relationships differ among landbridge islands, oceanic islands, and continents; (4) richness differs among biogeographic regions independently of climate and isolation.

We related numbers of breeding bird species in a worldwide sample of 240 continental parcels and 346 islands to several environmental variables. We found that richness varies similarly on islands and on continents as a function of mean annual temperature, an area x precipitation interaction, and the distance separating insular samples from the nearest continent ( $R^2=0.86$ ). Most studies to date have postulated that the slope of the richness-area relationship depends upon isolation. In contrast, we found no such interaction.

A richness-environment relationship derived using Old World sites predicts patterns of richness in the New World without bias, and vice-versa ( $R^2=0.85$ ).

Our results suggest that most of the global variation in richness is not strongly context-specific; rather, it reflects a small number of general environmental constraints operating on both continents and islands.

### Introduction

Consider a defined parcel of land: an island, a park, a county, a biome. How many different species in a given taxon (say, birds) should one expect to find there? The answer to this question may be important for conservation reasons (e.g., Brooks et al. 1997; Zurlini et al. 2002), or because one would like an expectation against which to test other hypothesized effects (e.g. Latham and Ricklefs 1993), or because identifying the main factors that influence variation in species richness may provide clues concerning the mechanisms driving species richness.

Recent syntheses suggest no general answer to this question (Huston 1995; Rosenzweig 1995; Whittaker 1998, chap. 7; Willig et al. 2003; Molles 2005; Begon et al. 2006, Chap 21). Reviews typically present long lists of factors hypothesized to influence diversity: productivity, spatial heterogeneity, disturbance, climatic variability, geometric considerations, etc. Moreover, richness-environment relationships often appear to be very context-dependent. For example, current evidence suggests that richness-environment relationships are scale-dependent (Palmer and White 1994; Lomolino 2000; Storch et al. 2005; Drakare et al. 2006). Further, Preston (1962) and MacArthur and Wilson (1967) suggested that the richness-area slope is steeper among isolated islands than

among mainland areas where easier dispersal increases the number of rare or transient species in small areas (see also Rosenzweig 1995:Fig. 8.40; Begon et al. 2006: Table 21.1). Other studies have suggested exactly the opposite: that area-richness slopes decrease with isolation because species pools are smaller in isolated situations (e.g. oceanic versus landbridge islands, Lawlor 1986; archipelagoes differing in isolation, Connor and McCoy 1979; islands versus mainlands, Drakare et al. 2006).

It has also been hypothesized that richness may be locally or regionally contingent on evolutionary history (Qian and Ricklefs 1999; Wiens and Donoghue 2004). Historical effects could include regional differences in speciation, long-distance dispersal, evolutionary differences in environmental tolerance, etc. (Rosen 1988; Adler 1992; Ricklefs and Bermingham 2004; Qian and Ricklefs 1999). Hawkins (2004; Hawkins and Porter 2003) proposed that contemporary patterns of bird richness in eastern North America reflect, to a degree, the history of Pleistocene glaciations.

Further, in local- to regional-scale studies, richness has been related to a variety of different factors. For example, some measure of habitat or topographic heterogeneity has been found to be a major correlate of diversity (Kerr and Packer 1997; O'Brien et al. 2000; Grytnes and Vetaas 2002). At the global scale, however, the proportion of the variation in richness that is related to measures of habitat diversity is usually small (Francis and Currie 2003; Kalmar and Currie 2006).

### *Avian richness on islands and continents*

In contrast, several recent studies have related substantial amounts of the broad-scale variation of richness to small sets of environmental variables. For example, among large, equal-area quadrats on continents, most of the variation in species richness (typically 70%-85%) can be related to climate or productivity (e.g., Francis and Currie 2003: angiosperms, global; Hawkins et al. 2003: birds, several continents; Field et al. 2005: woody plants, Africa). In sets of samples (islands or continental parcels) chosen to differ widely in area, an average of 64% of the variation in richness could be related to area (Drakare et al. 2006). Among islands, similarly large amounts of the global variation in richness can be related to climate and area (Wright 1983: global, mainly landbridge islands) or climate, area, and isolation (Kalmar and Currie 2006: global, landbridge and oceanic islands).

Even given these consistencies, Drakare et al. (2006) found that the slope of the species-area relationship (SAR) differed with scale, with latitude, among ecosystem types, and among types of organisms. They proposed that, "this variation ... strongly reflects the geographical, evolutionary and ecological context of the species considered."

Are richness-environment relationships truly so context-dependent, or can the bulk of the spatial variation in richness be related to a tractably small set of environmental variables in a single, general model? The answer is unknown because the studies above have used different sets of variables, or variables whose ranges differ dramatically, or they were conducted at different spatial scales. In particular, global insular and continental richness patterns have rarely

been statistically compared. The vast literature on island richness has focused mainly on archipelagos (e.g., all but one of the examples cited in Rosenzweig 1995, pp. 210-260) within which climate varies little, but area and isolation vary greatly. In contrast, recent broad-scale continental studies minimize variation in area, and vary greatly in climate.

In this study, we simultaneously examine the global variation of both insular and continental richness. We test the following hypotheses. (1) The functional relationship between richness and climate is different on continents and islands. We expect richness-area slopes to increase with temperature and precipitation on continents, as we found on islands (Kalmar and Currie 2006). (2) The richness-area slope varies with distance-based isolation (cf. Rosenzweig 1995:Fig. 8.40). (3) Richness-area slopes differ among landbridge islands, oceanic islands, and continents (cf. Krebs 2001:Fig.24.20). (4) Richness differs among biogeographic regions independently of (i.e., after controlling for) climate and isolation (cf. Qian and Ricklefs 2000). To do this, we statistically relate observed richness on 346 islands and in 240 continental sample areas to temperature, precipitation, elevation range, area, and isolation. As far as we know, this is the first study to incorporate continental and insular diversity variation into a single model using the global ranges of independent variables for both (Table 1).

## Methods

To investigate the relationship between global bird diversity and abiotic factors, we tallied land and freshwater bird species numbers from 586 locations around the world. The continental data consist of contiguous parcels of land delimited by physiographic, geographic or political boundaries. They neither overlap nor are adjacent to one another. Like islands, these continental parcels of land may encompass a single homogeneous habitat, or a mixture of habitats. The island data consist of single islands or atolls. We did not use richness pooled over archipelagos, although one or more islands from a given archipelago could be included (for a detailed description of the island data see Kalmar and Currie 2006).

Species numbers are based on annotated checklists, distribution tables and species distribution maps (when presence/absence could be determined unambiguously) published in international field guides and ornithological journals. Although we included data as we encountered them in the literature, we did actively seek to maximize the range of variability in predictor variables and attempted to sample all regions of the world as evenly as possible (Fig. 1, Table 1).

Our species counts included naturally occurring land and freshwater birds described as breeding, probably breeding, or having regularly bred in the past 400 years within the boundaries of a sample location. Marine species (for a list of families see Kalmar and Currie 2006), fossil species, introduced species, and established populations of domesticated birds are not included in our counts.

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The frequency distribution of species richness counts was strongly positively skewed (as most other studies have found). Although richness ( $S$ ) has been related to area ( $A$ ) by several different models, the power model  $S=cA^z$ , where  $c$  and  $z$  are empirical constants, is the most common (Arrhenius 1921; Schoener 1976; McGuinness 1984; Tjorve 2003). In pre-computer days, taking the logarithms of  $S$  and  $A$  led to a relationship that was convenient for linear regression:  $\log(S)=\log(c)+z\cdot\log(A)+\varepsilon$ , where  $\varepsilon$  is random error. Additionally,  $\log(S)$  was usually better distributed than  $S$ , and the residuals  $\varepsilon$  were less obviously skewed. The slope of this relationship, the  $z$ -value, became the subject of much subsequent literature (e.g., Connor and McCoy 1979; Rosenzweig 1995; Begon 2006, Chap 21, Drakare et al. 2006). However, we have found, using large samples, that  $\log(S)$  is negatively skewed and the residuals from models in which  $\log(S)$  is the dependent variable are not homoscedastic (e.g. H-Acevedo and Currie 2003; Kalmar and Currie 2006); We therefore tested power transformations  $S'=(S+0.5)^b$  where  $b$  varied from 0 to 1, and we assessed the normality of regression residuals using Kolmogorov-Smirnov (KS) tests. Conformity with a normal distribution was maximal using the power transformation with an exponent of 0.3 ( $p=0.29$ ), whereas the log transformation yields strongly non-normal residuals in our richness-environment models (KS  $p<10^{-10}$ ). Therefore, we use  $(S+0.5)^{0.3}$  as the dependent variable in our analyses. We added a half species to all cases, to reduce the weight of islands without any species in regressions. For the sake of comparison with

## *Avian richness on islands and continents*

earlier literature, we also carried out analyses using log-transformed richness. The two sets of analyses led to the same qualitative conclusions.

We related richness to four continuous variables (Table 1) common to both continental samples and islands: (1) total land *area* (km<sup>2</sup>, log transformed) of a sampled island or continental piece of land, (2) mean annual *temperature* (°C; untransformed), (3) mean annual *precipitation* (mm; raised to power 0.4). We averaged mean annual temperature and precipitation from weather station data (Wernstedt, 1972, Walter and Lieth, 1967). For sample areas without any weather station, temperature and precipitation were inferred from measurements at the nearest weather station(s) and from climate maps (Deichmann et al. 1991; USSR Committee for the International Hydrological Decade 1977). Finally, (4) we also related richness to the *range in elevation* within the boundaries of each sample area (m; raised to the power 0.4). We would have liked also to use a satellite-based vegetation classification, but these data are not available for many small islands. The transformations of independent variables were chosen to maximize normality of the variable (to avoid observations with extreme leverage in the regressions).

*Distance to the continent* and *neighbor index* are metrics of insular isolation. *Distance to the continent* corresponds to the shortest distance over open sea from an island's shore to the nearest continental shore. The *neighbor index* was calculated by the equation proposed by Kalmar and Currie (2006):

$$N = \sum \frac{A}{(D+1)^2}$$

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where  $N$  is the sum of the isolation-reducing effects of neighboring islands,  $A$  is neighbor area and  $D$  is the distance between the sampled island and a neighbor in kilometers. Since  $N$  was strongly right skewed, we log-transformed it for statistical analyses. For more details on quantifying insular isolation see Kalmar and Currie (2006). We also experimented with indices of continental isolation: areas surrounded by gradients of temperature, precipitation or elevation (e.g. mountain tops). We found that continental isolation was difficult to quantify unambiguously. Richness was significantly related to our continental isolation indices, but explained variance was relatively small (~7%). We therefore do not present analyses of continental isolation here. Rather, we assigned a value of 0 km for *distance to continent* to all continental samples.

We tested three categorical predictor variables in our models: (1) *insularity* (two levels: continent and island); (2) *faunal region*, boundaries based on Sclater 1858; (seven levels: Palearctic, Oriental, Ethiopian, Australasian, Nearctic, Neotropical and Antarctic/Sub-Antarctic). The Oriental-Australasian boundary follows Weber's line (Weber, 1902); (3) *historical isolation* (three levels: continent, landbridge island and oceanic island). We defined a "landbridge island" as an island located on a continental shelf contiguous with a present day continent. All other islands were classified as "oceanic". Since historical isolation is nested within insularity, the two were never used in the same model.

## Results

Spatial autocorrelation in our data is low. The mean distance among continental sample areas is 325 km (SD  $\pm$  249 km, n=240). Less than 14% of continental samples have other sample areas within a 100 km radius. Moran's I values for raw species richness in continental samples 50-100 km and 100-150 km distant from one another are 0.012 and 0.013 (10 and 34 number of pairs respectively). Autocorrelation in the residuals of our final models was also very low ( $\sim$ 0.12 from 0 to 1300 km). It may seem surprising that spatial autocorrelation in our data is low. However, as we show below, richness depends as strongly on area as on climate, and area is not spatially structured. Moreover, since these are local counts rather than regional distributions, "spillover" between samples separated by 325 km is likely to be low. Consequently, neighboring samples are not necessarily similar in species composition. For discussion of autocorrelation in the island data, see Kalmar and Currie (2006).

Collinearities among our predictor variables are also reasonably low (Table 2). Note however that area constrains elevation range because small areas are unlikely to have very high elevation range. Correlation between island area and distance to continent is moderate among oceanic islands ( $r=-0.31$ , n=172) and negligible among landbridge islands ( $r=0.026$ , n=174). For a discussion of other collinearities, see Kalmar and Currie (2006).

In agreement with earlier broad-scale studies, we have found that the global variation in avian richness is related to climate, (temperature and

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precipitation), area and isolation. Simple bivariate relationships between bird species richness and most abiotic predictors are restrictive (e.g., Fig. 2). Such triangular relationships reflect multiple possible limiting factors. For example, when we examine subsets of the data, the more we restrict the range of variation in climate and isolation, the more linear the relationship between richness and area becomes.

The effects of area and climate on richness are not simply additive: richness depends strongly upon area-climate interactions both on continents and on islands (Fig. 3). Within extremely small sample areas, richness is always low, irrespective of climate. In contrast, in large areas, richness increases dramatically with temperature and precipitation. Looking at it the other way, richness only increases with area if neither temperature nor precipitation is extremely low. As temperature and precipitation increase, SAR slopes become steeper (Fig. 3). If we model richness =  $f(\text{area, climate, area} \times \text{climate})$ , where climate is either mean annual temperature or precipitation<sup>0.4</sup>, the best model includes climate and the area-climate interaction (e.g., AIC= -51.01 using the area x precipitation interaction, versus AIC=2.07 with the linear combination of area and precipitation. The log area term drops out. Similar results are obtained with area and temperature). Thus, SAR slopes depend very strongly on climate.

To a smaller degree, richness also appears to depend upon an interaction between temperature and precipitation (Fig. 4). Richness increases with precipitation in warm regions, but not in cold regions. The richness-temperature relationship is peaked in dry areas, and it is monotonic positive in wet areas.

However, the temperature-precipitation interaction had little effect in multiple regression models (Table 3), probably because the shape of the interaction (Fig. 4) is difficult to model, and because this interaction is collinear with other terms in the final model (area x precipitation, temperature).

In contrast to most literature on species-area relationships, we found that the effects of area and isolation are additive, rather than multiplicative. Using area and distance to continent as predictor variables, the interaction term is non-significant ( $p=0.54$ ,  $n=586$ ). Results are similar if we use only the island data ( $p=0.23$ ,  $n=346$ ). In general, the area-distance to continent interaction term drops out from multiple regression models as non-significant (e.g. Table 3). The approximately parallel isoclines of a richness-area-isolation 3D plot illustrate the lack of interaction between isolation and area (Fig. 5).

As most other global studies have shown (e.g. Francis and Currie 2003; Kalmar and Currie 2006), broad-scale variation in richness is only weakly related to topographic heterogeneity. *Elevation range* and its interaction with temperature together explain 18% of the variance in global bird richness. However, in multiple regressions that include area, climate and isolation, elevation range accounts for so little variation that we did not retain the terms (Table 3).

A single, simple model can account for nearly all the global variation in avian species richness. Combining area, climate and isolation metrics in multiple regressions, we found that three terms (area-precipitation interaction, temperature and distance to continent) can explain 86% of the variation in non-

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marine bird diversity (Table 3; Fig. 6a). Using log-transformed richness instead of richness<sup>0.3</sup>, a model including the same terms accounts for 80% of the variation in log richness (see Appendix II for details). However, we found no model using log richness as the dependent variable in which the residuals showed no pattern (see, for example, the non-linearity in Fig. 6b) or were homoscedastic in their distribution (Kolmogorov-Smirnov  $p < 10^{-6}$ ).

After accounting for area, climate and isolation (Table 3), we detected no significant differences in richness among continental samples, landbridge islands and oceanic islands (Table 3). Also, there is very little variation in richness among faunal regions. The directions of the effects are often not consistent between islands and continents in the same region, nor do they seem consistent with any hypothesized historical explanation of which we are aware (Fig. 7). We therefore did not include faunal region in the final model.

Because our data do not necessarily represent a random sample of the global population of all areas to which the model applies, we tested the predictive ability of our three-term global model (Table 3) in two different ways. First, we used a cross validation procedure, fitting the statistical model to 2/3 of the data ( $n=391$ ), and calculating predicted richness for the remaining third of the samples ( $n=195$ ). We repeated this procedure 100 times, each time randomly assigning data to the training and testing data sets. The mean slope between predicted and observed richness was  $1.001 \pm 0.038$  (s.d.), the mean intercept was  $-0.009 \pm 0.128$ , and the mean  $r^2$  between predicted and observed richness in the test data was  $0.857 \pm 0.015$ .  $R^2$  and residual mean square values in the training and

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testing data was also very close (Table 4). This indicates that the model successfully predicts richness in areas not included in the analysis. Second, we divided the world into three regions with fairly distinct faunas: the New World, the western Old World (western Palearctic and Ethiopian faunal regions), and the eastern Old World (eastern Palearctic, Oriental and Australasian regions). Sub-Antarctic and Antarctic islands were joined to the nearest of these three regions. We fitted the three-term model in Table 3 to the data from two regions and used the fitted relationship to predict richness in the third region. We found that a richness-environment relationship in 2/3 of the world could predict richness in the remaining 1/3 with  $R^2=0.85$ , despite the fact that these areas have largely distinct faunas and evolutionary histories (Fig. 8).

### Discussion

The methods used in this study contrast with earlier literature in that we used a power transformation of species richness. Reanalysis of our data using the log transformation of species richness yielded very similar results: area-climate interactions are strong and area-isolation interactions are non-significant (legends of Figs. 3 and 5; Fig. 9; also cf. Table 3 and Appendix III). The difference between the two transformations is that the transformation to the power 0.3 led to homoscedastic, linear relationships, whereas the log transformation did not (e.g., Figure 6b). Additional terms included in the log model can improve its linearity somewhat (at the expense of parsimony), but not its heteroscedasticity. Also, the percentage of explained variation in regression

models is always higher using the 0.3 power transformation. Drakare et al. (2006), compared the statistical fit of  $S$  as a function of  $\log(A)$ , versus  $\log(S)$  as a function of  $\log(A)$ . Examining 794 species-area relationships, they found that the two models each provided better fit in ~50% of the studies. We suspect that this is because  $\log(S)$  is often over-transformed, and  $S$  is under-transformed.

Our most important findings are: (1) A single model based on descriptors of area, climate, and insular isolation can predict reasonably well bird diversity in any defined area larger than ~2 km<sup>2</sup> anywhere in the world (we return to this lower limit below). (2) The slope of the richness-area relationship (SAR) does not depend upon isolation. (3) SAR slopes do depend strongly on climate, both on continents and on islands. (4) After accounting for the effects of climate and distance-based isolation, richness does not differ significantly among continental samples, landbridge islands and oceanic islands, and differs very little among biogeographic regions. We explain each of these points below.

Our first main finding – a globally consistent richness-environment relationship (Fig. 8) – is consistent with a growing literature. In continental- to global-scale studies, most of the broad-scale variation in richness of most major groups of organisms can be related to climate and area (Hawkins et al. 2003). Relationships derived in given regions of the world successfully predict richness in other regions (Currie and Paquin 1987; Francis and Currie 2003; Field et al. 2005). We find comparable results. We have also demonstrated that the extension of continental models to islands is possible because the effects of area and insular isolation are additive (Figs. 5-6).

Our 2-D contour diagrams of area and climate effects explain why regional richness-climate studies can yield apparently different results. For example, bird species richness increases with temperature in cool and moist parts of North America (Currie 1991; cf. the bottom half of Fig. 3a). In contrast, bird species richness decreases with temperature in hot and dry Australia (Schall and Pianka 1978; cf. the lower right portion of Fig. 4a). Kerr and Packer (1997) suggested that continental bird richness increases with temperature only up to about 5°C, and then plateaus. We find that there is a threshold of temperature above which richness plateaus or decreases, but that this threshold increases with precipitation (Fig. 4). Thus, regional studies that include different subsets of the global ranges of temperature and precipitation may appear to contradict one another.

We observed only small differences between islands and continents in richness-environment patterns: the area-temperature interaction is stronger on islands (Fig. 3b), whereas on continents the area-precipitation interaction is very strong (Fig. 3c). This probably reflects global geography more than any biological differences between islands and continents. For example, in polar and sub-polar regions, precipitation has considerably more variance among islands than among continental samples, which can lead to small differences in the statistical models between these systems.

Our second main finding – that the richness-area relationship does not depend upon isolation – contrasts with much earlier literature (Preston 1962; MacArthur and Wilson 1967; Connor and McCoy 1979; Rosenzweig 1995). It is

possible that the lack of an isolation effect on the richness-area slope reflect the fact that this study focused on birds, a group with particularly strong dispersal ability. However, much of the earlier literature that observed this interaction dealt also with birds (Connor and McCoy 1979:806 and references cited there). Moreover, Drakare et al. (2006), in a meta-analysis of 749 species-area relationships, also observed that the species-area relationship did not differ systematically between insular and continental samples. Their analysis included many taxonomic groups of differing dispersal ability.

Why did many earlier studies find that SAR slopes vary with isolation? We propose three distinct reasons for this. The first and most important is our third main finding – that SAR slopes depend on precipitation and temperature. Data from isolated oceanic islands typically come from tropical regions (e.g., hot and humid South Pacific islands) where SAR slopes are steep because of area-climate interactions (Fig. 3b, 3d). Continental data, on the other hand, typically come from temperate North America or Europe, where the same area-climate interactions predict lower SAR slopes (Fig. 3a, 3c). Continental and insular SAR slopes do not differ significantly when the samples are drawn from the same region, within which climates are similar (Fig. 9). However, even within a given region, islands often tend to be somewhat warmer and rainier (Appendix III), leading to minor differences in SAR slopes when richness is (inappropriately) log-transformed (Fig. 9c,e).

We also suspect that SAR slopes often appear to be lower on continents than on islands because of a sampling bias at small spatial scales. During our

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data collection we found no continental checklists with fewer than 10 breeding landbird species. Surely, there are small continental areas (10 ha - 2.0 km<sup>2</sup>) with fewer species (e.g., in deserts or in cold regions). However, these areas appear not to attract birdwatchers to compile very short checklists. For islands of similar size, checklists with very few or no landbirds are available because these islands attract birdwatchers by their seabird colonies. This bias is a continental equivalent of the "zero effect" reported by Williams (1996) for islands, according to which the exclusion of islands with zero species numbers decreases z values.

There also appears to be a methodological artifact due to the difference between log- and power-transformed data (e.g. Fig. 9). This is likely to be particularly problematic when sample areas are small because the difference between log- and power-transformed data is largest there. Since continental areas and land-bridge islands may be large or small, whereas oceanic islands are invariably small, comparisons of slopes between continents and oceanic islands will depend strongly on the transformation used.

In striking contrast to our results, Storch et al. (2005) recently reported a negative interaction between the effects of productivity (as characterized by NDVI) and area on species richness. They tallied bird species richness in nested quadrats of increasing area in Great Britain and South Africa. They reasoned that, if individual species occupy a higher proportion of sites in more productive areas, then the SAR slope must decrease with productivity. At the limit, the slope is zero when all species occupy all sites. Storch et al. observed shallower slopes using large quadrats, and they inferred that occupancy increases, and

therefore beta diversity decreases, with increasing productivity. However, the literature has much more commonly reported positive interactions between productivity and SAR slope (Weiher 1999; Drakare et al. 2006), and negative relationships between beta diversity and latitude (Koleff et al. 2003; Rodriguez and Arita 2004).

We suggest that the results of Storch et al. (2005) reflect an artifact of their study design: when quadrats capture most of the regional species pool, richness becomes independent of any environmental variable. In their British data, the largest quadrats (6400 km<sup>2</sup>) capture 65%-83% of the entire British species pool, irrespective of NDVI. Richness per quadrat appears to be independent of NDVI because it is constrained by the size of the species pool. In smaller quadrats, richness increases with NDVI, but the relationship is clearly non-linear, approaching a plateau near the level of richness in the large quadrats. This leads to the apparent negative interaction between NDVI and area on richness. The South African species pool (651 species) is much larger than that in Britain (189 species). Large quadrats in low NDVI areas of South Africa encompass ~50% of the total species pool. Richness increases with NDVI until the quadrats encompass  $\geq 65\%$  of the species pool, when richness again apparently becomes independent of NDVI (their Fig. 2a). With richness per quadrat constrained by pool size only in the highest NDVI quadrats, the negative interaction between the richness-NDVI relationship and area is much weaker. In global analyses, such as ours, even the largest, most speciose samples capture <10% of the global species pool. With richness unconstrained by the size of the species pool, we

observe that richness depends upon a positive area-temperature or area-precipitation interaction.

Our fourth main finding – that regional influences on richness, after accounting for climate, are small – suggests that contemporary factors are mainly responsible for broad-scale variation in richness. Our study cannot exclude the possibility that contemporary richness-climate correlations may reflect effects of historical climate, because historical climatic gradients since the Eocene are strongly correlated with contemporary broad-scale variation in climate (Hawkins et al. 2006). This collinearity arises because the latitudinal positions of the continents have changed little since the Eocene (Scotese 2004). However, other evidence suggests that richness responds to contemporary climate. Richness changes seasonally in a way that is consistent with seasonal changes in climatic variables and productivity (H.-Acevedo and Currie 2003; Hurlbert and Haskell 2003). Also, richness may be responding to recent climate change (Parmesan and Yohe 2003; Root et al. 2003). Convincing statistical evidence that numbers of species (as opposed to *which* species) show a historical signature is still lacking (*pace* Qian and Ricklefs 1999; Wiens and Donoghue 2004).

The small signal that we do detect (the significance and predictive value of *faunal regions*, Table 3) is mostly due to lower than expected diversity in the Sub-Antarctic – Antarctic region. This may be caused by the absence of a local center of radiation or by particular climatic conditions in the region. Trees are absent from most Sub-Antarctic islands because of strong winds and the lack of summer heat, even though mean annual temperatures are not particularly cold

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(Watson 1975). In consequence, an impoverished flora may be responsible for low bird species richness on Sub-Antarctic islands. *Faunal region* is also correlated with climate (Table 2) and its statistical significance may be due to a minor lack of fit of richness to climate. This may explain why the regional effect is slightly stronger when richness is log-transformed (Appendix II).

In summary, this study was the first global analysis of continental and insular diversity of which we are aware. It yielded a consistent model whose strong area-climate interactions explain the apparent differences among earlier regional studies. We found that although distance-based isolation is a very strong predictor of insular bird richness, its effect is additive to other factors. Consequently, richness-climate and richness-area relationships are commensurable on islands and continents.

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Tables and figures

Table 1. Dependent and independent variables used in our regression models explaining non-marine bird species richness. N=240 continental samples and 346 islands. For variables describing insular isolation see Kalmar and Currie (2006).

	islands			continents		
	min.	max.	median	min.	max.	median
number of species	0	547	28.5	10	1348	134.0
area [km <sup>2</sup> ]	0.085	820033	625.0	0.061	1001000	11527.5
elevation [m]	3	5030	710.5	1	7348	635.5
temperature [°C]	-26.0	30.0	20.3	-14.3	30.0	14.5
precipitation [mm]	25	5470	1077.5	8	4000	662.5

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Table 2. Pearson correlations between predictor variables used in our regression models. For  $n = 586$ , correlations at  $|r| \geq 0.081$  are significant at  $p = 0.05$ , and at  $|r| \geq 0.136$  they are significant at  $p = 0.001$ . Note: *faunal region* is a categorical variable: the numbers in the last row are ANOVA  $r^2$  values.  $N = 586$ .

	log area	elev.	temp.	precip.
elevation range <sup>0.4</sup>	0.534			
average annual temperature	-0.155	0.024		
total annual precipitation <sup>0.4</sup>	-0.157	0.122	0.509	
faunal region	0.094	0.100	0.547	0.349

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Table 3. A global model predicting (bird species richness)<sup>0.3</sup> for continental samples and islands around the world (n=586). The three retained terms are listed in order of inclusion by forward selections with cumulative R<sup>2</sup> values. Increase in R<sup>2</sup> and p values of excluded terms are also shown if they were to be included as a fourth term.

	cumulative r <sup>2</sup>	p
<b>retained terms:</b>		
distance to continent <sup>0.2</sup>	0.526	<10 <sup>-15</sup>
log area x precipitation <sup>0.4</sup>	0.824	<10 <sup>-15</sup>
temperature	0.857	<10 <sup>-15</sup>
<b>excluded terms:</b>		
faunal region (7 levels)*	+ 0.013	<10 <sup>-9</sup>
sample category (continental or insular)*	+ 0.001	0.019
geohistory (continental, landbridge, oceanic)*	+ 0.002	0.055
distance to continent <sup>0.2</sup> x log neighbor index	+ 0.006	<10 <sup>-5</sup>
distance to continent <sup>0.2</sup> x log area	0.000	0.894
elevation range <sup>0.4</sup> **		0.003
elevation range <sup>0.4</sup> x temperature **	} + 0.006	<10 <sup>-5</sup>
temperature x precipitation <sup>0.4</sup> **		<10 <sup>-7</sup>
temperature x (precipitation <sup>0.4</sup> ) <sup>2</sup> **	} + 0.011	<10 <sup>-9</sup>

\* categorical variable

\*\* 2 terms included simultaneously

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Table 4. R square and residual mean square comparisons between training and testing subsets of our data used in the cross-validation test of our three-term global model (Table 3). N=100 trials.

		mean	standard deviation
training data	R <sup>2</sup>	0.857	0.0081
	residual mean square	0.253	0.0163
test data	R <sup>2</sup>	0.857	0.0155
	residual mean square	0.257	0.0324

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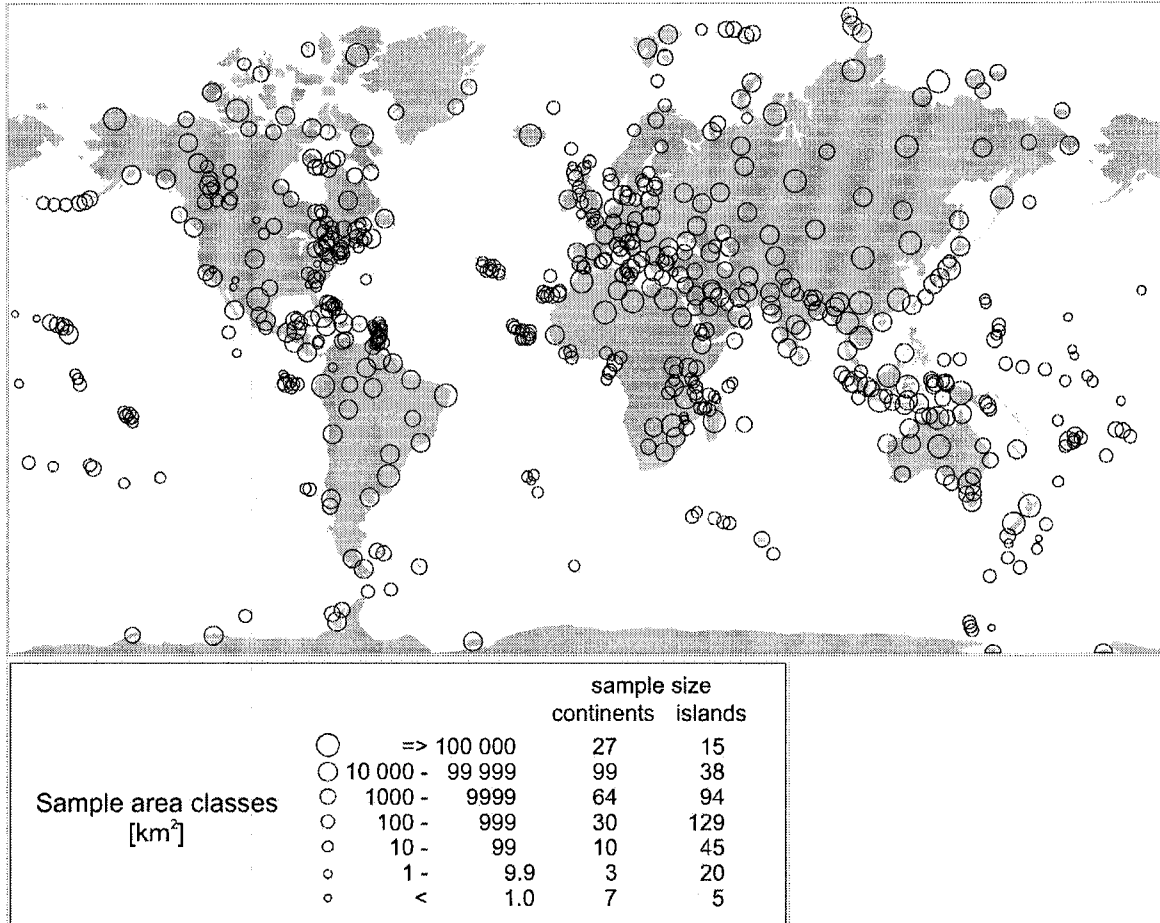


Figure 1 Spatial distribution of the 240 continental sample areas and the 346 islands included in this study.

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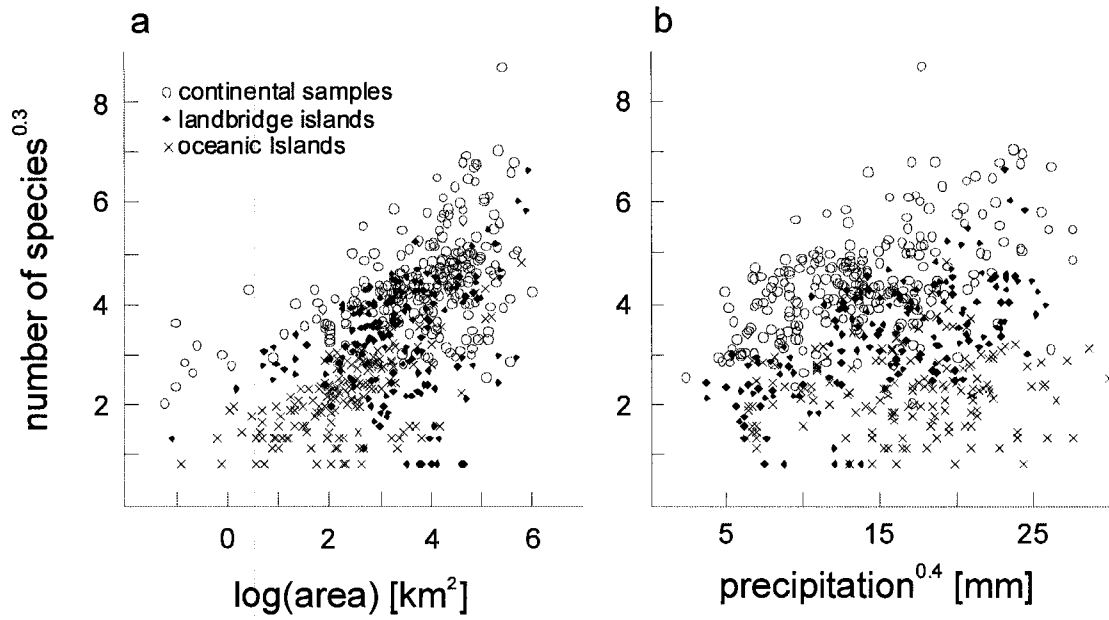


Figure 2. Restrictive global relationships of non-marine bird richness with area (a) and precipitation (b). N= 240 continental samples, 174 landbridge islands and 172 oceanic islands.

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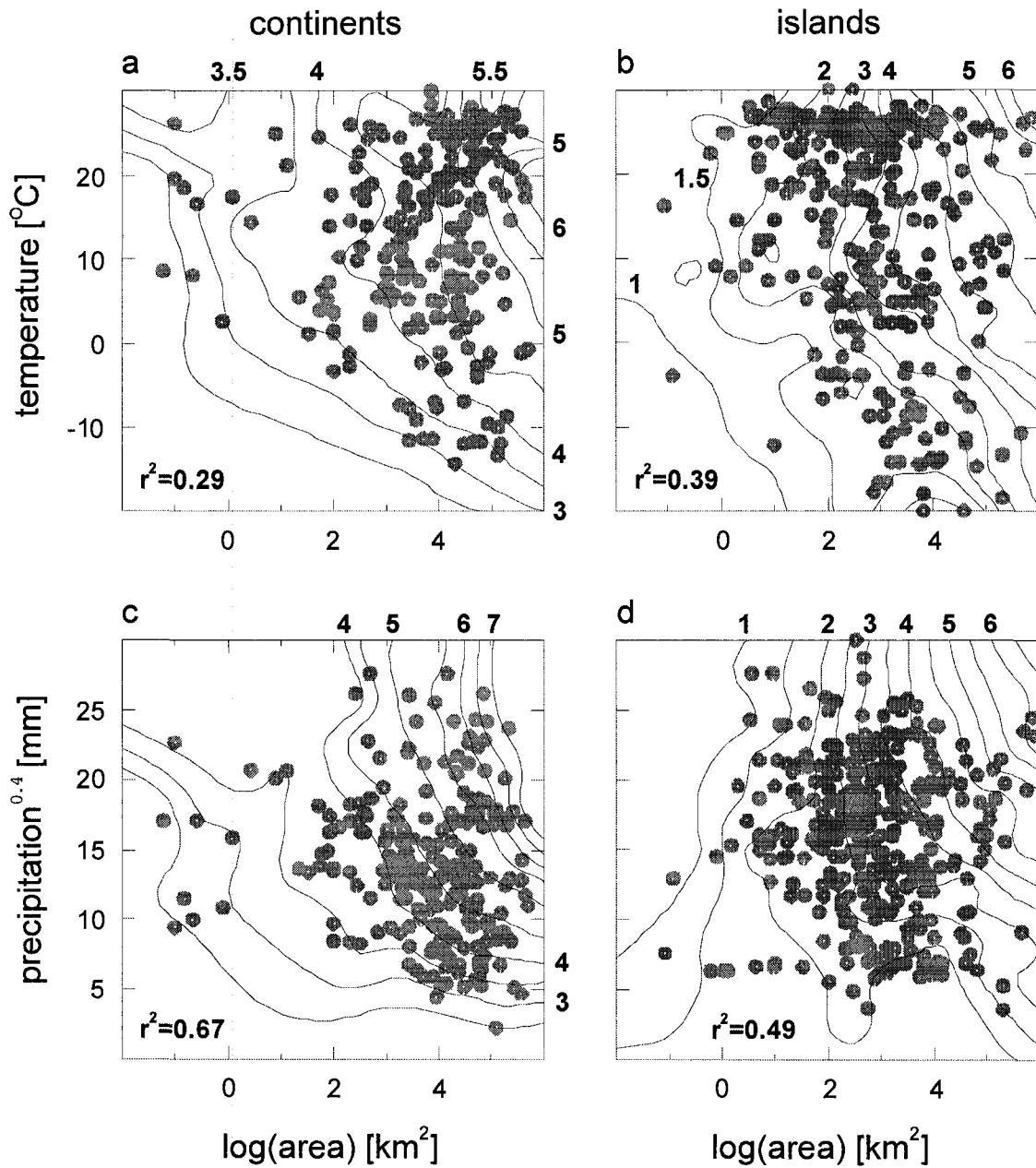


Figure 3. Area-climate interactions are strong both on continents and on islands. Bold numbers are isocline values for bird species richness raised to the power of 0.3. Smoother method: DWLS, tension 0.7. N=240 (a,c), N=346 (b,d). Using logarithmic transformation of richness, these interactions remain strong with similar explained variance: (a)  $r^2=0.27$ , (b) 0.38, (c) 0.66, (d) 0.36.

*Avian richness on islands and continents*

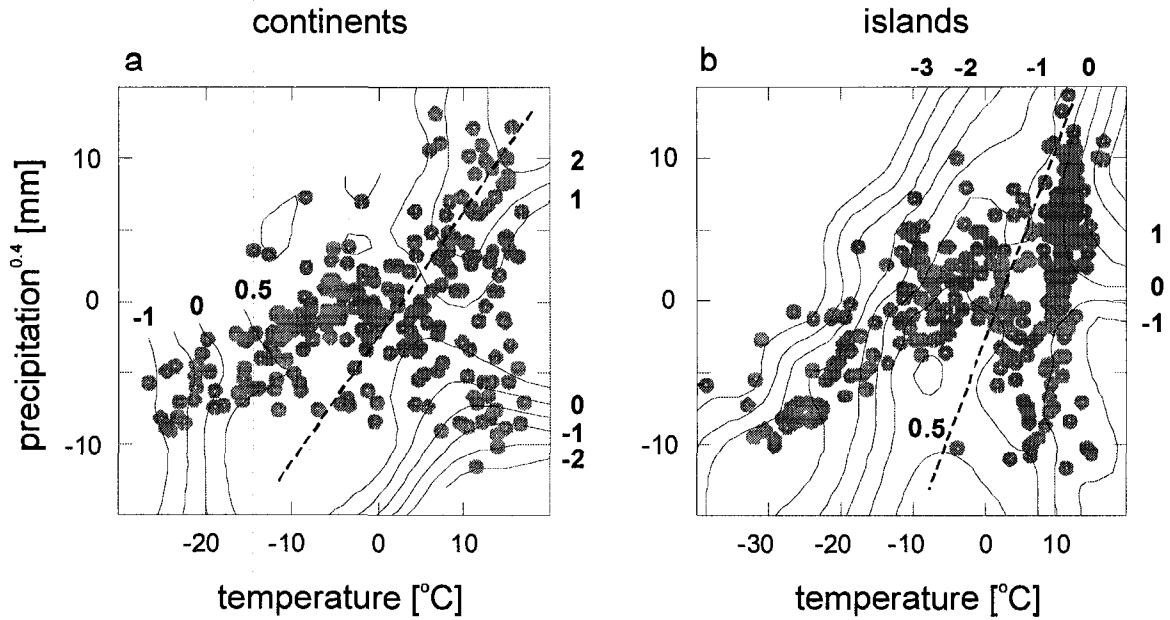


Figure 4. Effect of the temperature-precipitation interaction on bird species richness. The dashed lines indicate apparent ridges. The axes represent residuals after controlling for the effects of *area* and *distance to continent*. Bold numbers are isocline values for residuals of bird species richness raised to the power of 0.3. Smoother method: DWLS, tension 0.7. N=240 (a), N=346 (b).

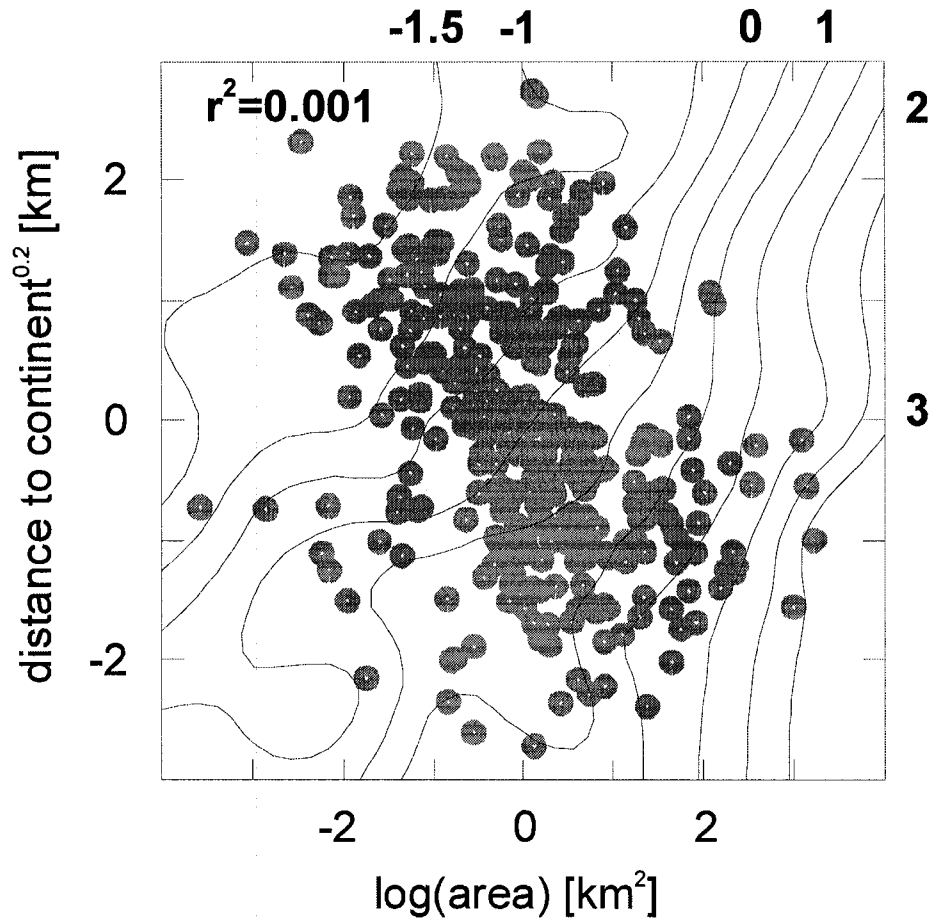


Figure 5. Lack of interaction between area and distance-based isolation (c.f.  $r^2$  with those of Fig. 3). Bold numbers are isocline values for insular bird species richness raised to the power of 0.3. Note that low the  $r^2$  value and approximately parallel isoclines suggest lack of interaction. Smoother method: DWLS, tension 0.7. N=346 islands. The surface would look virtually identical with the inclusion of the 240 continental samples for which *distance to continent* = 0 km. Note also that the interaction is similarly non-significant if richness is log-transformed:  $r^2=0.0003$ ,  $p=0.76$ , N=346.

*Avian richness on islands and continents*

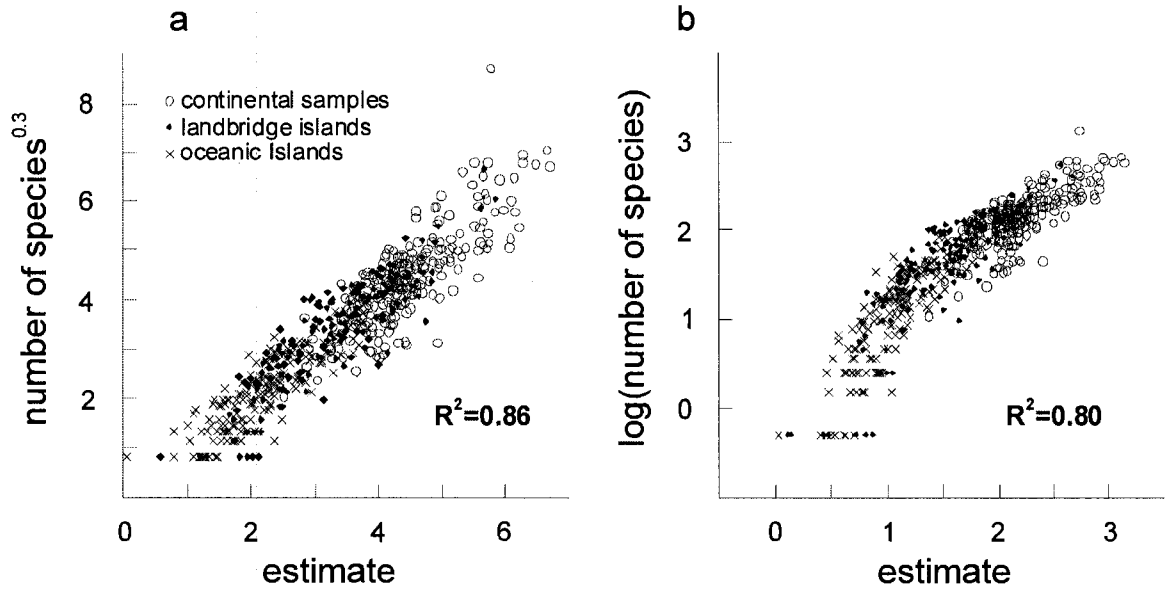


Figure 6. Bird species richness and the estimate of our power model of global avian diversity of 3 terms: area-precipitation interaction, temperature and distance to continent (a). In comparison, the use of logarithmic transformation of richness yields a curved, heteroscedastic relationship, with lower predictive value (b). N=586.

Avian richness on islands and continents

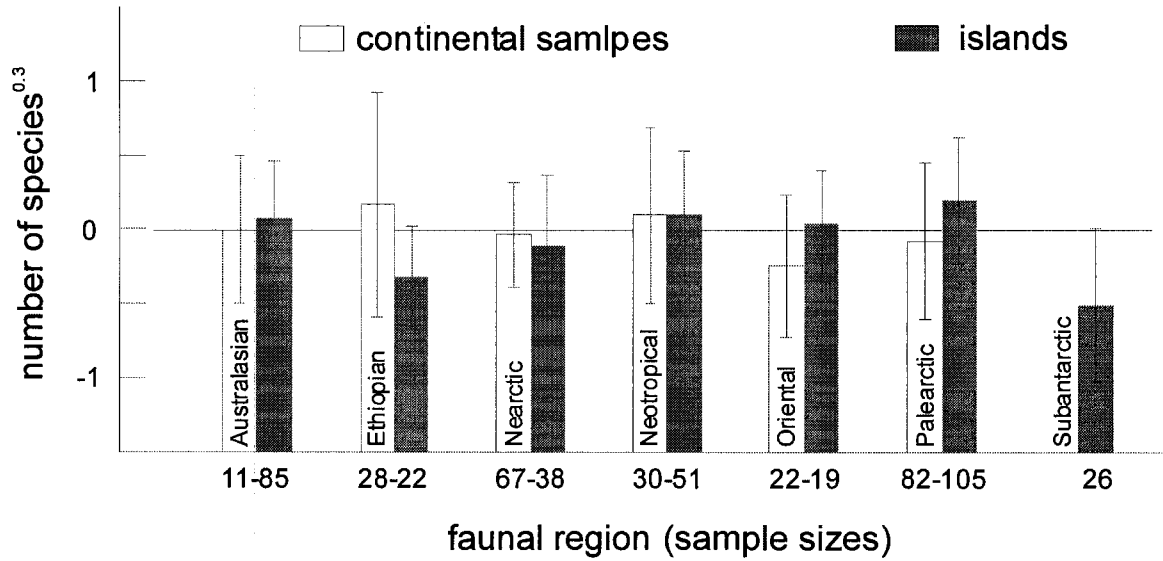


Figure 7. Regional differences of bird species richness among continental samples and islands. The ordinate represents species richness residuals after controlling for the 3 terms of our global model: area-precipitation interaction, temperature and distance to continent. Error bars: SD.

*Avian richness on islands and continents*

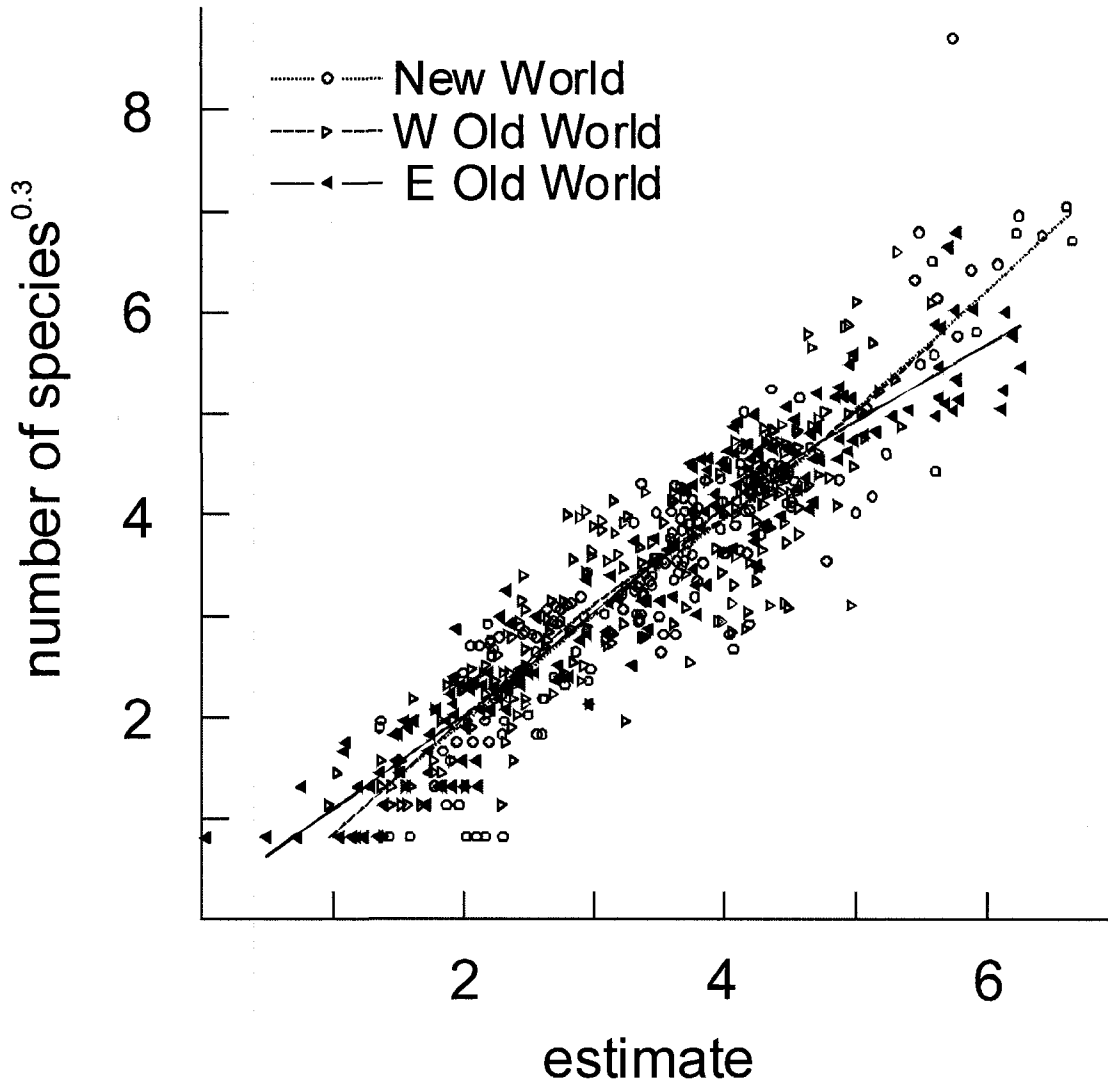


Figure 8. A test of the predictive power of the three-term model based on climate, area and isolation (Table 3). We divided the world into three regions: the New World (N=188), the western Old World (N=188) and the eastern Old World - Australasia region (N=183). We fitted the model to the data from two regions and predicted richness in the excluded region. Global agreement between predicted and observed richness:  $r^2=0.85$ . Smoother method: Lowess, tension 0.7.

Avian richness on islands and continents

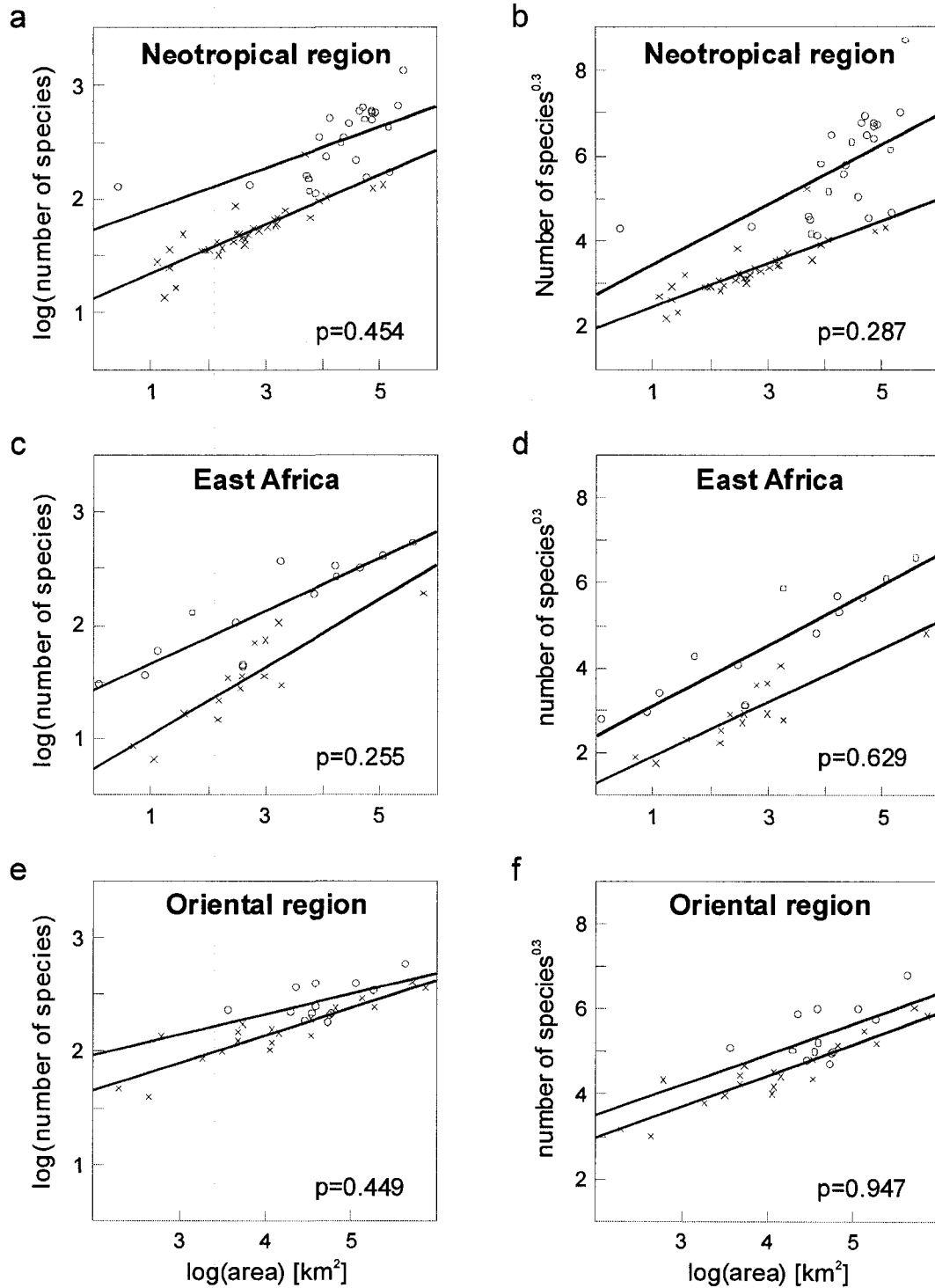


Figure 9. Are species-area slopes different in regional subsets of our global data, where continental (o) and insular (x) samples have similar climates? Regardless of the transformation used, slopes do not differ significantly between continents and islands (ANOVA p values for interaction terms are indicated). Curve fitting: linear. N= 59 (a,b), N= 28 (c,d), N=32 (e,f). See Appendix III for details of the samples used.

Appendix I

Sources of continental bird species richness data

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Electronic data resources

Brasilia, Brazil: <http://www.bdt.fat.org.br/zoologia/aves/avesdf/>

Accessed on March 3, 2006.

Cambodia: <http://phnompenhdaily.com/3c.htm>

Not accessed since 2000. Link no longer active.

Canberra, Australia: <http://canberrabirds.org.au/chklist.htm>

Accessed on March 3, 2006.

Cedar Creek, Minnesota: <http://cedarcreek.umn.edu/birds/>

Accessed on March 3, 2006.

Contra Costa county, California: <http://fog.ccsf.cc.ca.us/~jmorlan/ccclist.htm>

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Fernbank Forest, Georgia: <http://fsc.fernbank.edu/Birding/checklist.htm>

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GNV174, digitized precipitation data: <http://www.grid.unep.ch/data/data.php>

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Platte River Valley, Nebraska:

<http://www.npwrc.usgs.gov/resource/distr/birds/platte/platte.htm>

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Rudall River N.P. Western Australia:

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SNARL, California: <http://vesr.ucnrs.org/pages/snarlbirds.html>

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Stirling Range N.P. Western Australia:

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For sources of insular bird species richness see Kalmar and Currie (2006).

Appendix II

A global model predicting log-transformed bird species richness

A global model predicting log-transformed bird species richness for continental samples and islands around the world (n=586). The three retained terms are listed in order of inclusion by forward selections with cumulative  $R^2$  values.

Increase in  $R^2$  and p values of excluded terms are also shown if they were to be included as a fourth term. Note that these results are very similar to the results shown in Figure 3, in which richness<sup>0.3</sup> is the dependent variable. Tests of the residuals for homoscedasticity show that the residuals using log-transformed richness are strongly non-normal ( $p < 10^{-10}$ ), whereas residuals using richness<sup>0.3</sup> are normal ( $p = 0.29$ ).

See table on next page.

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retained terms:	cumulative $r^2$	p
distance to continent <sup>0.2</sup>	0.534	<10 <sup>-15</sup>
log area x precipitation <sup>0.4</sup>	0.749	<10 <sup>-15</sup>
temperature	0.803	<10 <sup>-15</sup>
excluded terms:		
faunal region (7 levels)*	+ 0.062***	<10 <sup>-10</sup>
sample category (continental or insular)*	+ 0.018	<10 <sup>-10</sup>
geohistory (continental, landbridge, oceanic)*	+ 0.019	<10 <sup>-10</sup>
distance to continent <sup>0.2</sup> x neighbor index	+ 0.033	<10 <sup>-15</sup>
distance to continent <sup>0.2</sup> x log area	+ 0.011	<10 <sup>-7</sup>
elevation range <sup>0.4</sup> **	} + 0.012	<10 <sup>-4</sup>
elevation range <sup>0.4</sup> x temperature **		<10 <sup>-8</sup>
temperature x precipitation <sup>0.4</sup> **	} + 0.012	<10 <sup>-7</sup>
temperature x (precipitation <sup>0.4</sup> ) <sup>2</sup> **		<10 <sup>-8</sup>

\* Categorical variable

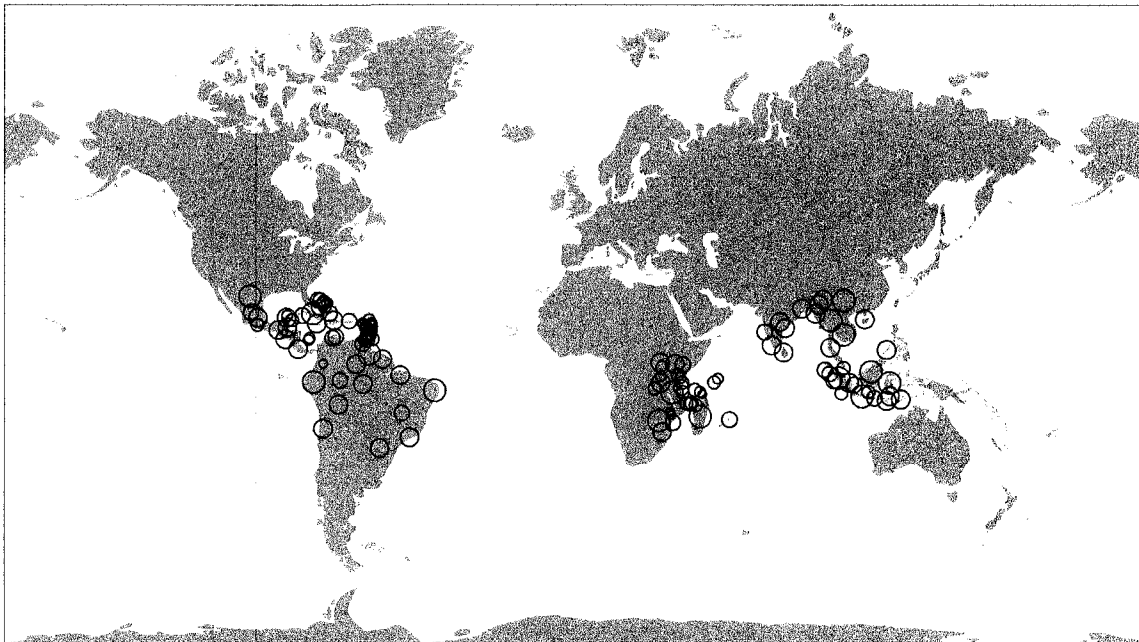
\*\* Two terms included simultaneously

\*\*\* This term would be retained in this model (cf. Table 3)

Appendix III

Regional subsets of our data used for SAR slope comparisons

We compared species-area slopes between islands and continents in the Neotropics, in East Africa, and in the tropical Indo-Pacific (Fig. 9). These samples were selected from our global data to yield regional subsets within which islands and continental samples had similar temperature and precipitation. The spatial distribution of these samples is shown on the map below. Means and medians of annual temperature and precipitation for islands and continental samples in each of the three regions are indicated on the next page.



Spatial distribution of regional subsets of our data used for figure 9.

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**Neotropical region**

Islands (n=34)

	Temp. [°C]	Precipitation [mm]
Median	25.900	1294.500
Mean	25.809	1435.088

Continental samples (n=25)

	Temp. [°C]	Precipitation [mm]
Median	22.300	1901.000
Mean	22.536	1757.840

**East African region**

Islands (n=14)

	Temp. [°C]	Precipitation [mm]
Median	26.300	1959.500
Mean	25.825	1920.714

Continental samples (n=14)

	Temp. [°C]	Precipitation [mm]
Median	23.150	1231.500
Mean	22.400	1169.857

**Oriental region**

Islands (n=19)

	Temp. [°C]	Precipitation [mm]
Median	26.000	2131.000
Mean	25.889	2268.368

Continental samples (n=13)

	Temp. [°C]	Precipitation [mm]
Median	26.400	1491.000
Mean	25.031	1716.538

## Chapter 3

# Relative and absolute completeness of the continental fossil record

Abstract

Did organisms diversify in different ways on land and in the marine realm over the Phanerozoic, or do the different diversification curves of continental and marine organisms reflect primarily methodological artifacts? To answer this question, a quantitative assessment of the completeness of the global continental fossil record is indispensable. We used comparisons between continental and marine fossil diversity and between past and present day patterns of continental diversity to assess the absolute and relative completeness of the continental fossil record. Collector's curves of the number of described families over the past 200 years suggest that the global continental fossil record, and even that of European and North American tetrapods, is still highly incomplete. Nevertheless, relative proportions of major continental and marine taxa, patterns of tetrapod endemism and familial durations suggest that the family-level continental fossil record may be fairly representative. We also found that, although continental fossil richness is correlated with the amount of terrestrial clastic sediment available for sampling, the exponential diversification curve of continental metazoans is unlikely to be an artifact of this rock bias.

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### Introduction

The Phanerozoic fossil record presents a picture of the history of life on Earth that reflects both the life that was once present on our planet and the vagaries of preservation of that life. Variations in fossil diversity have been traditionally interpreted from a biological point of view (e.g., Miller, 1998; Jablonski 1999; Benton et al. 2000). The rock record was thought to reflect a primarily biotic signal because "several kinds of data sets converged on the same pattern" (Sepkoski et al. 1981). Recent studies, however, suggest that the rock record is subject to taphonomic megabias (Peters and Foote, 2001; Smith et al. 2001; Adrain and Westrop 2003; Smith 2003). Methods have been proposed to correct for incompleteness and sampling bias in the Phanerozoic marine fossil record (e.g. Alroy et al. 2001; Kidwell and Holland, 2002) so that the remaining signal can be interpreted biologically. Most of these efforts, however, are focused on marine taxa only. The continental fossil record, on the other hand, has received relatively little attention.

There are contrasting views regarding the quality of the continental fossil record. Traditionally, the continental fossil record is considered "far poorer" than the marine fossil record (Padian and Clemens 1985). The overall fossil record of terrestrial organisms - and that of insects in particular - is widely regarded as very incomplete (Vermeij and Leighton 2003). Over three-fourths of the earth's terrestrial habitats do not influence the fossil record except as downstream weathering products (Badgley 2003). However, while terrestrial sediments provide only a relatively small portion of the available fossil record (Raup 1976a, 1976b),

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the completeness of continental sections is often comparable or even superior to that of marine sections (Sadler 1981, Schindel 1982).

Recent studies suggest that the completeness of the fossil record of various continental taxa may be comparable to that of marine organisms. Alba et al. (2001) found that the completeness of the genus-level Neogene mammal record from the Iberian Peninsula is higher than that of Ordovician-Devonian Crinoids. According to Benton and Simms (1995), the overall tetrapod fossil record is as complete as that of echinoderms. Fountaine et al. (2005) argue that the record of Mesozoic birds is “just as good as that of many other terrestrial vertebrates”. Clade metrics assessing completeness and congruence between cladistic and stratigraphic data both suggest that the continental record may be comparable to the marine record (Benton et al. 1999; Benton 2001).

These findings give rise to the question: Is it reasonable to use the continental fossil record to test hypotheses about Phanerozoic diversification patterns? To answer this question, we need to assess the completeness of the continental fossil record. In this study, we will use the marine fossil record and present day diversity as points of reference to find quantitative answers to the above question.

### Methods

We tabulated stage-level fossil family richness over the Phanerozoic based on Benton (1993). Benton's compendium indicates the first and last observed stratigraphic occurrences of fossil families in a standardized, stage-level format. It

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also includes a categorical index of habitat (marine, freshwater, terrestrial) and the date of first description for family-level metazoan taxa. We treated the stratigraphic ranges of families as continuous from the stage of first appearance to the stage of last appearance, ignoring gaps in the record, i.e. intervening stages where fossils of a given family have not been discovered yet. Data on intervening stages are not presented for many taxa (Benton 1993).

As expected for such an extensive collection of data, the quality of the information presented by Benton (1993) is heterogeneous to some extent. First and last occurrences are based on various published and unpublished data. For specific details see the chapter introductions in Benton's (1993) compendium. As preservation potentials vary, so does the completeness of the record among phyla and classes (e.g. Benton 1994; 2001). However, this family-level database is likely more robust to preservation bias than genus-level data. According to Benton et al. (2000), stage- and family-level data is uniform in quality over the Phanerozoic.

We categorized as "continental" all families that occur only in terrestrial and/or freshwater environments. We categorized as "marine" all families that occur in marine and/or brackish water habitats only. Families present in both *continental* and *marine* habitats, and families without habitat specified, make up about 4% of all metazoan families in Benton's (1993) compendium. We excluded these from analyses that distinguished between marine and continental taxa.

Sample size in most analyses corresponds to the number of stage-level stratigraphic units of the Phanerozoic (Harland et al. 1990) adopted in Benton's (1993) compendium, minus the Holocene (n=122 stages). We excluded the

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Holocene, because the quality of both fossil and environmental data is likely to be much better than for older stages, and because of the ambiguity of distinguishing between fossil and sub-fossil remains of extant families. For most statistical analyses of continental families, we excluded the Cambrian and Ordovician stages, because there are no known continental families in these periods (thus leaving  $n=97$  stages).

The great majority of continental fossil families belong to three taxonomic groups. Tetrapods (excluding the lobe-finned fishes) make up 36% of continental families. For these, data on spatial distribution is also available (Benton 1996a, 1996b). Most of the remaining families belong to the arthropod subphyla Hexapoda (51%) and Chelicerata (8%). While the temporal resolution of first and last records are generally at the stage level in Benton's (1993) compendium, for Hexapods, they are at the series level only.

Global estimates of the amount of sedimentary and other major rock types, generally at the sub-period-level, are taken from Ronov et al. (1980). Within each of their stratigraphic intervals, we assumed that sediments were distributed among stratigraphic stages in proportion to their estimated duration (i.e., we assumed constant rates of sedimentation within sub-periods). This introduces some error, likely to reduce the weight of these variables in regressions. We retained sediment volume in our models because, in our opinion, underestimating the effects of sediment volumes is less of a problem than ignoring them altogether. Stage-level fluctuations in preservation potentials have been previously demonstrated for marine taxa (Foote 2003; Lu et al. 2006). However, this does not appear to be the

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case with the continental fossil record (Fara 2002).

Most of the variables described above had strongly positively skewed frequency distributions. To make these distributions more symmetric, we used power or log transformations, as specified in Table 1.

### Results

In absolute terms, the global Phanerozoic record of fossil metazoan families is still very incomplete. A cumulative curve of fossil metazoan families described during the past 200 years shows no tendency to plateau (Fig. 1a). This is in sharp contrast with the curve of extant families (i.e. families having a fossil record and living representatives), which is reaching an asymptote at about 1600 families. The data in figure 1 cover 80% of all metazoan families having a fossil record. Most of the remaining families are hexapods for which dates of first description are not indicated in Benton's (1993) compendium.

Even the tetrapod fossil record, which is probably the best documented continental record, appears to be incomplete. Collector's curves of fossil tetrapod families show approximately linear increases in Europe and North America, as well as in other, presumably undersampled continents (Fig. 2). The general absence of plateauing trends illustrates the incompleteness of the tetrapod fossil record and/or constant taxonomic revisions.

Relative representation of families in fossil, versus contemporary, records also suggests that the continental record is less complete than the marine one. Continental families make up about 36% of all living metazoan families. Among

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fossil metazoan families, the continental families amount to 24% only. The difference may indicate either that the continental record is less complete than the marine record, or that terrestrial life is more diverse today than in the past. The difference is relatively small either way.

A comparison of the spatial distributions of fossil and living tetrapods also suggests that undersampling of the fossil fauna is probably not so severe as to mask the history of diversification. The raw numbers of fossil and living families per geographic region clearly differ: most fossil tetrapods have been unearthed in Europe and North America, where sampling intensity is presumably the highest (Fig. 3a). Proportions of endemics per continent are also generally higher for fossil families than for living families (Fig. 3b). This probably reflects incomplete sampling. Globally, 53% of all fossil families are endemic to a single continent versus 44% of all living families. However, trends of endemism among continents are similar. Both for fossil and living families, the proportion of endemics per continent is highest in South America and Australasia (Fig. 3b). The portion of families with world-wide distributions is also very similar among fossil and living tetrapods (12.5% vs. 13.5% respectively). Overall, these results suggest that, albeit incomplete, the global record of fossil tetrapod families may be still fairly representative.

The major continental and marine taxonomic groups are also represented in similar proportions in living and fossil families (Fig. 4). We found that Tetrapoda, Hexapoda and Chelicerata (the 3 major continental taxa) together make up about the same proportion of all living and fossil metazoan families. The same can be

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said about the three largest predominantly marine groups: Mollusca, Crustacea and Pisces. Although the relative proportions of these groups vary somewhat (e.g. Chelicerata and Crustacea), they do not suggest gross under-sampling of the family level continental fossil record.

If the continental fossil record were less complete than the marine one, we would expect familial durations (i.e., the temporal ranges of families) to be shorter for continental animals than for marine ones. We found that median durations of continental families of metazoans was 34.0 Myr vs. 40.1 Myr for marine families. Although the difference is statistically significant in an ANOVA ( $p < 10^{-10}$ ,  $n = 6031$  families), the difference between marine and continental taxa accounts for only 1.2% of the total variance of familial durations ( $\text{Myr}^{0.2}$ ) over the Phanerozoic. This difference could have been attributed also to the fact that marine families often originate in the Lower Paleozoic where continental families are still absent. Thus, these long ranging marine families would increase median familiar durations for marine taxa. To test this possibility, we excluded marine families originating in the Cambrian and Ordovician. Surprisingly, we found that by excluding the Lower Paleozoic marine taxa, the difference in median familiar durations actually increased: 34 vs. 49 Myr for continental and marine families respectively (ANOVA:  $r^2 = 0.021$ ,  $p < 10^{-10}$ ,  $n = 6031$  families). These results suggest that familial durations, and presumably the completeness of the marine record as well, are superior to the continental one, although the difference is not large, given the standard deviations (continental: 56.2 Myr; marine: 75.0 Myr, excluding the Ordovician and the Cambrian periods).

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The above use of familial durations to assess completeness is based on the assumption that rates of origination do not differ between continental and marine metazoans. Although speciation rates are known to vary over time, among taxa and among climatic regions (Sepkoski 1998), we found that, overall, origination rates of families do not differ on continents and in the marine realm. Based on Benton (1993), we counted a total of 3541 marine metazoan families that have originated since the Vendian, yielding a mean of 5.80 fam/Myr until the Holocene. Broadly speaking, while marine diversity began to increase in the Vendian, life on continents started to radiate only in the Devonian. The 2399 continental families that appeared from the Devonian to the Holocene, yields a very similar mean origination rate to that of marine animals (5.87 fam/Myr). These rates are based on the time scale of Harland et al. (1990). They would only slightly differ according to the newer ICS time scale (Gradstein et al. 2004): 5.48 fam/Myr (marine); 5.77 fam/Myr (continental).

Absolute age is the strongest predictor of family richness both for continental and marine families (Table 1). The diversification of continental families over the Phanerozoic increased approximately as a power function of time (Fig. 5a). Stage order, i.e. a simple numerical ranking of stratigraphic stages in temporal order, can statistically explain 91.6% of the variance in continental family richness<sup>0.4</sup> since the apparition of terrestrial metazoans in the Devonian (n=97).

We found that per stage family richness of continental animals was unrelated to stage duration (Myr<sup>0.2</sup>). The relationship was not significant for either continental families ( $r^2 < 10^{-4}$ ,  $p = 0.965$ ,  $n = 97$ ) or marine families ( $r^2 = 0.021$ ,  $p = 0.11$ ,

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n=122). Results are only slightly stronger after controlling for the effect of time (continental families:  $r^2=0.061$ ,  $p=0.014$ ,  $n=97$ ; marine families:  $r^2=0.047$ ,  $p=0.017$ ,  $n=122$ ). Therefore, a sampling effect of time, according to which stages of longer duration would yield more fossils, is very small.

Continental fossil richness is correlated with the amount of terrestrial clastic sediment (Table 1). However, this appears to be the case only when there are less than about 1.8 million  $\text{km}^3$  of sediment per stage (Fig. 6). Note that the pre-Devonian stages, from which there are no known terrestrial families, fall nicely on the same relationship. This means that the absence of terrestrial families from the Cambrian and Ordovician periods could be attributed in part to the very small amount of terrestrial clastic sediment associated with these periods.

After controlling for the volume of terrestrial clastic sediment, continental family richness still increases monotonically with time (Fig. 7). Moreover, stages adjacent to major extinction events (typically dated for system boundaries) do not seem to be outliers. Aside from terrestrial clastic, no other sediment type shows a strong positive correlation with continental family richness (carbonate<sup>0.2</sup>:  $r=-0.22$ ; carbonate and clastic<sup>0.2</sup>:  $r=-0.32$ , marine clastic<sup>0.2</sup>:  $r=0.084$ . total rock volume<sup>0.2</sup> of all sediment types:  $r=-0.015$ ;  $n=97$ ). Thus, the exponential diversification curve of continental families does not appear to be a preservation artifact.

After controlling for the amount terrestrial clastic sediments, marine family richness also shows exponential growth (Fig. 8). Although both of these relationships appear linear, the slope of the marine curve is much less steep (0.0015 for marine vs. 0.030 for continental metazoans). Unlike the continental

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data, the residual variance of the marine samples increases with age. This positive correlation between marine fossil richness and terrestrial clastic sediments is not necessarily surprising (Thesis conclusion: Table 1). On the other hand, controlling for the amount of marine clastic sediments would not alter substantially the familiar logistic curve of marine animals (Fig. 5 vs. Fig. 9). A similar curve can be obtained by controlling only for carbonate and clastic sediments which are most strongly correlated with variation in marine fossil richness (Chapter 4, Table 3a).

### Discussion

In this study, we used collector's curves to assess the completeness of the fossil record. This approach is analogous to the use of species accumulation curves in contemporary ecology to estimate species richness in a sampling area as a function of the number of captured specimens (e.g. Sanders 1968; Palmer 1990). Similarly, as the fossil record becomes more and more complete with every passing decades of research activity, collector's curves can serve as a tool to assess its completeness. If a leveling off pattern is present, an estimate of the number of families still awaiting discovery becomes possible. For example, it is unlikely that the number of extant metazoan families will increase considerably in the future (Fig 1a). On the other hand, the fossil record of metazoans, and especially that of continental animals, appears to be still very incomplete. The rate of accumulation of marine fossil families may show some sign of slowing in the late 20<sup>th</sup> century, although it may be too early to advance a figure on the number of

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families remaining to be discovered (Fig. 1b). In contrast, the continental curve is still accelerating. This is consistent with the traditional view that the terrestrial fossil record is much less complete than the marine record (Padian and Clemens 1985). Family-level collector curves reflect, to some degree, taxonomic uncertainties as well. Fossil genera have often been documented years or decades prior to the formal establishment of their respective families.

Even the best sampled continental organisms, the tetrapods, appear to be under-sampled. Although some tetrapod taxa have been shown to have a relatively complete record at the regional scale (Alba et al. 2001, Benton and Simms 1995), the global tetrapod record appears to be still very incomplete (Fig. 2). The number of described tetrapod families per continent is increasing more or less linearly even in Europe and North America, where the record is generally believed to be most complete. For other continents, the degree of undersampling may be reflected by lower slopes (Fig. 2). This would support the general view that tropical regions are strongly undersampled (Raup 1976a, Signor 1990, Johnson 2003, Smith 2003).

Under-sampling notwithstanding, several characteristics of the continental fossil record suggest that it reflects the history of diversification of life almost as accurately as does the marine record. First, we found familial durations to be only moderately shorter among continental families than among marine families. Relative increases in familial durations, due to new discoveries and taxonomic revisions, also appear to be similar among continental and marine families: family range increase is about twice as common as family range decrease, both among

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tetrapods (excluding birds, Maxwell and Benton 1990) and among marine families (Sepkoski 1992).

Patterns of endemism are not dramatically different between living and fossil tetrapods (Fig. 3b). The high proportion of endemic families from Europe and North America may be partly the result of intense research activity on these continents (Fig. 3b). Nevertheless, this regional bias may have limited impact on the overall adequacy of the tetrapod fossil record, because these continents, enjoying a warmer climate in the past, presumably shared a larger proportion of the global diversity than they do today.

Major continental and marine taxonomic groups have very similar proportions between living and fossil metazoan families (Fig. 4). The decreasing proportion of tetrapods (15% of fossil vs. 7% of living families) is likely an evolutionary trend. Chelicerates clearly make up a much more important fraction of living families than of fossil families (Fig. 4). This could be the results of low preservation potential for these predominantly soft-bodied animals. Alternatively, it could also indicate a recent explosion of diversity. Chelicerate family richness fluctuates at around 20 families per stage since the Lower Paleozoic up until the Rupelian (Early Oligocene), when it increases dramatically to about 130 families and maintains this higher level of richness until the present.

The continental fossil record may be biased by the amount of terrestrial clastic sediment available for sampling, but probably not severely so. In particular, the near absence of terrestrial clastic sediments in the lower Paleozoic means that it is effectively impossible to determine whether a small number of continental

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families existed during the lower Paleozoic or none at all (Fig. 6). Despite this rock bias, however, our results support Benton's claim (1997, 2001) that the exponential diversification curve of continental organisms over the Phanerozoic is unlikely to be the result of preservation artifact (Fig. 7).

Stage order alone explains 91.6% of the temporal variation in continental family richness<sup>0.4</sup> since the Devonian. This does not imply, however, that the quality of the record is a mere function of time. Bivalves, one of the best preserved marine groups, show a similar monotonic increase in richness over the Phanerozoic. Stage order similarly explains 96.2% of the variation in the number of Bivalve families<sup>0.5</sup> over the Phanerozoic. In contrast, the logistic diversification curve of all marine metazoan families is very similar to that of marine genera (Fig. 5b).

In summary, quantitative and graphical comparisons of the continental fossil record with the marine fossil record and with present day patterns of diversity (summarized in Table 2) suggest that the continental record may well worth some attention in global paleodiversity studies. From an absolute point of view, the continental record is certainly less complete than the marine record. Nevertheless, at the taxonomic level of the family, the difference in relative completeness between the continental and the marine record does not appear to be marked. In agreement with Benton (1997), we found that the logistic diversification curve of continental metazoans is unlikely to be the result of a poor fossil record (Fig. 7). Therefore, we propose that, at the suprageneric level, the use of continental taxa for computing global diversity metrics is appropriate.

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Tables and figures

Table 1. Correlations between the number of marine and continental metazoan fossil families and factors potentially responsible for the temporal variation in richness. Since the physical variables are collinear with time, the partial correlations between richness and the physical variables, controlling for a linear effect of time, are also presented. We excluded the Cambrian and the Ordovician stages from the analysis for correlations with continental family richness: n=122 (marine families), 97 (continental families). Correlations stronger than  $r=0.18$  are significant at  $p<0.05$  for  $n=122$ , and at  $r=0.20$  for  $n=97$ .

	marine <sup>0.2</sup>		continental <sup>0.4</sup>	
	simple r	partial r   time	simple r	partial r   time
geological time [Myr]*	0.655	---	0.960	---
stage order	0.594	---	0.957	---
stage duration [Myr] <sup>0.2</sup>	-0.143	-0.216	0.004	-0.248
terrestrial clastic sedim. [ $10^3\text{km}^3$ ] <sup>0.2</sup>	0.135	-0.443	0.622	-0.004

\* untransformed, based on Harland et al. (1990)

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Table 2. Summary of graphical and quantitative comparisons to assess the completeness of the family-level fossil record of continental metazoans.

comparison	assessment
collector's curves of metazoan families (Fig. 1)	highly incomplete
regional collector's curves of tetrapods (Fig. 2)	highly incomplete *
tetrapod endemism (Fig. 3)	representative *
past-present proportions of continental families	moderately incomplete
past-present proportions of major taxa (Fig. 4)	representative
familial durations	moderately incomplete
family range increases **	representative *
exponential diversification (Fig. 5,7)	representative

\* Tetrapods only

\*\* Based on Maxwell and Benton (1990) and Sepkoski (1992)

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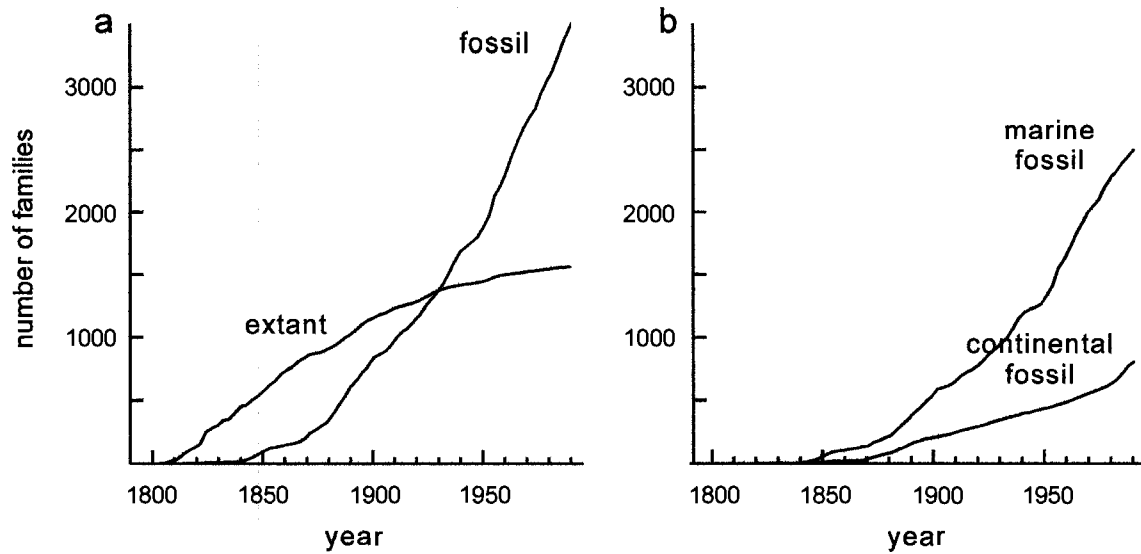


Figure 1. Cumulative collector's curves of the number of metazoan families as a function of the year of first description in the scientific literature. The two curves in panel 1a include all marine and/or continental taxa. Extant families have both fossil and living representatives, as indicated by Benton (1993). b) The cumulative numbers of described fossil families in marine and continental habitats (families occurring both in continental and marine habitats have been excluded).

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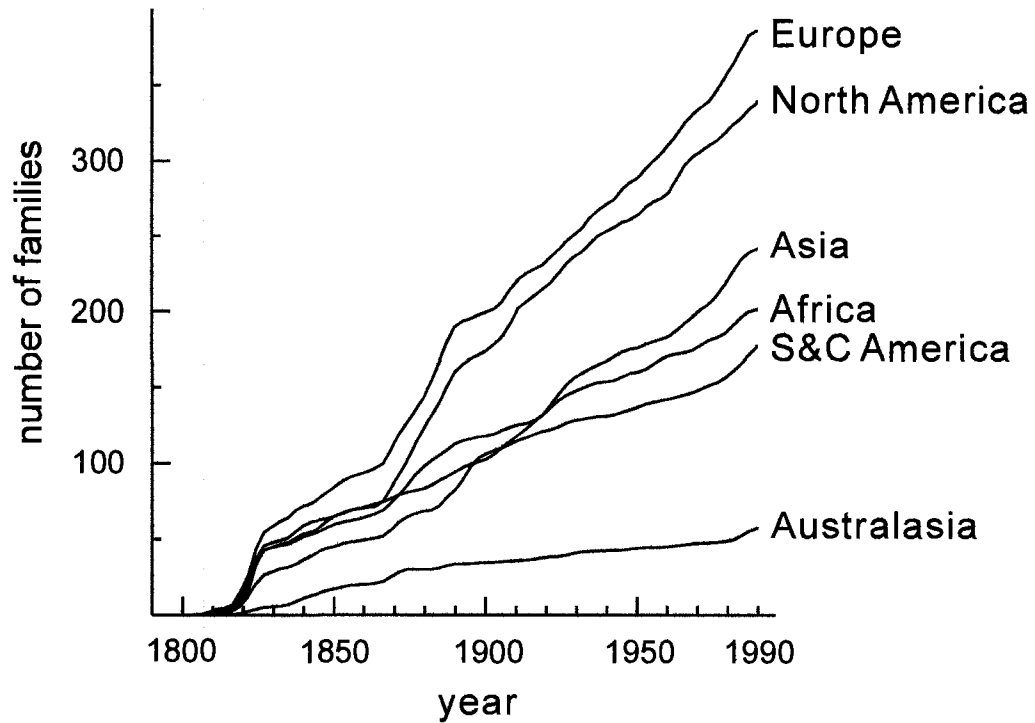


Figure 2. Cumulative regional collector's curves of the number of fossil tetrapod families as a function of the year of first description in the scientific literature. Singleton families are included. Data from Benton (1993, 1996a, 1996b).

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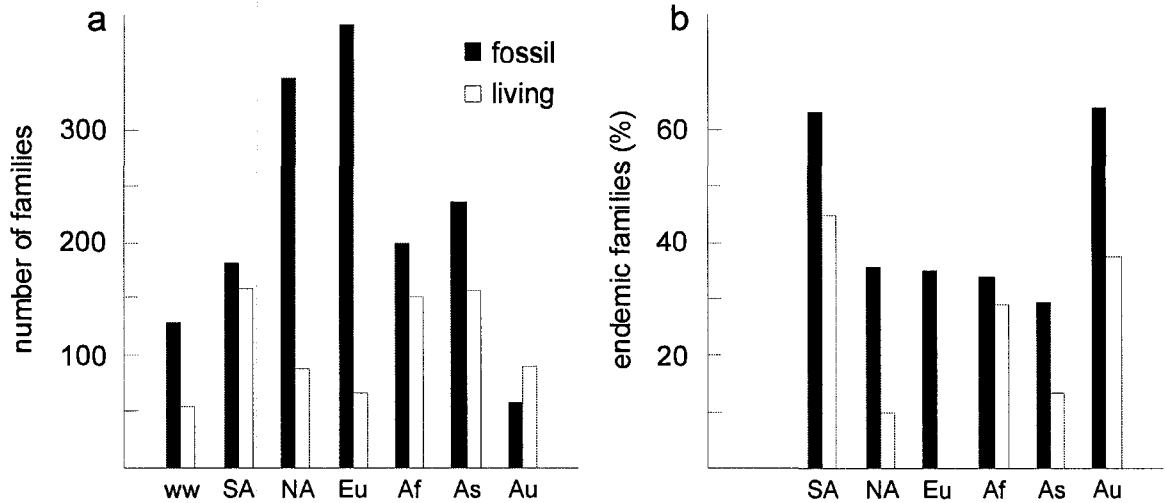


Figure 3. Geographic distribution of fossil and living tetrapod families. (a) Most fossil tetrapods have been unearthed on continents where sampling intensity is presumably the highest: North America and Europe. (b) Endemism is apparently higher among fossil families than among living families, probably reflecting the incompleteness of the fossil record. Fossil families occurring on at least four continents are counted in the world-wide category only (data from Benton 1993, 1996a, 1996b). Singleton families are included.

Abbreviations: ww - world-wide; SA – South America (including Central America, West Indies and Galapagos); NA - North America; Eu – Europe, Af - Africa (including Madagascar and Indian Ocean); As – Asia; Au – Australasia (including New Guinea, New Zealand and the South Pacific).

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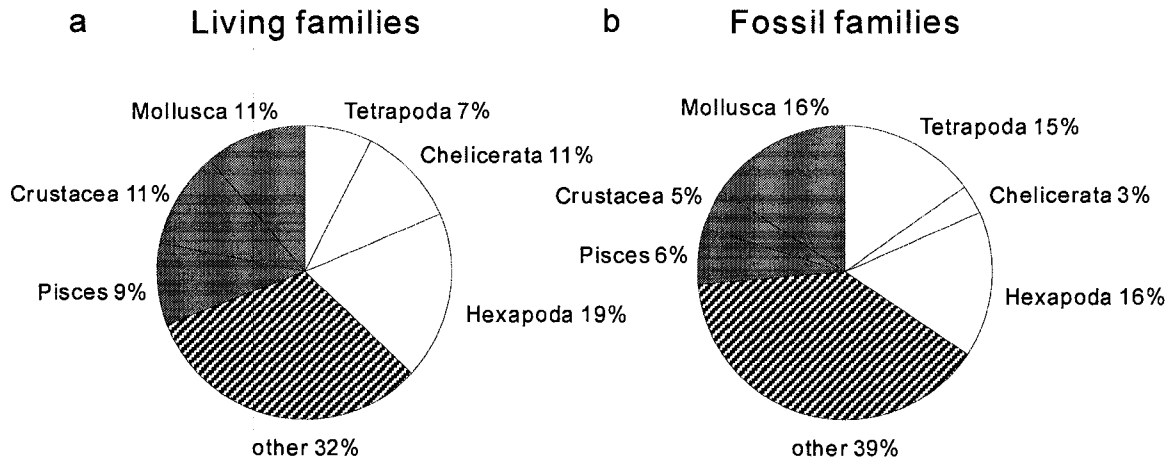


Figure 4. (a) Relative proportions of the three largest predominantly continental taxa (white) and the three largest predominantly marine taxa (gray) of living metazoan families. (b) Relative proportions of these same taxa among fossil families. Counts include 5242 living families (Parker 1982) and 6815 fossil family level taxa (Benton 1993).

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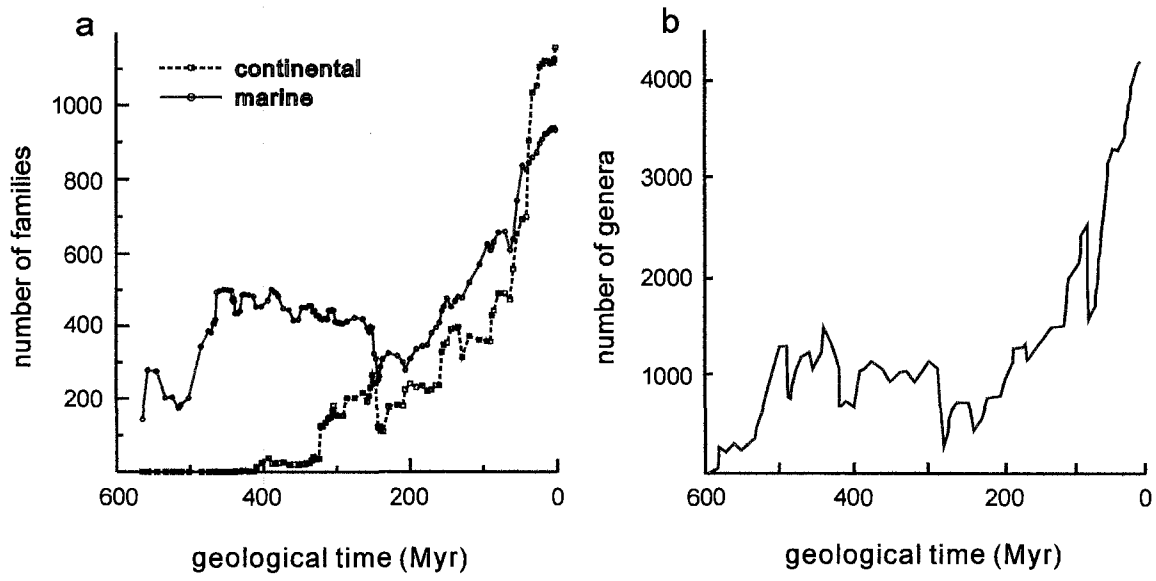


Figure 5. (a) Global Phanerozoic diversification curves of continental and marine metazoan families (data from Benton 1993). (b) The logistic curve of well-skeletonized marine genera (Fig. 6c of Benton 1997, based on data from Sepkoski, 1996) is similar to that of marine families.

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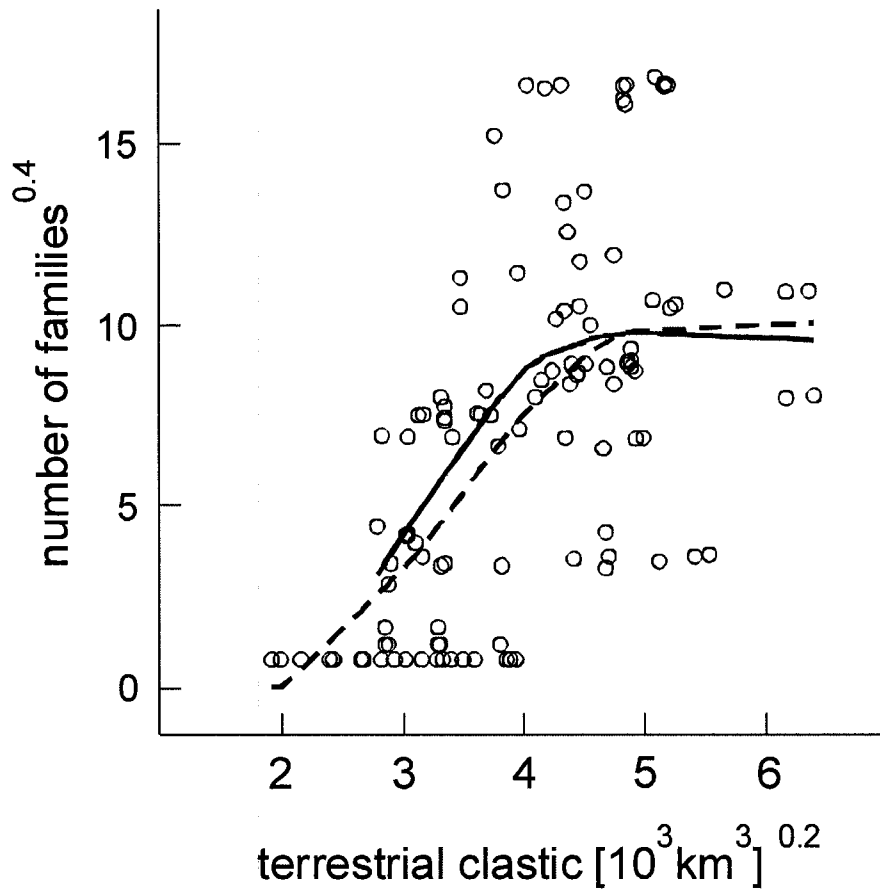


Figure 6. Global richness of continental metazoan families as a function of the amount of terrestrial clastic sediment associated with stratigraphic stages. Family richness plateaus at about 1.8 million  $\text{km}^3$  of sediment per stage, corresponding to about 4.5 on the X axis. Solid line: Curve fitted excluding the Cambrian and Ordovician stages where continental family richness = 0 ( $n=97$ ). Dashed line: curve fitted including the Cambrian and Ordovician stages. These Lower Paleozoic stages are without any continental families, and correspond to  $0.5^{0.4}=0.758$  on the Y axis.  $N=122$ . Tension for both curves = 0.7 (LOWESS fit).

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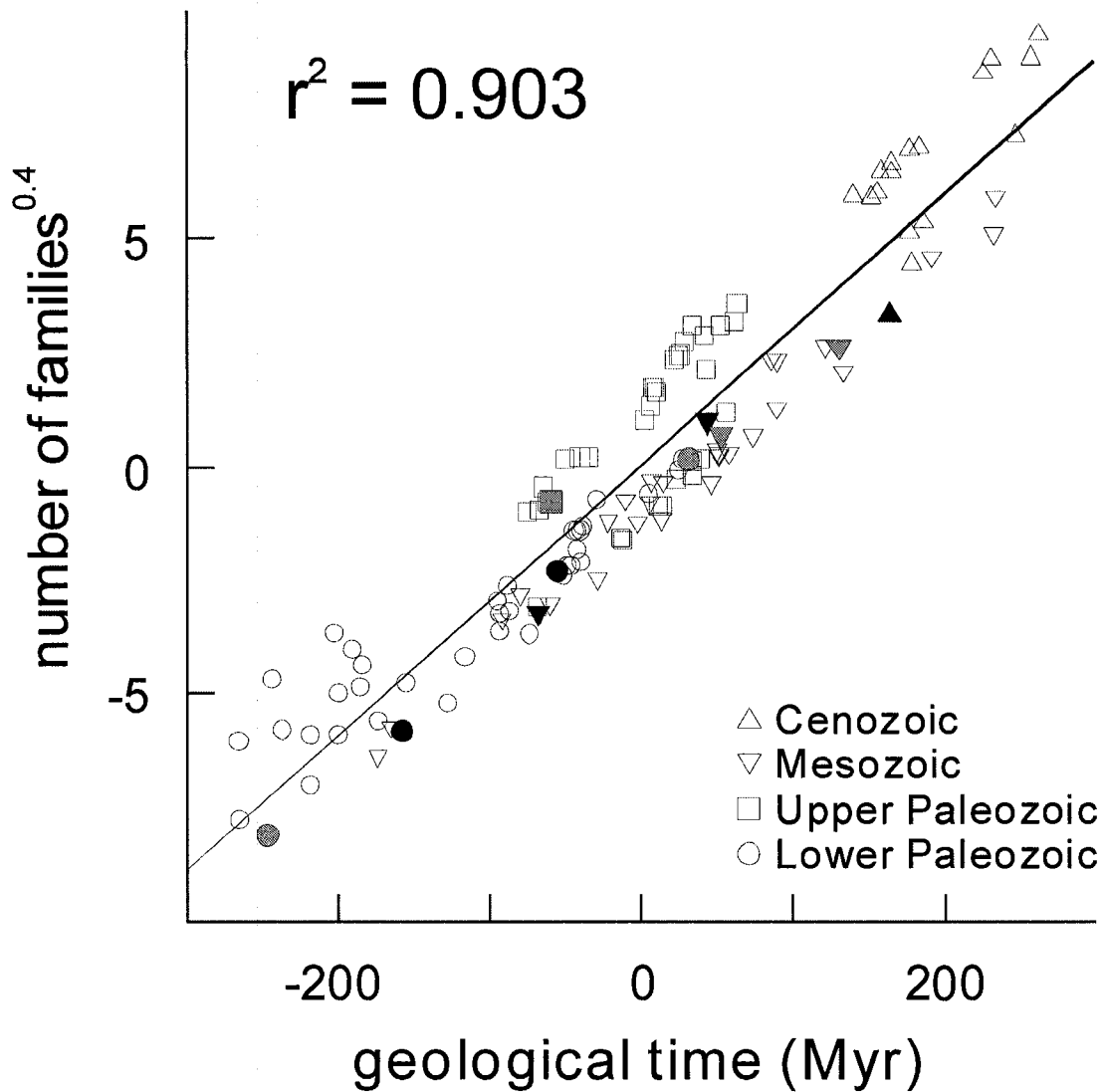


Figure 7. Global richness of continental metazoans over the Phanerozoic, as a function of geological time. The axes represent residuals, after controlling for the amount of terrestrial clastic sediment associated with stratigraphic stages. Stages preceding and following the Big Five mass extinction events, associated with stage boundaries, are indicated in grey and black respectively. N=122.

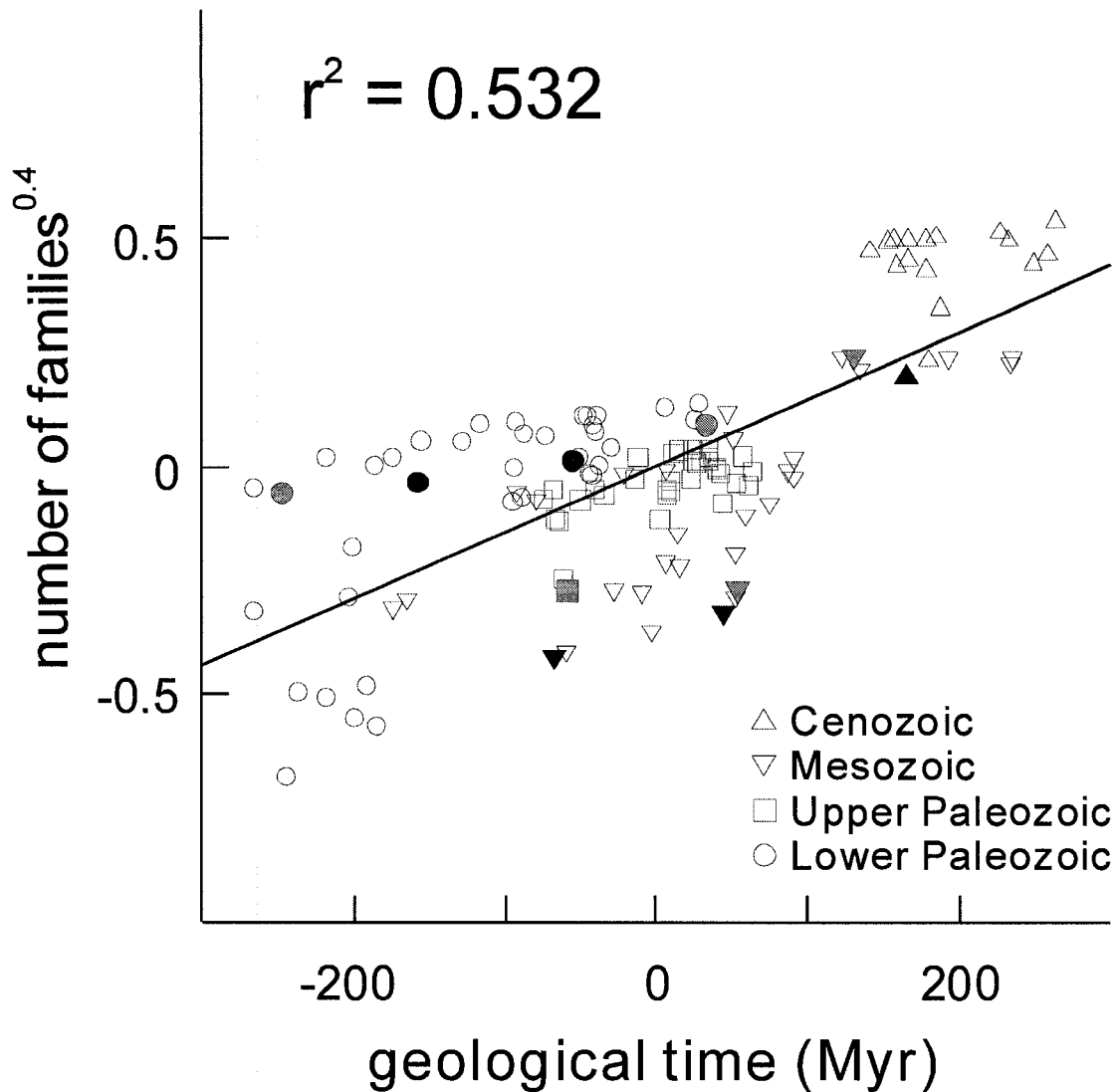


Figure 8. Global richness of marine metazoans over the Phanerozoic, as a function of geological time. The axes represent residuals, after controlling for the amount of terrestrial clastic sediment associated with stratigraphic stages. Stages preceding and following the Big Five mass extinction events, associated with stage boundaries, are indicated in grey and black respectively. N=122.

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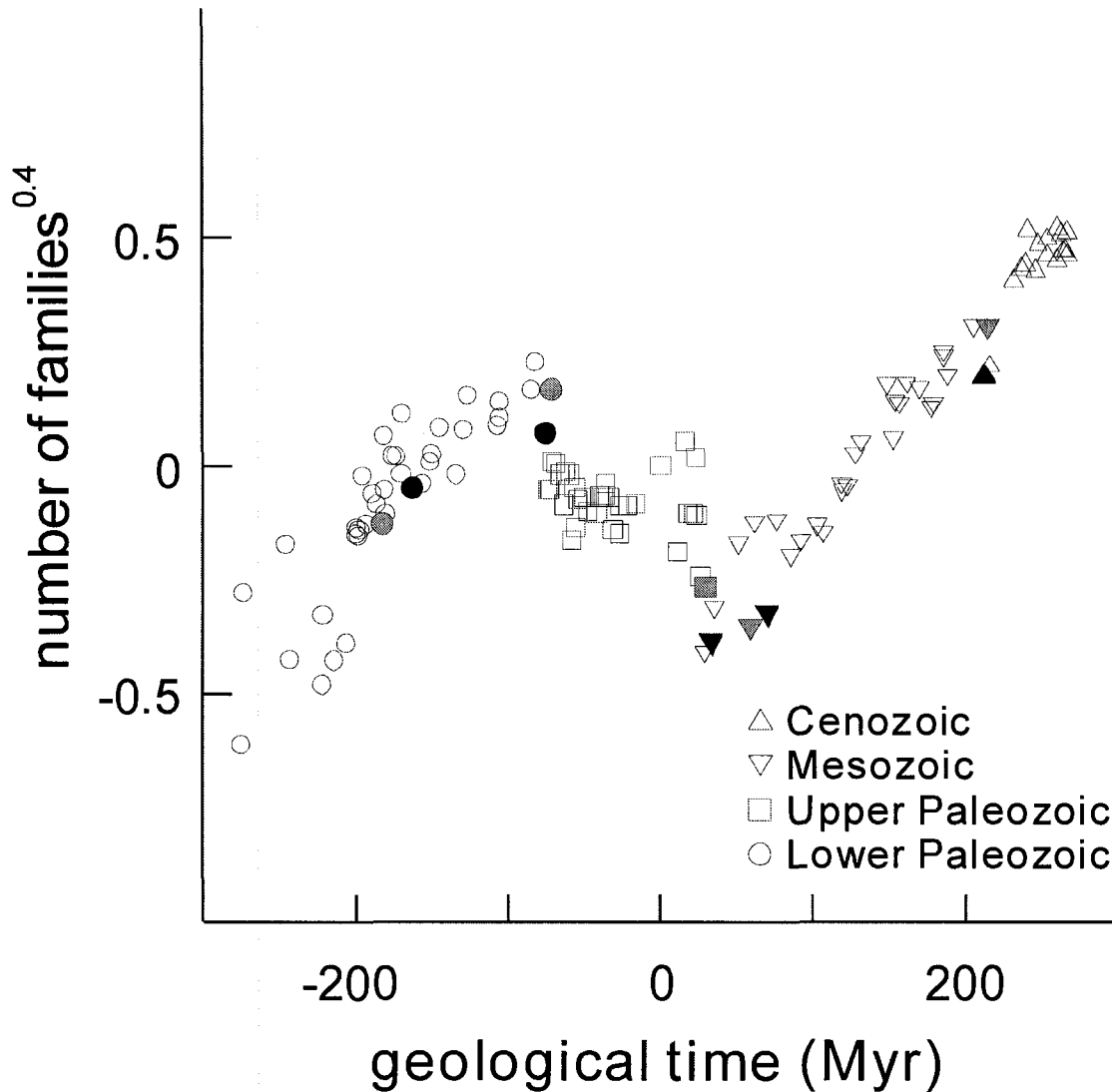


Figure 9. Global richness of marine metazoans over the Phanerozoic, as a function of geological time. The axes represent residuals, after controlling for the amount of marine clastic sediments associated with stratigraphic stages, including carbonate, carbonate and clastic and marine clastic sediments (based on Ronov et al. 1980). Stages preceding and following the Big Five mass extinction events, associated with stage boundaries, are indicated in grey and black respectively. N=122.

## Chapter 4

A global relationship between variation in fossil  
richness and magnetic polarity reversals

Abstract

Although single extinction events have long been related to magnetic polarity reversals, no globally consistent relationship have been conclusively demonstrated between variation of fossil diversity and reversal intensity over the entire Phanerozoic. Here we document a global correlation between the number of magnetic polarity reversal records and change in the number of metazoan families per stage ( $r=0.73$ ). To illustrate the predictive value of the magnetic data, we also evaluate cratering intensity, atmospheric CO<sub>2</sub> ratios, stratigraphic stage duration and abundances of various sediment types as potential predictors of per stage rates of originations, extinctions and change in number of families, of marine and continental metazoans. We found that reversal intensity stands out as a strong predictor of all these metrics in multiple regression models. Our results suggest that either variation in fossil diversity and the magnetic record are both subject to preservation bias in the rock record, or alternatively, a perturbation regime can statistically explain most of the variation in fossil richness over the Phanerozoic. Strong stage-level cyclicity in the fossil record, as well as in cratering and magnetic reversal intensity, are compatible with both of these hypotheses.

## Introduction

What factors control variation in fossil richness? The answer to this question is no doubt even more complex than its contemporary equivalent: what controls spatial variation in species richness? Fossil richness not only reflects past diversity, but also, to a great extent, preservation bias. Since preservation bias is often triggered by climatic, geologic and extra-terrestrial perturbations, quantitative and predictive models are needed to understand how the biosphere responds to these environmental perturbations (Flessa 2000). Here, we document a strong correlation between change in fossil composition and an index of magnetic polarity reversal intensity over the Phanerozoic.

Magnetic polarity reversals are interchanges in the orientation of the magnetic fields of stellar and planetary bodies. On Earth, the history of reversals is recorded in the orientation of crystals in layered deposits of ferromagnetic minerals. Rates of magnetic polarity reversals varied greatly in Phanerozoic times; from about 5/Myr (Miocene) to 0.05/Myr (Middle and Upper Cretaceous) [Coe and Glatzmaier 2006]. The process of reversal in itself is relatively short, ca. 1000-6000 yrs (Glatzmaier et al. 1999). The causes and mechanisms behind magnetic polarity reversals are still not well understood (for reviews see Glatzmaier 2002; Glatzmaier et al. 2004).

Extinctions of individual taxa - especially that of Radiolarians - have been associated with magnetic polarity reversals in earlier literature (Uffen 1963; Hays and Opdyke 1967; Hays 1971; Hays and Shackleton 1976). Raup (1985) showed a global scale correlation between increased magnetic polarity reversal

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activity and mass extinctions over the past 165 million years. Raup (1985) also proposed that variations in reversal activity and extinction events are both consistent with ca. 30 million years stationary periodicity. Although many studies have examined the question of periodicity in the fossil record (Fisher and Arthur 1977; Hallam 1984; Kitchell and Pena 1984; Raup and Sepkoski 1984, 1986, 1988; Sepkoski and Raup 1986; Patterson and Smith 1987, 1989; Shaw 1987; Stigler and Wagner 1987, 1988; Sepkoski 1987, 1990), few have attempted to assess the strength of the correlation between reversal intensity and extinction rates. Plotnick (1980) found that the apparently strong correlation between number of reversals and fossil marine invertebrate species richness is not significant after factoring out their correlation with the duration of stratigraphic series.

Using the global paleomagnetic data from Pisarevsky (2005), we test the hypothesis that a global scale correlation may exist between variation in fossil metazoan family richness and magnetic polarity reversal intensity for the entire Phanerozoic. If such a correlation can be demonstrated, its relative predictive value can also be tested against other classic predictors of variation in fossil diversity. In particular, we intend to assess the predictive values of atmospheric CO<sub>2</sub> ratios, bias caused by the available amount of rocks for sampling (Raup 1976), stage duration and bolide impact intensity.

Variation in atmospheric RCO<sub>2</sub> (past/present ratio) have been shown to be positively correlated with fractional origination rates of marine animals (Cornette et al. 2002). Paleolevel estimates of atmospheric CO<sub>2</sub> are based on volcanic

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activity, chemical weathering, paleoclimate, solar radiation, plant biomass and other factors (Berner and Kothavala 2001). Therefore, if perturbations, such as volcanic activity or increased sea-floor spreading, and climate drive origination and/or extinction rates, this might account for a correlation with RCO<sub>2</sub>.

Several major Phanerozoic extinctions events have been related to bolide impacts (e.g. Rampino and Stothers 1984; Alvarez et al. 1980; Alvarez 1987; Hodych and Dunning 1992). Becker et al. (2001) reported fullerenes with carbonaceous chondrite-like helium and argon isotopic ratios for the Permian-Triassic boundary. Unusually high iridium concentration, a possible indicator of bolide events, was reported to coincide with numerous Phanerozoic extinction events (Walliser 1996). For example, iridium anomalies are present at the terminal Eocene (Alvarez et al. 1982), the Ordovician/Silurian boundary (Wang and Chai 1989), the Devonian/Carboniferous boundary (Wang 1993), etc. Most earlier studies on bolide impact effects have focused on demonstrating single-event causation or long term periodicities. Here we assess the predictive value of the Phanerozoic cratering data alongside the magnetic record and other potential predictors in a multivariate analysis.

### Methods

Benton's (1993) global compendium, *The Fossil Record 2*, indicates the first and last stratigraphic record of fossil families in a standardized, stage-level format (for more details regarding Benton's database see Chapter 3: Methods). Based on these data, we counted the number of first and last appearances of

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family-level metazoan taxa in each Phanerozoic stage. We will refer to these as origination and extinction rates (per stage) respectively. *Change in number of families* is the total number of metazoan families per stage having a different stratigraphic distribution status (absence or presence) with respect to the preceding stage. Many families are known from a single stratigraphic stage only. We did count these for *change in number of families*, but not for origination and extinction rates. In either way, the inclusion or exclusion of these "temporal endemics" has little impact on the statistical relationships we present (see results). We treated all other families as having a single appearance and extinction (save extant groups) in the stratigraphic record, as indicated by Benton (1993). Thus, we did not count gaps in the record (intervening stages) for any of our fossil metrics.

For our index of magnetic polarity reversal intensity, we counted the number of known magnetic polarity reversal records per stratigraphic stage, based on Pisarevsky's *Global Paleomagnetic Database* (GPMDB 2005). This database indicates the lower and higher age estimates for 7513 rock units. About 80% of these records are Phanerozoic. We found that age estimates of polarity reversals tend to cluster at stage boundaries, making them difficult to assign to a particular stage. We therefore counted the number of reversals that occurred between the midpoints of successive stages (rather than during a given stage). We assigned this number to the later stage. Pisarevsky's magnetic data follow the 2004 ICS time scale (Gradstein et al. 2004). Consequently, we had to adjust reversal intensity rates to the stratigraphic stages of the Harland

time scale (Harland et al. 1990) followed by Benton (1993). The method of time scale adjustment is described in Appendix I.

Cratering data are from the *Earth Impact Database* (2006) of the Planetary and Space Science Center. This database indicates crater diameters and age estimates for 172 dated impact craters from around the world. About 90% of these records are Phanerozoic. For our index of *cratering intensity*, we summed all recorded crater diameters per stages, based on the dates of the EID (2006), without considering the error estimates on the dates. Note that crater ages have a clustered distribution. While a few stages have numerous dated craters, about 58% of all Phanerozoic stages have no recorded impact craters at all. Therefore, *cratering intensity* has a large variance. To reduce the weight of stages without any dated craters in statistical analyses, we added a hypothetical value of 0.75km (i.e. half the size of the smallest sum of crater diameters in our data, on the assumption that this represents the effective limit of detection) to all stages.

We also experimented with other indices of cratering intensity. For example, we summed crater diameters from midpoint to midpoint of successive stages or just counted the number of dated impact craters per stage, based on the *Earth Impact Database* (2006). Since all these statistics yielded very similar or lower correlations with fossil diversity metrics, we do not present them here. Although in this chapter we present results using the EID (2006), we also assessed cratering intensity from Hamilton's (1995) *Terrestrial Impact Crater List*. The statistical relationships with other variables were virtually identical using either cratering data source.

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Estimates of atmospheric CO<sub>2</sub> ratios are from Berner and Kothavala (2001). We recalculated this 10 million year interval data for stratigraphic stages as simple arithmetic averages, taking into consideration the slight differences between the time scale (Gradstein and Ogg, 1996) followed by Berner and Kothavala (2001) and the Harland time scale (Harland et al. 1990) followed by Benton (1993).

Data on abundance of lithological associations is based on Ronov et al. (1980). This comprises a global estimate of the amount of sedimentary and other major rock types associated with sub-period-level Phanerozoic stratigraphic intervals. Within each of these intervals, we distributed the total amount of sediments among stratigraphic stages, according to their estimated duration: i.e. we assumed constant rates of sedimentation for all stages of a given subperiod. Therefore, our goal here is limited to test for the presence of large-scale sampling effects (cf. Raup 1976). Sampling effect at the (sub)stage level, due to cyclic fluctuation in preservation potentials, has been previously demonstrated (Foote 2003; Lu et al. 2006).

We related the numbers of originations, extinctions and *change in number of families* per stratigraphic stage to the predictor variables described above in multiple regressions. All variables were transformed to best conform to normal distributions (transformations specified in Tables 1 and 3). We also compared the results of ordinary least squares (OLS) regression to conditional autoregressive models (CARs; Rangel et al. 2006). CARs increased explained variation by <<1%, compared to OLS, and the parameter estimates changed very

little. For simplicity's sake, we present only OLS results below. Although we focus on absolute rates of variation in fossil diversity, we also present results for fractional rates, i.e. the absolute values divided by the total number of taxa occurring in a stage and by stage duration (Tables 2b, 3b). We avoided time series analyses for reasons explained below.

Cross correlation analysis shows that change in number of families and origination rates are most strongly correlated with predictor variables at lag=0. Extinction rates, however, are most strongly correlated with predictor variables at lag=+1. This is because the stage of interest for a response variable is where the distribution status of a taxon changes - in the case of extinctions, from present to absent - in the stratigraphic record. Consequently, we related extinction metrics at lag=+1 to predictor variables in all of our statistical analyses.

## Results

Temporal autocorrelation in our data was generally weak. The strongest autocorrelation was in the *change in number of marine and continental families combined* with a lag of two stratigraphic stages:  $r=0.433$  ( $n=120$ ,  $p<10^{-6}$ ). This autocorrelation reflects the alternating pattern of extinction and origination intervals observed in earlier studies (e.g. Carr and Kitchell 1980; Lu et al. 2006). Procedural errors that might induce temporal autocorrelation would tend mainly to affect first order autocorrelation (lagged by one stratigraphic stage) because occurrences of families are more likely to be unobserved for one stage than for two or more successive stages. However, this was much weaker:  $r=0.279$

( $n=121$ ,  $p=0.002$ ). In general, the same can be said about our other fossil metrics (Table 1). In the regression models that follow, first-order autocorrelation in model residuals was always  $r<0.15$ .

Stage-to-stage change in the total number of fossil metazoan families fluctuates in parallel with polarity reversal intensity (Fig. 1). The relationship is surprisingly consistent over almost the entire Phanerozoic, with the exception of the Devonian (Fig. 1c). All other absolute metrics of variation in fossil diversity show highly significant and fairly strong correlations with reversal intensity ( $p<10^{-7}$ , Table 2a). Fractional rates, on the other hand, have markedly weaker correlations with reversal intensity (Table 2b).

We found that reversal intensity was more strongly correlated with change in number of families than with extinction or origination rates (Table 2a). Theoretically, this may be the result of our methodology of counting temporal endemics. About 10% of all metazoan families are “temporal endemics”, i.e. they are found in one stratigraphic stage only. Recall, that we counted these families for change in number of families per stage, but not for rates of originations and extinctions. However, subtracting the temporal endemics from *change* of all metazoan families does not decrease substantially its correlation with reversal intensity ( $r=0.713$ , c.f. Table 2a). Also, adding temporal endemics to origination or extinction rates would not increase their correlations with reversal intensity (originations:  $r=0.677$ , extinctions:  $r=0.661$ , c.f. Table 2a). Therefore, the stronger correlation we found between change in number of families and reversal intensity is not an artifact of handling the single stage

families.

Correlations between variation in fossil diversity and reversal intensity are not a consequence of variation in stage duration. Stage duration<sup>0.2</sup> is collinear with reversal intensity<sup>0.33</sup> ( $r=0.455$ ,  $n=122$ ,  $p<10^{-6}$ ); however, the correlation between *change in number of families*<sup>0.4</sup> and reversal intensity<sup>0.33</sup> remains strong after controlling for the effect of stage duration ( $r=0.658$ ,  $n=122$ ,  $p<10^{-14}$ ). The same can be said about the correlations between reversal intensity and origination rates of all families ( $r=0.635$ , cf. Table 2a) and extinction rates of all families ( $r=0.668$ , cf. Table 2a).

Variation in fossil diversity is weakly but significantly correlated with cratering (Table 2a,  $p<0.005$ ). As is the case with magnetic reversal intensity, cratering intensity appears to be the most strongly correlated with *change in number of families*, marine and continental families combined. Note that continental metrics are more strongly correlated with cratering than the marine metrics (Table 2a). On the other hand, none of the fractional rates show significant correlations with cratering (Table 2b). These relatively weak correlations may be due to the poorer quality of the cratering record, relative to the record of magnetic reversals.

Fractional metrics of change in number of marine families and origination rates of marine families are significantly correlated with RCO<sub>2</sub> ratios (Table 2b). On the other hand, fractional metrics of continental families are unrelated to RCO<sub>2</sub>. Among the absolute metrics, only change in number of marine families was significantly correlated with RCO<sub>2</sub> ( $r=0.334$ ,  $n=122$ ,  $p=0.0036$ ). Nonetheless,

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this relationship does not appear to be an artifact of stage duration, since  $\text{RCO}_2$  is only weakly correlated with stage duration ( $r=0.213$ ,  $n=122$ ,  $p=0.018$ ). As for the other absolute metrics, a weak but consistent pattern can be discerned: marine metrics are positively correlated with  $\text{RCO}_2$ , while continental metrics are negatively so. Because of these opposing trends, there is practically no correlation between combined metrics and  $\text{RCO}_2$  (Table 2a).

In multiple regressions reversal intensity is the strongest predictor for most fossil metrics (Table 3). Atmospheric  $\text{CO}_2$  ratio has significant residual effects on the change in number of marine families and on marine origination rates, both for absolute and for fractional metrics. Carbonate and clastic sediment volumes also have significant residual effects on several absolute metrics (Table 3a). Cratering intensity and terrestrial clastic sediment volumes drop out as non-significant from all models. In models predicting fractional metrics,  $R^2$  values are generally lower than in models predicting absolute metrics (Table 3a-b).

Autocorrelation functions show strong negative correlations at lag=+1 stage for both biotic and abiotic variables (Fig. 2). Combined metrics of continental and marine families and change in number of families also show similarly strong negative correlations at lag=+1 (not illustrated). These patterns suggest a general stage level cyclicity in global geo- and bioevents, and/or in preservation potentials over the Phanerozoic.

## Discussion

In this paper, we documented a consistent global correlation between stage to stage variation in the fossil record and the frequency of magnetic polarity reversal records over the Phanerozoic (Fig. 1). We also demonstrated that, in general, the number of reversal records is a stronger predictor of variation in fossil metrics than many other predictors thought to be correlated with variation in fossil diversity (Table 3a). Although we have shown that these correlations are not artifacts of stage duration (cf. Plotnick 1980), their meaning remains open to interpretation.

One possibility is that fluctuations in fossil diversity and the number of reversal records both reflect a predominantly stage-level taphonomic megabias (Smith et al. 2001; Peters and Foote 2002). An argument for this possibility may be that reversal intensity and volumes of terrestrial clastic sediments are collinear ( $r=0.596$ ,  $n=122$ ). In theory, causal modeling (e.g., path analysis) could help to elucidate the relationship between fossil metrics, reversal intensity and rock volumes. However, such an approach may be inappropriate at the present because the precision of the rock data is substantially worse than the precision of the reversal data, potentially influencing the strength of their correlations with other variables. Recall that we assumed constant rates of sedimentation within sub-periods (methods section). Stage-level data on the global abundances of sediment volumes may be needed to ascertain the effect of preservation bias on reversal intensity and fossil richness.

Bias aside, *reversal intensity* may serve as an indicator of global scale,

non habitat selective perturbations. The fact that the combined data of marine and continental families yield stronger correlations with reversal intensity than they do separately (Table 2) may suggest a complementarity in the response of marine and continental biota to global-scale perturbations. As marine fossil richness is positively correlated with (underwater) shelf area (Sepkoski 1976), continental fossil richness is likely to be positively correlated with above water shelf area. Therefore, complementarity in marine and continental fossil metrics can be the result of opposite area effects on marine and continental diversity. An example of this may be the dramatic decline in the number of terrestrial reptile families, and the concomitant increase in marine reptile family numbers in the Lower Triassic (Fig. 3).

Finally, some third environmental factor may drive both reversal intensity and extinction events. We have found that polarity reversal records tend to cluster at stage boundaries. This may be an artifact of stratigraphical rock dating, or alternatively, it may be an indicator of pulses in reversal intensity. Various biotic and geologic phenomena have been shown to exhibit similar per stage pulses. According to Foote (2005), single extinction and origination pulses per stage appear to be the norm in the marine fossil record. Eustatic events also often coincide with stage boundaries (e.g. Hallam 1994: p.200: Figure 3; Barnes et al. 1996). Ultimately, sea level change and reversal intensity may both be driven by astronomical phenomena. Strong negative correlations at lag=+1 stage (about 4 Myr) in cratering intensity and other variables (Fig. 2) suggest stage-level dynamics in geo- and bioevents, possibly driven by astronomical

phenomena. At a longer scale, a ca. 33 Myr periodicity is also observable in geotectonic activity, geomagnetic reversals and cometary showers (Tiwari and Rao1999).

Unfortunately, data regarding terrestrial impact craters are apparently both incomplete and imprecise in comparison to the magnetic record. Crater age estimates from the *Earth Impact Database* (2006) have, in many cases, large error. Also, there is a restrictive, triangular relationship between cratering and geologic time ( $r=0.36$ ), which probably reflects the worsening preservation of older craters. Therefore, lack of significance for the impact record in multiple regressions (Table 3) may be due to the poor quality of the data. In summary, the data at hand are probably insufficient to demonstrate a possible causal relationship for astronomical phenomena.

Alternating patterns of global bio- and geoevents (Fig. 2) suggest that stratigraphic stages often correspond to discrete chapters in Phanerozoic history. However, stage-level cyclicality is difficult to demonstrate by conventional time series analyses as stages are often split or grouped according to various time scales. For example, Harland et al. (1990) divided the Carboniferous into 25 stratigraphic stages while Gradstein et al. (2004) recognized only 7 stages for the same system. Also, the duration of Phanerozoic (sub)stages is not known accurately (Newman and Palmer, 1999), making a million year based time series analysis unreliable. We found that even the estimated durations of Phanerozoic systems vary by about 16% between the above mentioned two time scales. In our opinion, strengthening the correspondence between the concept of

stratigraphic stage and global bio- and geoevents may help to detect cyclic and/or periodic phenomena over the Phanerozoic. We will explore this possibility further in Chapter 5.

We found *change in number of marine families and fractional rates of originations of marine families* positively correlated with atmospheric CO<sub>2</sub> levels (Table 2a, 2b). This is in agreement with Cornette et al. (2002), who reported a correlation of  $r=0.66$  between fractional origination rates of marine genera and atmospheric RCO<sub>2</sub>. There may be several reasons why their genus-level data showed stronger correlation with RCO<sub>2</sub> than our family-level data. First, genus-level data may be more sensitive to (gradual) climate change and related environmental phenomena than family-level data. There may be also some statistical reasons. For example, a skewed distribution is likely to yield higher  $r$  values, as Cornette et al. (2002) apparently did not normalized their variables. More importantly, however, family-level fractional metrics fluctuate more strongly from stage to stage than genus-level metrics do. In the family-level data we used, fractional origination rates often vary from near zero to extremely high values from stage to stage. Apparently, the genus level data does not take extremely low values (Fig. 1. of Cornette et al. 2002). For the same reason, in general, fractional metrics at the family-level are less suitable for modeling than absolute metrics (Table 3a vs. 3b).

In summary, today, when Phanerozoic diversification patterns receive much attention from various sections of the scientific community, the continuous improvement of geological and paleontological data makes the revision of causal

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and artifactual relationships not only possible but timely. We hope that the analysis we presented illustrates the potential of the *Global Paleomagnetic Database* (GPMDDB 2005) to estimate reversal intensity, and the use of this data to predict fossil richness. The paleomagnetic record may also help to assess the extent of taphonomic bias in the fossil record. Finally, our results (Fig. 2) underline the need to strengthen the correspondence between global bio- and geo-events and the concept of stratigraphic stage. This would enhance the detectability of cyclic phenomena in stage-level statistical analyses, possibly leading to a better understanding of the underlying mechanisms.

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Tables and figures

Table 1. Temporal autocorrelations in change in number of fossil metazoan families, extinction and origination metrics. N=119-121 (marine and combined metrics), 94-96 (continental metrics).

	1st order	2nd order	3rd order
change <sup>0.4</sup> (all families)	0.279	0.433	0.351
change <sup>0.4</sup> (marine families)	0.320	0.464	0.348
change <sup>0.2</sup> (continental families)	0.337	0.423	0.350
originations <sup>0.2</sup> (all families)	0.284	0.378	0.285
log(originations) (marine families)	0.298	0.484	0.313
log(originations) (continental families)	0.367	0.298	0.276
log(extinctions) (all families)	0.138	0.284	0.197
log(extinctions) (marine families)	0.179	0.288	0.177
log(extinctions) (continental families)	0.139	0.313	0.250

*Fossil richness and magnetic polarity reversals*

Table 2a. Pairwise correlations of absolute metrics of fossil metazoan families (total numbers of families) with magnetic polarity reversal intensity, cratering intensity and RCO<sub>2</sub>. N=122 (marine and combined metrics), 97 (continental metrics). Non-significant correlations are in parentheses (Bonferroni-corrected p>0.05).

	reversals <sup>0.33</sup>	cratering <sup>0.2</sup>	log(RCO <sub>2</sub> )
change <sup>0.4</sup> (all families)	0.734	0.395	(0.054)
change <sup>0.4</sup> (marine families)	0.585	0.302	0.334
change <sup>0.2</sup> (continental families)	0.582	0.361	(-0.183)
originations <sup>0.2</sup> (all families)	0.693	0.359	(-0.001)
log(originations) (marine families)	0.587	0.300	(0.240)
log(originations) (continental families)	0.542	0.348	(-0.179)
log(extinctions) (all families)	0.678	0.303	(-0.019)
log(extinctions) (marine families)	0.546	(0.243)	(0.188)
log(extinctions) (continental families)	0.581	0.335	(-0.160)

*Fossil richness and magnetic polarity reversals*

Table 2b. Pairwise correlations of fractional metrics of fossil metazoan families with magnetic polarity reversal intensity, cratering intensity and RCO<sub>2</sub>. N=122 (marine and combined metrics), 97 (continental metrics). Non-significant correlations are in parentheses (Bonferroni-corrected p>0.05).

	reversals <sup>0.33</sup>	cratering <sup>0.2</sup>	log(RCO <sub>2</sub> )
change <sup>0.2</sup> (all families)	0.421	(0.095)	(0.199)
change <sup>0.2</sup> (marine families)	0.377	(0.095)	0.324
change <sup>0.2</sup> (continental families)	0.322	(0.039)	(0.060)
originations <sup>0.2</sup> (all families)	0.461	(0.141)	(0.103)
originations <sup>0.2</sup> (marine families)	0.431	(0.140)	0.286
originations <sup>0.2</sup> (continental families)	(0.303)	(0.099)	(0.008)
extinctions <sup>0.2</sup> (all families)	(-0.056)	(-0.065)	(0.120)
extinctions <sup>0.2</sup> (marine families)	(-0.090)	(-0.045)	(0.245)
extinctions <sup>0.2</sup> (continental families)	(-0.046)	(0.130)	(-0.002)

*Fossil richness and magnetic polarity reversals*

Table 3a. Multiple regression models predicting *change in number of families*, extinction and origination rates, using absolute metrics as dependent variables (total numbers of families). Standardized coefficients of terms retained both by forward selection and by backward elimination are shown. Dependent variables are transformed as indicated in Table 1. N=122 (marine and combined metrics), 97 (continental metrics).

	change			originations			extinctions		
	marine	contin.	all	marine	contin.	all	marine	contin.	all
reversal intensity <sup>0.33</sup>	0.586	0.577	0.685	0.501	0.343	0.693	0.497	0.581	0.734
cratering <sup>0.2</sup>									
log(CO <sub>2</sub> )	0.363			0.257					
mid-point age [Myr]					0.402				
stage duration [Myr] <sup>0.2</sup>				0.273					
carbonate *									
carbonate and clastic *	0.242	0.062	0.217				0.221		0.431
marine clastic *									
terrestrial clastic *									
total amount of rock *									-0.353
R <sup>2</sup>	0.575	0.343	0.583	0.508	0.416	0.480	0.344	0.338	0.499

\* (10<sup>3</sup>km<sup>3</sup>)<sup>0.2</sup>

*Fossil richness and magnetic polarity reversals*

Table 3b. Multiple regression models predicting fractional rates of fossil metrics. Standardized coefficients of terms retained both by forward selection and by backward elimination are shown. All dependent variables are raised to the power of 0.2. N=122 (marine and combined metrics), 97 (continental metrics).

	change			originations			extinctions		
	marine	contin.	all	marine	contin.	all	marine	contin.	all
reversal intensity <sup>0.33</sup>	0.436	0.481	0.631	0.486	0.303	0.590			-0.046
cratering <sup>0.2</sup>									
log(CO <sub>2</sub> )	0.390			0.360					
mid-point age [Myr]		-0.322	-0.411			-0.252			
carbonate *							0.314		0.248
carbonate and clastic *									
marine clastic *									
terrestrial clastic *									
total amount of rock *									
R <sup>2</sup>	0.290	0.182	0.302	0.312	0.092	0.260	0.099	0.002	0.061

\* (10<sup>3</sup>km<sup>3</sup>)<sup>0.2</sup>

*Fossil richness and magnetic polarity reversals*

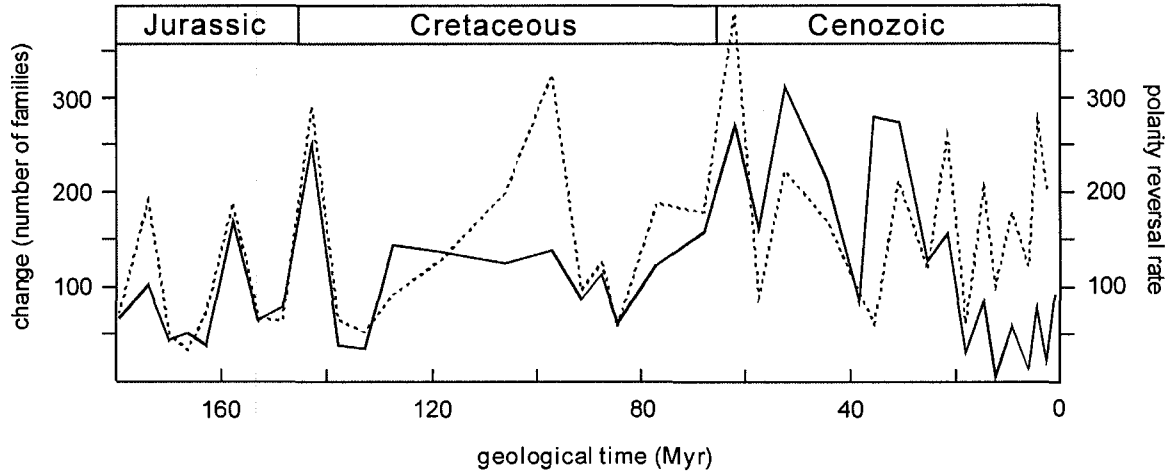


Figure 1a.

Figure 1. Change in number of fossil metazoan families (solid line) and magnetic polarity reversal records (dashed line) per stratigraphic stage over the Phanerozoic. The mid-point ages of the stratigraphic stages of the Harland time scale (Harland et al. 1990) have been adjusted to the ICS time scale (Gradstein et al. 2004).

See 1b and 1c on the following pages.

*Fossil richness and magnetic polarity reversals*

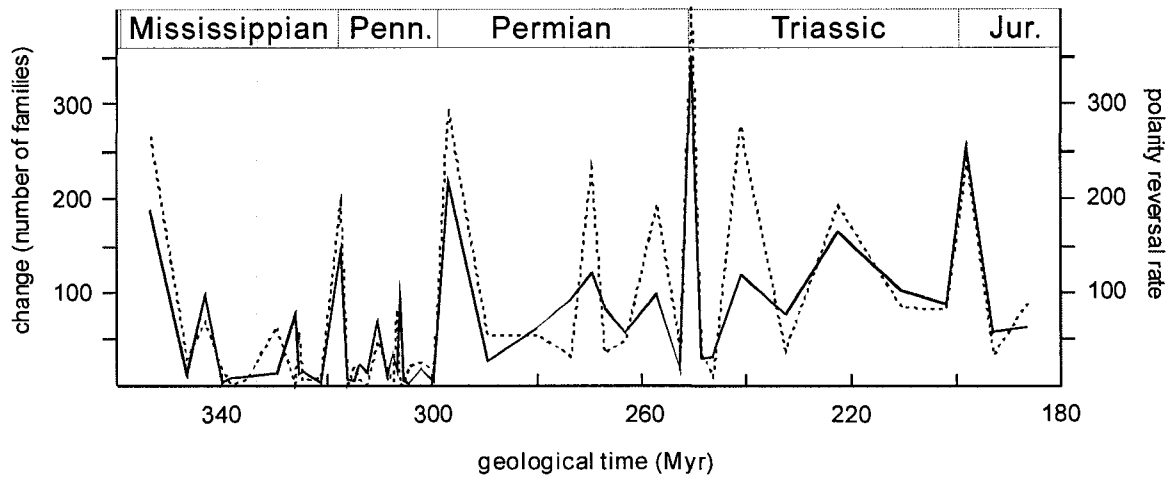


Figure 1b.

*Fossil richness and magnetic polarity reversals*

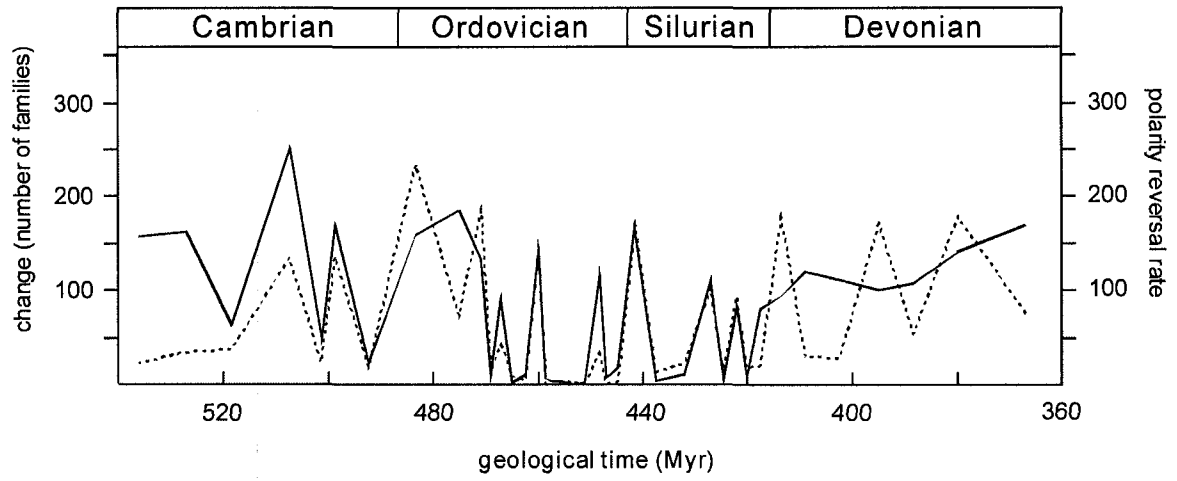


Figure 1c.

*Fossil richness and magnetic polarity reversals*

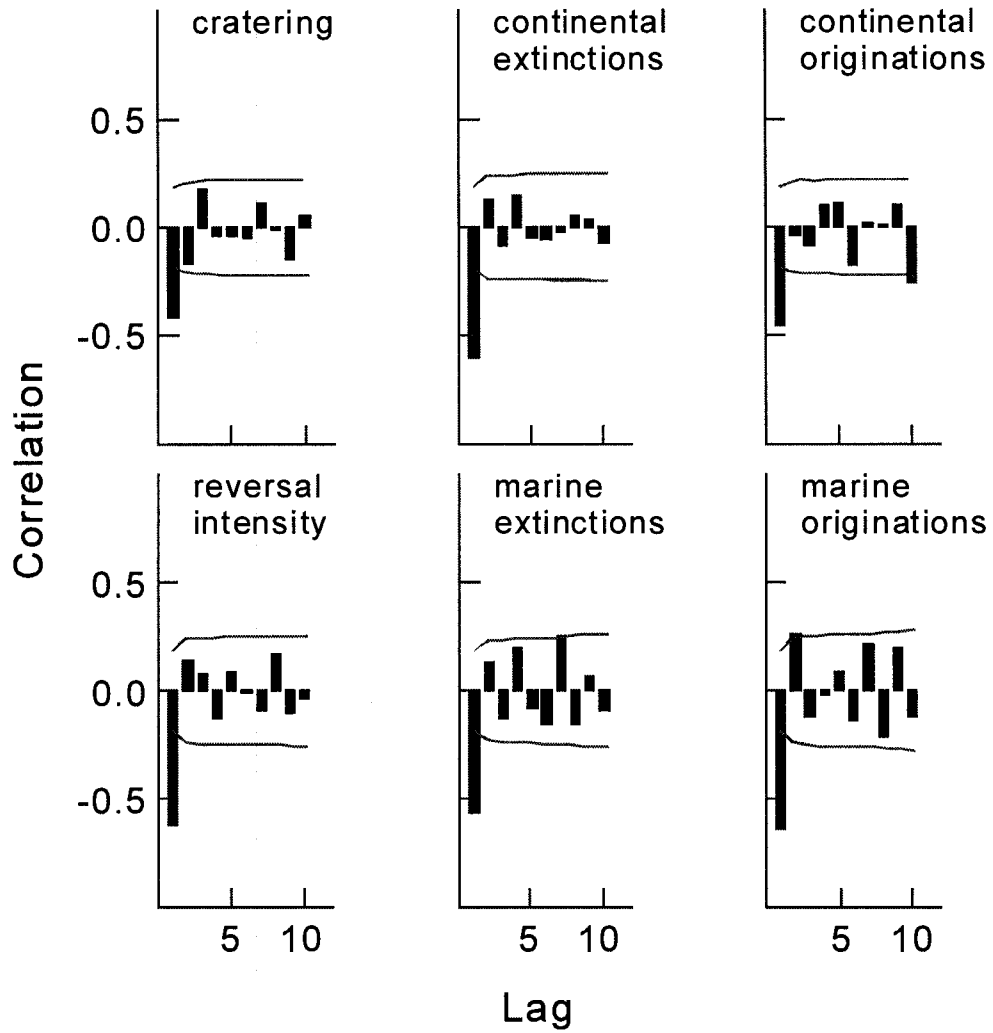


Figure 2. Autocorrelation functions of per stage cratering intensity, magnetic reversal intensity, and extinction and origination rates of metazoan families over the Phanerozoic. All variables were differenced to remove temporal trends.

*Fossil richness and magnetic polarity reversals*

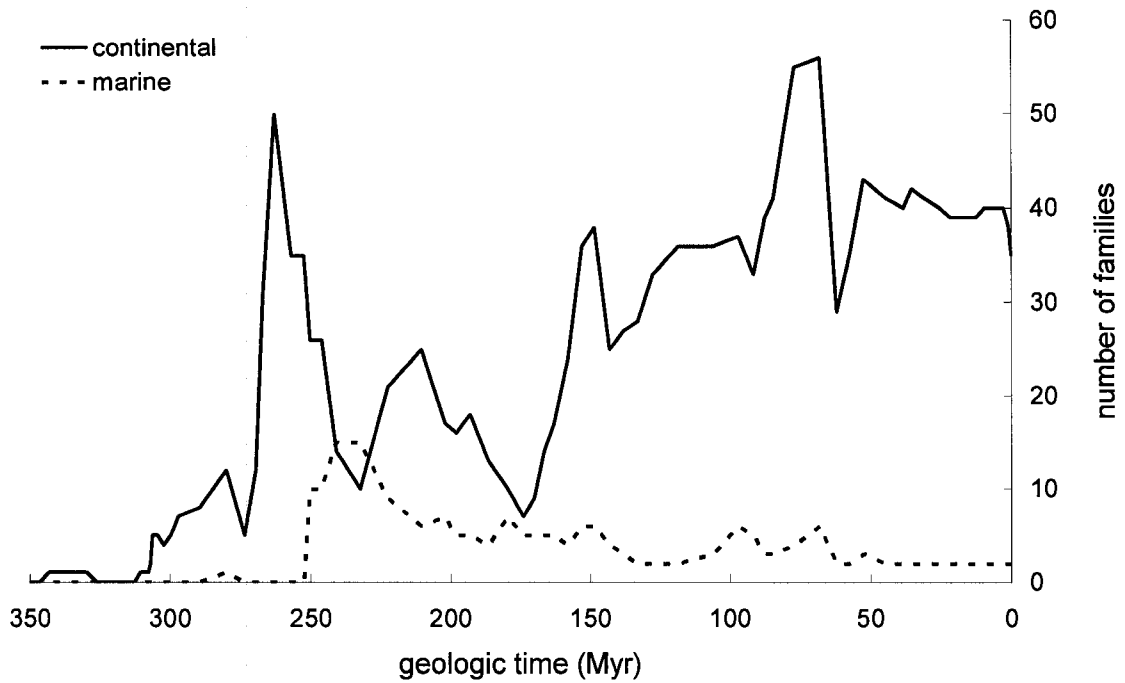


Figure 3. Global richness of continental and marine reptile families from the Carboniferous to the Holocene. Note that marine family richness apparently peaked at a time when continental richness experienced its most dramatic decline. Data from Benton (1993).

Appendix I

Time scale adjustment

Time scale adjustment is a technique analogous to rubber-sheeting maps in geography. Rubber-sheeting needs to be done prior to overlaying two maps with different projections. For example, one may want to overlay a species range map and a climatic map. If the two maps are in different projections, one must first recalculate the coordinates of the two maps so that they correspond to the projection of a common base map.

Similarly, dates of events in geological history differ according to different authors. Magnetic polarity reversals from Pisarevsky's (2005) database, used in chapters 4 and 5 of the present thesis, were dated with respect to the time scale of Gradstein et al. (1996). Thus, a magnetic event dated, for example, to be at the base of the Cambrian will have an age of 540 Myrs. Benton's (1993) fossil data, however, followed the time scale of Harland et al. (1990). On the Harland time scale, 540 Myrs would fall in the middle Cambrian, because the base of the Cambrian is estimated to be at 570 Myrs in the Harland time scale. Therefore, paleontological data classified according to different time scales need to be standardized prior to statistical analysis.

The most important difference between rubber-sheeting and time scale adjustment is that, in contrast to map projections, time scales do not relate to one another according to simple mathematical functions. There are considerable differences between time scales regarding the durations of stages and periods.

### *Fossil richness and magnetic polarity reversals*

Also, the number of stages vary. Although many stages are identical (by name and stratigraphic position) between the Harland and Gradstein time scales, others differ. Gradstein et al. (1996) relegated many of the Harland stages to the substage level. Other stages were considered as regional stages, synonyms, or artificial units. Therefore, to overlay the number of magnetic polarity reversals per stage, which follows the new ICS time scale of Gradstein et al. (1996), on the Harland time scale, we matched up every ICS (sub)stages to the corresponding stratigraphic units of the Harland time scale, as described by Rohde (2005).

We converted the more recent Gradstein ages into the older Harland time scale because Benton's compendium follows Harland et al (1990). Further, the Harland time scale is divided more finely than the Gradstein time scale. In Chapter 5, it would have been impossible to establish extinction-origination cycles based on the time scale of Gradstein et al. (1996) because their stages are often longer than half-cycles. Looking at the Lower Paleozoic and the Carboniferous, Gradstein stages typically correspond to one or two full extinction-origination cycles (Chapter 5, Fig. 10).

## Chapter 5

# Supercyclicity over the Lower Paleozoic, the Upper Paleozoic and the Mesozoic

Abstract

We present a previously undocumented, apparently cyclic pattern over the Lower Paleozoic, the Upper Paleozoic and the Mesozoic. To make statistical comparison among these three large segments of the geologic column possible, we have classified stratigraphic stages into alternating extinction and origination half-cycles, a pattern in agreement with the results of partial autocorrelation functions (Chapter 4, Fig. 2). We found that per half-cycle rates of magnetic polarity reversal intensity, as well as originations, extinctions, and richness of metazoan families are correlated among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic. Randomization tests suggest that these correlations are not merely the result of our stage classification procedure. We found that cyclic patterns are synchronous among marine, freshwater and terrestrial metazoan families, and that magnetic reversal intensity peaks at the end of extinction half-cycles. Although we have constructed the Phanerozoic Time Synchronization Chart to make statistical comparisons among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic possible, it has other potential applications. We propose this reorganization of stratigraphic stages to improve the chances of detecting cyclic patterns over the Phanerozoic. The PTSC may also help in the formulation of a general multidisciplinary model to identify the abiotic mechanisms driving paleodiversity.

## Introduction

In this chapter we present an apparent cyclic pattern in magnetic polarity reversal intensity and variation in fossil diversity over three large segments of the geologic column, corresponding to the Lower Paleozoic, the Upper Paleozoic and the Mesozoic. To our knowledge, this pattern is undocumented elsewhere in scientific literature. Therefore, we begin by presenting a very brief review of related topics, such as the origin of the geologic column and previously documented cyclic phenomena.

Phanerozoic rocks are classified into ten primary and world-wide chronostratigraphic units called "systems". These are the Cambrian, Ordovician, Silurian, Devonian, Carboniferous (including the Mississippian and Pennsylvanian sub-systems), Permian, Triassic, Jurassic, Cretaceous and the Cenozoic (including the Tertiary and the Quaternary). The ten systems are subdivided into series, and series are subdivided into stages. These stratigraphic i.e. rock units have corresponding temporal equivalents. The temporal equivalent of a "system" is referred to as a "period". The temporal equivalents of "series" and "stage" are "epoch" and "age" respectively (Articles 69-74, North American Commission on Stratigraphic Nomenclature, 1983).

Most of the Phanerozoic systems were described by geologists between 1822 and 1841 (Table 1). Perhaps surprisingly, the works of two creationists, Steno's (1669) three laws on original horizontality, original continuity and superposition and William Smith's faunal successions of 1799 (Prothero 1990, p. 11) were major contributions to the vertical ordering of the Geologic column. By

## *Phanerozoic supercycle*

the time of Darwin's *On the Origin of Species* (1859) all but the Ordovician system had been described (Table 1). This illustrates the general agreement among paleontologists concerning the vertical arrangement of the ten systems since the early days of the science of stratigraphy. We are not aware of any recent work proposing a different arrangement for Phanerozoic systems or even for stages.

Cyclic patterns in geology and in the fossil record have long been recognized. Cuvier - a creationist and founder of vertebrate paleontology - proposed that antediluvian history was a succession of revolutions with alternating short extinction periods and longer quiescent periods (Rudwick 1972, p. 131). Originally, Lyell - a uniformitarian, often credited with the first geologic time scale - also insisted that early history was cyclical (Prothero 1990, p.10). It is now known that transgressive-regressive sequences bounded by unconformities occur along continental margins world-wide. These stratigraphic cycles can be classified into four major categories (Vail et al. 1977). First order cycles, also called "supercycles", have multi-period (i.e. multi-system) duration. Second order cycles roughly correspond to the duration of a single period. Finally, third and fourth order cycles occur on the scale of (sub)stages. These are thought to be caused by rapid changes in sea-level, due to changing ice volume (Vail et al. 1977; Prothero 1990, p.195).

Extinctions and originations also exhibit an alternating, cyclic pattern over most of the Phanerozoic (e.g. Carr and Kitchell 1980; Lu et al. 2006). This is reflected by a see-saw pattern at the stage level, i.e. the majority of Phanerozoic

## *Phanerozoic supercycle*

stages correspond to either a peak in extinctions or to a peak in originations (Fig. 1). According to Foote (2005), these per stage peaks represent single pulses in extinctions and originations rather than several distinct bio-events within individual stages. In Chapter 4 we have shown strong negative autocorrelations at lag+1 in per stage rates of extinctions, originations, magnetic polarity reversal intensity and cratering (Chapter 4, Fig. 2). All these results suggest general stage level mechanics in variation of fossil richness and certain geologic phenomena. In this chapter, we will propose a classification of stratigraphic stages into extinction-origination cycles to formalize and strengthen the correspondence between stratigraphic units and bio-events.

Supercycles have been proposed for various geologic, climatic and biotic processes. For example, a supercontinent cycle of 400-600 Myr duration, consists of continental accretion and fragmentation (Worsley et al. 1984; Nance et al. 1988; Veevers 1990). The oceanic equivalent of a supercontinent cycle is referred to as a Wilson cycle. As for climate, a 300 Myr supercycle between icehouse and greenhouse states have been proposed, spanning the entire Phanerozoic (Fischer 1984). In paleoecology, biochemical cycles of ca.100 Myr have been proposed for the early Paleozoic and late Mesozoic. These are characterized by an initial diversification of predators and burrowers, followed by a rise in planctonic organisms in the marine realm (Vermeij 1995).

Our interest in supercyclicality arose from observation of per million year frequencies of magnetic polarity reversal records over the Phanerozoic (based on Pisarevsky, 2005). We saw what appeared to be repeated temporal

## *Phanerozoic supercycle*

patterns over the Lower Paleozoic, the Upper Paleozoic and the Mesozoic.

These could not be demonstrated by conventional time series analyses because they appeared to be "stretched" differently, both on a million year-based time scale and on a stage-based time scale. Therefore, we decided to construct a new time scale based on the general seesaw pattern in extinction and origination rates, present over most of the Phanerozoic (Fig. 1). We used million year-based paleomagnetic reversal frequencies as calibration nodes, but defined the alternating extinction and origination half-cycles based on variations in per stage rates of extinctions and originations. We limited this study to the Lower Paleozoic, the Upper Paleozoic and the Mesozoic because our preliminary observation of magnetic polarity reversal frequencies did not suggest supercyclicity extending beyond the early Tertiary or into the Precambrian.

### The Phanerozoic Time Synchronization Chart

We represent our modified timescale in a Phanerozoic time synchronization chart (PTSC), which reclassifies the stratigraphic stages of the Harland time scale (Harland et al. 1990) into alternating extinction and origination intervals. We will refer to these as half-cycles, to reflect the dynamics of bio-events over the Phanerozoic. Half-cycles generally correspond to one or more stratigraphic stages of the Harland time scale (Harland et al. 1990). According to this modified time scale, coupled origination and extinction half-cycles form a continuous succession of cycles over the entire Phanerozoic.

The labeling of half-cycles as "extinction" or "origination" does not imply

## *Phanerozoic supercycle*

the exclusive occurrences of these bio-events. Family-level extinctions do occur during origination half-cycles and originations do occur during extinction half-cycles. However, in average, originations are six times more common than extinctions in origination half-cycles. And, extinctions are 1.7 times more common than originations in extinction half-cycles.

We constructed the PTSC to eliminate some recurrent problems in stage-based and million year-based data for temporal analyses. First, stratigraphic stages do not always correspond to one complete extinction or origination event in Phanerozoic history. There is also considerable uncertainty concerning the durations of stratigraphic stages (Newman and Palmer 1999, p. 4). Thus, conventional time series analyses may not be suitable to detect cyclic phenomena. On the other hand, the PTSC regroup (sub)stages in agreement with bio-events, and so, it is designed to test for cyclicity. Alternating extinction and origination half-cycles can also be phased or aligned, yielding even sample sizes for pairwise comparisons of various segments of the geologic column. Thus, our spectral stage classification procedure can be also termed *time synchronization*.

Our primary stage classification criteria are based on stage-to-stage variation in extinctions and originations of Metazoan families. We classified a stage into an extinction half-cycle if there were more extinctions and fewer originations than in the preceding stage. Conversely, we defined an origination stage by an increase in originations and a decrease in extinctions (Fig. 2a). Stratigraphic ranges of families are from *The Fossil Record 2* (Benton 1993).

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We treated stratigraphic ranges of taxa as continuous from the record of first appearance to the record of last appearance. Thus, we did not consider gaps in the record.

We applied our primary stage classification criteria to marine, fresh water and terrestrial families separately for each Phanerozoic stages. In the Lower Paleozoic the primary classification criteria are generally met by marine families only. This is due to the small number of continental families in the Lower Paleozoic. In the Upper Paleozoic, the primary classification criteria are often shown by marine, fresh water and terrestrial families as well. Finally, in the Mesozoic, the primary stage classification criteria are most often detected among terrestrial families (PTSC chart, pp. 211-212). Note that the three habitats rarely gave contradictory signals.

The general pattern is that marine, freshwater and continental families exhibit synchronous extinction-origination trends. During this exercise we could have encountered frequently opposite patterns among marine, freshwater and terrestrial families in a same stage. This would make our stage classification problematic or even pointless. In practice, however, this happens so rarely that we can refer to them as exceptions. We found only three cases in which the primary stage classification criteria gave contradictory signal from different habitats. These are indicated by red bordered cells in the PTSC.

When classification was difficult based on patterns of extinctions and originations in all three habitats, we used a secondary stage classification criteria: We looked for patterns of increase and decrease in originations and

extinctions within the marine taxa with a good fossil record, and especially in the system where the stage(s) in question are located (Table 2). We also widened our classification criteria (Fig. 2b). These wider definitions gave sometimes false positives. Therefore, we weighted their signals in consideration with the total numbers of originations and extinctions per stages (Table 2). We also considered patterns of extinctions and originations of Foraminifera, even though they are not metazoans and thus excluded from our total family counts and statistical analyses.

Some Harland stages are relatively uneventful, in terms of extinctions and originations. These "quiescent" stages generally follow origination stage(s). We therefore merged them with the preceding origination stage (Table 3). Most of these quiescent stages are in the Ordovician and the Carboniferous, and they have been relegated to the sub-stage level in more recent time scales (Gradstein and Ogg, 1996; Gradstein et al. 2004).

We found that more than 90% of Harland stages can be categorized as extinction or origination stages, based on one of the above described three methods (primary criteria, secondary criteria and quiescent post-origination stages). The remaining *problematica* include three stages of the Late Cretaceous and the Cenozoic, where we suspect that extinction signals are masked by a general rise in diversity (Campanian, Priabonian and Santonian). Two stages, the Chokierian and the Arenig, were classified based on a particularly strong, stage-to-stage spectral pattern in extinctions alone, spanning over numerous adjacent stages. Finally, there are four Ordovician (sub)stages

## *Phanerozoic supercycle*

with very small numbers of family-level originations and extinctions. We have classified these tentatively, as indicated in Appendix I (Harnagian, Longvillian, Rawtheyan and Soudleyan).

We left three stages unclassified. We have left the Norian (of the Triassic) unresolved on the cyclic scale, as it probably covers a complete extinction-origination cycle. As a consequence of this, sample size in the Mesozoic time segment is reduced from 22 to 20 for all of our Mesozoic fossil metrics and pairwise correlations involving the Mesozoic. We also left the two most recent stages of the Cenozoic unclassified. Based on mixed patterns of extinctions and originations, climatic and magnetostratigraphic data, the Pleistocene appears to be a multi-cyclic stage. The Holocene probably corresponds to an extinction half-cycle, but its assessment, based on our criteria, is difficult due to the multi-cyclic nature of the Pleistocene and the lack of distinction between newly originated families and families without a fossil record.

In summary, we have classified the stratigraphic stages of the Harland time scale into alternating extinction and origination half-cycles in view to test for supercyclicity. We classified 80 stages based on our primary stage classification criteria for marine, fresh water and terrestrial metazoan families. Twenty two stages have been classified based on our secondary stage classification criteria (Table 2). Nine "quiescent" stages were classified as origination stages (Table 3). Another nine stages have been tentatively classified, considering a variety of factors, and three remained unresolved or unclassified. All stages and their classifications are listed in Appendix I.

# Phanerozoic Time Synchronization Chart

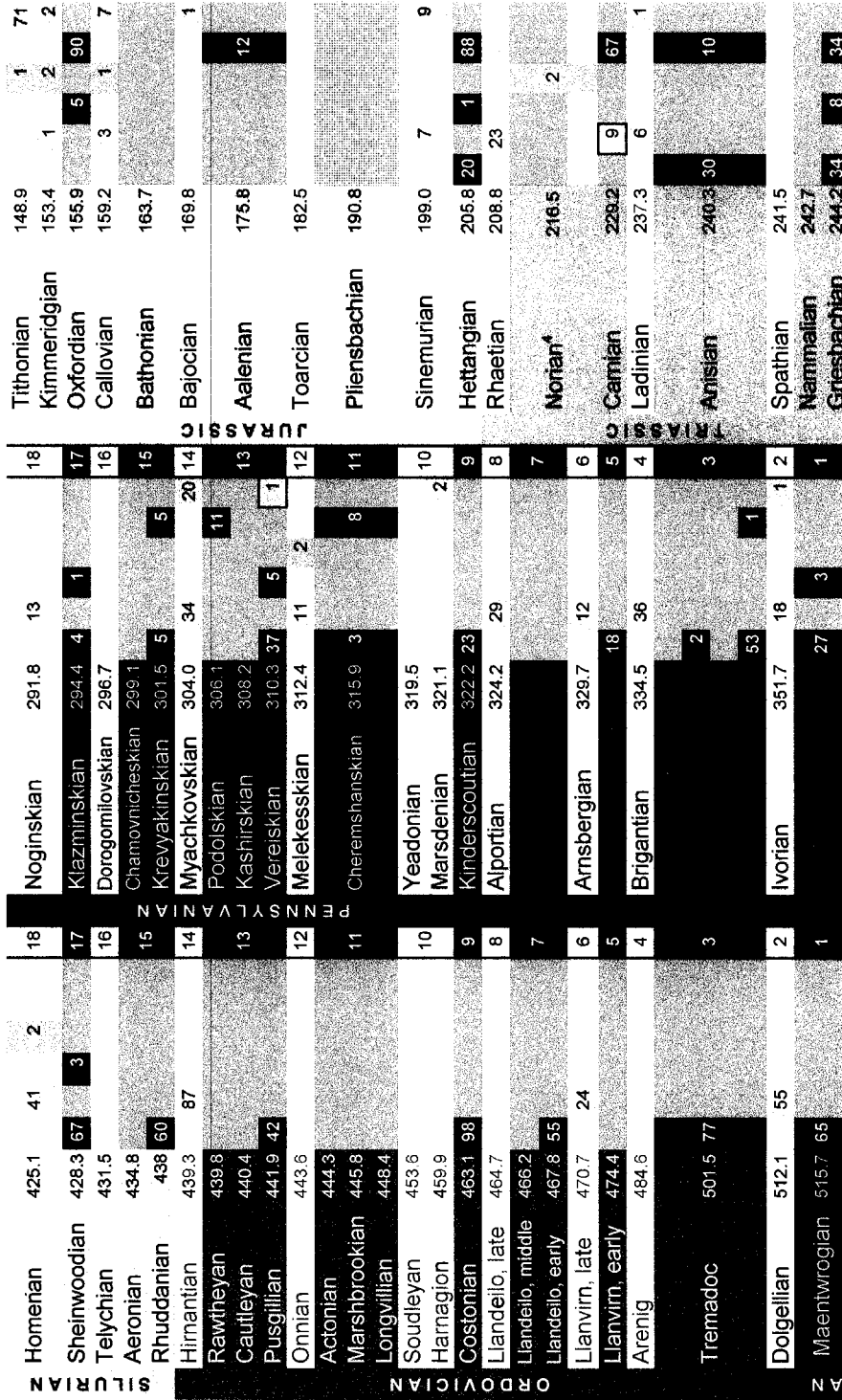
A classification of stratigraphic stages<sup>1</sup> into alternating extinction and origination half-cycles aligned to test for supercyclicity over three segments of the geologic column.

## Legend

Primary classification signal	
<b>MO</b>	marine originations
<b>ME</b>	marine extinctions
<b>FO</b>	freshwater originations
<b>FE</b>	freshwater extinctions
<b>TO</b>	terrestrial originations
<b>TE</b>	terrestrial extinctions
<b>colored rows</b>	origination half-cycles
<b>white rows</b>	extinction half-cycles
<b>bordered cell</b>	contradictory signal among habitats

stage name	Age <sup>2</sup>				number of families <sup>3</sup>				Half-cycle	
	MO	ME	FO	TE	MO	ME	FO	TE		
<b>Famennian</b>	364.8									
<b>Frasnian</b>	372.2									
<b>Givetian</b>	379.1	15								22
<b>Eifelian</b>	383.4	18								
<b>Emsian</b>	388.2	10								
<b>Pragian</b>	393.4	9	1							
<b>Lochkovian</b>	402.4	20								
<b>Pridoli</b>	409.6	8								
<b>Ludfordian</b>	412.9	40								
<b>Gorstian</b>	419.6	34								
<b>Wordian</b>	253.8		3							
<b>Ufimian</b>	255.6	2								21
<b>Kungurian</b>	257.9									
<b>Artinskian</b>	264.3	13								
<b>Sakmarian</b>	275.2	14	2							
<b>Asselian</b>	285.8	19	7							19
<b>Changxingian</b>	246.3									
<b>Longtanian</b>	248.8									
<b>Capitanian</b>	251.3	61								22
<b>Ypresian</b>	53.3	71								41
<b>Thanetian</b>	58.5									
<b>Danian</b>	62.8									32
<b>Maastrichtian</b>	69.5									
<b>Campanian</b>	78.5									
<b>Santonian</b>	84.8									
<b>Coniacian</b>	87.6									59
<b>Turonian</b>	89.5									
<b>Cenomanian</b>	93.7									1
<b>Albian</b>	104.5									
<b>Aptian</b>	118.3									
<b>Barremian</b>	128.2									1
<b>Hauterivian</b>	133.4	12								86
<b>Valanginian</b>	137.9									
<b>Berriasian</b>	143.2		9							101
<b>Pleistocene<sup>4</sup></b>	0.8		2							
<b>Placenzian</b>	2.5	8	1							18
<b>Zanclean</b>	4.3	8	2							11
<b>Messinian</b>	6.0	16	2							19
<b>Tortonian</b>	8.6	11								11
<b>Serravallian</b>	12.3	6								21
<b>Langhian</b>	15.3	6								22
<b>Burdigalian</b>	18.9	5								21
<b>Aquitanian</b>	22.4	16								10
<b>Chattian</b>	26.3	2								
<b>Rupelian</b>	32.4	7								
<b>Priabonian</b>	37.0									
<b>Bartonian</b>	40.4		1							2
<b>Lutetian</b>	46.1	10								1

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- 1 Based on Harland et al. (1990)
- 2 Midpoint age of stratigraphic stage [Myr]
- 3 Increase indicated when primary signal is present
- 4 unresolved stage

Supercyclicity in magnetic polarity reversal frequency

We counted the number of magnetic polarity reversal records per extinction and origination half-cycles, based on Pisarevsky (2005). For each half-cycle, we summed the number of records from the corresponding stratigraphic stage(s), according to the PTSC. Per stage reversal frequency was counted from mid-point to mid-point of successive stages, as described in Chapter 4. For more information on the paleomagnetic data, see the *Methods* section in Chapter 4. We raised the number of records per half-cycles to the power of 0.3 to normalize their distribution.

We found strong correlations of magnetic polarity reversal frequency among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic segments of the geologic column (Figs. 3-4). Reversal frequency exhibits a see-saw pattern similar to that of extinctions and originations (Fig. 1). Origination half-cycles correspond to highs and extinction half-cycles correspond to lows in reversal frequency (Fig. 3). Since reversal frequencies are clustered at stage and half-cycle boundaries, this essentially means that reversal frequency is high at the end of extinction periods and low at the end of origination periods.

Randomization tests for habitat-specific fossil metrics

We suspected that our classification of stratigraphic stages into extinction and origination half-cycles might induce some correlations in the variation of fossil diversity among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic segments synchronized in the PTSC. This is because our defining

## *Phanerozoic supercycle*

criteria (Fig. 2) will necessarily yield higher numbers of originations for origination half-cycles, and higher numbers of extinctions for extinction half-cycles, regardless of any temporal trend in originations and extinctions. Therefore, we run randomization tests, using habitat-specific fossil metrics, to estimate how much of the observed correlations can be attributed to our spectral stage classification methodology.

We have created 27 habitat-specific metrics to describe variation in fossil diversity over the Lower Paleozoic, the Upper Paleozoic and the Mesozoic (Table 4). These are counts of number of family-level taxa based on Benton (1993). Benton's compendium indicates the first and last appearances of family-level taxa in a standardized, stage-level format. In variable names, we will refer to first appearances as originations and to last appearances as extinctions. A half family was added to each datum of all habitat-specific metrics and a fifth-root transformation was uniformly applied to normalize distributions.

Some of the variables listed in Table 4 have very little variation over the Lower Paleozoic. This is because no exclusively terrestrial or freshwater families have been described for the Cambrian and Ordovician periods (Benton 1993). We have excluded these from the randomization tests that follow, as indicated in Table 4.

We have also excluded families found in both marine and continental (including terrestrial and/or fresh water) habitats. These families and others with unspecified habitat amount to less than 4% of the 3610 Paleozoic and Mesozoic families in Benton's (1993) database. Families occurring in both

fresh water and terrestrial habitats have been counted as fresh water families. Families occurring in marine and brackish water have been counted for the marine category.

To avoid any ambiguity in richness metrics, we only counted families whose temporal ranges do not overlap the division we have established between the Lower Paleozoic, the Upper Paleozoic and the Mesozoic. These excluded taxa constitute 12.6% of all Paleozoic and Mesozoic families in Benton's database (1993). Note however, that all these were counted for extinction and origination metrics.

For the randomization test we separated the values (number of families per half-cycles) into two separate bins corresponding to extinction and origination half-cycles. Then, for each of the 15 comparisons in Figure 5, we randomized the values within these two bins and ran Pearson correlations. We repeated this process 100 times. Based on these 100 trials, we calculated mean correlations in the randomized data and compared it to the observed correlations (Fig. 5).

As expected, our methodology induced some correlations for extinction and origination metrics, but not for total richness metrics (Fig. 5). Nevertheless, for all 15 comparisons, the observed correlations are stronger than the mean correlations of the randomized data. This means that the artifactual correlations introduced by our stage classification method can not account for the similarities in variation of fossil diversity over the Lower Paleozoic, the Upper Paleozoic and the Mesozoic (binomial test  $p = 0.5^{15} < 10^{-4}$ ).

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The above described metrics and results are based on absolute numbers of metazoan families. Alternatively, the same statistics can be run for fractional rates of originations and extinctions as well. Fractional rates of originations and extinctions are calculated by dividing the number of originations or extinctions per half-cycle by total family richness and by the duration of half-cycles (Myr, based on estimated stage durations of the Harland time scale). We calculated these fractional equivalents of our habitat-specific metrics of originations and extinctions. A log-transformation was generally applied to normalize distribution. We found that correlations, using the fractional metrics, were generally weaker in comparison to the absolute metrics described above (Table 5).

### Combined habitat fossil metrics

Combining marine, freshwater and terrestrial habitats makes it possible to include fresh-water and terrestrial families from the Lower Paleozoic into our analysis (6 excluded metrics indicated in Table 4), and also families occurring in both continental and marine habitats. As in the case of the 27 habitat-specific metrics, a fifth-root and a log transformation was uniformly applied to absolute and fractional metrics respectively.

All of our fossil metrics showed positive correlations among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic. Originations were moderately correlated among the three time segments (Fig. 6). Note the bimodal distribution of the absolute metrics in the Upper Paleozoic and the Lower Paleozoic (Fig. 6a). Extinctions showed even stronger correlations than

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originations (cf. Fig. 6 and 7). The Lower Paleozoic - Upper Paleozoic fit is especially good for the absolute metrics ( $r=0.87$ ,  $p<10^{-6}$ , Bonferroni, Fig. 7a). Family richness metrics are also strongly correlated over the Lower Paleozoic, the Upper Paleozoic and the Mesozoic (Fig. 8). Here, the strongest fit is between the Upper Paleozoic and the Mesozoic ( $r=0.88$ ,  $p=10^{-5}$ , Bonferroni). The fifth-root transformation, we uniformly applied to all absolute metrics, was apparently too strong for the Lower Paleozoic and the Upper Paleozoic (Fig. 8). Finally, as it was the case with the habitat-specific metrics, fractional metrics of origination and extinction showed generally weaker correlations than absolute metrics (Figs. 6b and 7b).

In summary, correlations among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic were even stronger using the combined habitat metrics than correlations using the habitat-specific metrics. For absolute metrics of combined habitat, mean  $r=0.70$  ( $n=9$  comparisons), and for habitat-specific metrics, mean  $r=0.57$  ( $n=15$  comparisons). These results suggest that extinction-origination dynamics are synchronous in the marine and continental realms.

### Discussion

We have demonstrated that variation in fossil diversity and magnetic polarity reversal intensity exhibit highly similar cyclic fluctuations in the Lower Paleozoic, the Upper Paleozoic and the Mesozoic (Figs. 3-4, 7a, 8). We have also shown that these correlations are unlikely to be only the result of our stage

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classification methodology (Fig. 5). The similarities in patterns of extinction, for example, are striking: half-cycles 2-4-6 show a gradual decrease in extinctions, while in half-cycles 10-12-14-16-18-20-22 there is a general increase in extinctions with a marked low at half-cycle 16 for each of the three time segments (Fig. 9).

We see two possible explanations for these patterns: (1) They can be interpreted as supercyclicity, a pattern which probably require a geological or astronomical mechanism of very long duration. (2) Theoretically, these patterns can be the result of contemporaneity among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic. This latter hypothesis, however, is at serious odds with current views on the history of life in our planet. We found only one reference related to this possibility: Flori and Rasolofomasoandro (1974) suggested that certain Phanerozoic systems may be contemporaneous with one another, corresponding to distinct habitats rather than to distinct time intervals in Phanerozoic history.

Contemporaneity of the Lower Paleozoic, the Upper Paleozoic and the Mesozoic would essentially imply that diversification of marine and continental organisms occurred simultaneously, and not sequentially, in the marine, coastal and terrestrial realms on Earth. It would also require a revision of the geologic column. One scenario for this may be, without violating the established order of vertical superposition of stages, that the Devonian and the Lower Triassic systems are composed of temporarily heterogeneous rocks.

One advantage of the contemporaneity theory, as a working hypothesis, is

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that it is testable. Contemporaneity implies that allegedly contemporary half-cycles (and corresponding stages), aligned in horizontal rows in the PTSC, should not be found in vertical successions. If violations to this exclusion principle are routinely found in vertical successions around the world, the contemporaneity hypothesis can be safely rejected. On the other hand, if violations of this "exclusion principle" are very rare, the contemporaneity hypothesis may need to be seriously considered.

Unfortunately, we found that the general pattern of vertical successions in the world present a peculiar pattern which makes the rejection of the contemporaneity hypothesis more difficult than expected. While making a preliminary study, we found that good Cenozoic record is commonly found on either Upper Paleozoic or Mesozoic systems. It is very rare, however, to find a good Mesozoic record on top of a well preserved Upper Paleozoic. For example, Precambrian - Lower Paleozoic - Cenozoic successions are not uncommon. Precambrian - Mesozoic - Cenozoic successions are also not uncommon. However, an area with rich Paleozoic record almost never has a well preserved Mesozoic topping it. This scarcity of Mesozoic deposit on Upper Paleozoic rocks in vertical successions is predictable by the contemporaneity hypothesis.

Many other features of the Phanerozoic fossil record are also rather compatible with the contemporaneity hypothesis. These are unlikely to offer distinguishing criteria between the supercyclicality and the contemporaneity hypotheses. For example, the rarity of terrestrial sediments from the Lower

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Paleozoic and the distinct (epicontinental) nature of the Mesozoic marine fauna are predicted by the contemporaneity hypothesis. The extreme scale of the Permian extinction and of the Tertiary explosion of diversity could be interpreted as the results of splitting and reuniting the geologic time line. Continental accretion by the end of the Paleozoic may also be explained by identifying the Pangean supercontinent with Gondwana. Therefore, the best distinguishing criteria between the two hypotheses may be still the exclusion principle based on the PTSC.

Unlike the contemporaneity hypothesis, the concept of supercyclicity among the Lower Paleozoic, the Upper Paleozoic and the Mesozoic does not violate established theories about Phanerozoic evolution. Its disadvantages are that it is difficult to offer statistically testable mechanisms which would operate over very long (>100 Myr) time intervals, and that it can offer only a very small number of full cycles for statistical analyses. Thus, the formal disproving of the contemporaneity hypothesis may still provide the strongest indirect evidence to confirm the supercyclicity theory.

Theories and possible explanations aside, the Phanerozoic time synchronization chart is a major feature of this chapter in itself (pp. 211-212). We constructed the PTSC independently from trends in revisions of the geologic time scale. Nevertheless, the PTSC appears to combine elements of the Harland time scale (Harland et al. 1990) and of the new ICS time scale (Gradstein et al. 2004). These two time scales differ widely in their classification of the Lower Paleozoic (Cambrian and Ordovician) and of the

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Carboniferous. While stages of the Harland time scale generally coincide with our half-cycles, those of the ICS typically correspond to one or two full cycles on the PTSC (Fig. 10). Based on these patterns, we propose to consider the recognition of half-cycles as bio- and chronostratigraphic units. In our opinion, this categorical distinction between origination and extinction intervals may greatly enhance the detectability of (super)cyclic and periodic phenomena over the Phanerozoic.

Another interesting feature of the PTSC is related to magnetostratigraphy. It may be noteworthy that the largest number of stages grouped within a single half-cycle (six stages of half-cycle 21 of the Mesozoic time segment of the PTSC) approximately coincides with the longest and best documented superchron, the Cretaceous Normal. The Permian section of another proposed superchron, the Kiaman superchron, also covers stages corresponding to half-cycle 21, in the Upper Paleozoic time segment (McElhinny and McFadden 2000, p.162: Fig. 4.12). Finally, a large "superzone" described by Molostovsky et al. (1976, Fig. 1), coincide with sections of the PTSC where four or more Harland stages are grouped per half-cycles (Middle Devonian to Middle Mississippian). In summary, these patterns suggest a possible link between half-cycles and magnetostratigraphic units.

The PTSC may also provide a clue to abiotic mechanisms driving cyclic bio-events. Based on a Triassic sea-level curve from Arctic Canada, stages and half-cycles appear to correspond to eustatic cycles, and sea-level fall is most pronounced at the end of extinction half-cycles (Hallam 1996: Fig. 2). Also,

based on the same figure of Triassic stages, sea-level is higher during origination half-cycles than during extinction half-cycles (Hallam 1996: Fig. 2). We found that magnetic polarity reversal intensity peaks at the end of extinction half-cycles but not at the end of origination half-cycles (Fig. 3). Cratering intensity also exhibit a similar pattern: we found that the largest impact craters are usually from late extinction half-cycle - early origination half-cycle boundaries. Unfortunately, the cratering record (Earth Impact Database, 2006) is too incomplete for a statistical analysis at the half-cycle level because most half-cycles, like most stages, have no dated impact craters at all (Chapter 4, Methods). Nevertheless, we will interpret these patterns within the framework of a general astronomical model driving variation in fossil richness over the Phanerozoic in the last chapter of the thesis.

In this chapter, we used the method of classifying stratigraphic stages into alternating extinction and origination cycles, to test for supercyclicity. Another application of our proposed stage classification would be to improve model fitting in multivariate analyses explaining variation in fossil diversity (Appendix II). Results suggest that the mere labeling of stages as "extinction" or "origination" carries a great deal of information in itself.

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### Tables and Figures

Table 1. First description by name of the eleven Phanerozoic systems and the two Carboniferous sub-systems. Based on Prothero (1990), with modifications.

system	year	author
Tertiary*	1760	Giovanni Arduino (1713-1795)
Jurassic**	1795	Alexander von Humboldt (1769-1859)
Carboniferous***	1822	William D. Conybeare (1787-1857) and William Phillips (1775-1828)
Cretaceous	1822	J.B.J. D'Omalius D'Halloy (1783-1875)
Quaternary	1829	Jules Desnoyers (1800-1887)
Silurian	1834	Roderick Impey Murchison (1792-1871)
Cambrian	1834	Adam Sedgwick (1785-1873)
Triassic	1834	Friedrich August von Alberti (1795-1878)
Devonian	1839	A. Sedgwick (1785-1873) and R.I. Murchison (1792-1871)
Permian	1841	Roderick Impey Murchison (1792-1871)
Ordovician	1879	Charles Lapworth (1842-1920)
Mississippian	1870	Alexander Winchell (1824-1891)
Pennsylvanian	1891	Henry Shaler Williams (1847-1918)

\* term formerly used to describe rocks formed after the Noachian flood.

\*\* Leopold von Buch established the Jurassic proper in 1839 based on Humboldt's "Jura-Kalkstein"

\*\*\* D'Halloy described the coal seams of Belgium ("Terrain Bituminifere") in 1808

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Table 2. Secondary stage classification criteria applied to various marine taxa for stage classification. We interpreted a stage to stage increase in family-level originations coupled with a decrease in extinctions as an origination signal. Per stage originations (number of families) are indicated in black squares. Conversely, an increase in extinctions accompanied by a decrease in originations is interpreted as an extinction signal. Per stage extinctions (number of families) are indicated in white squares. We have interpreted these signals jointly with the total number of originations and extinctions of metazoan families (Foraminifera not included) per stage to classify 10 stages into origination half-cycles and 12 stages into extinction half-cycles, as they are grouped and listed alphabetically on the left of the table.

	Foraminifera	Porifera	Anthozoa	Gastropoda	Cephalopoda	Bivalvia	Trilobita	Crustacea	Ostracoda	Brachiopoda	Bryozoa	Echinodermata	total originations	total extinctions
Albian	1			2		2		3			2		72	32
Aptian					6	9			1		1		104	29
Atdabanian							1						128	12
Bathonian							1				3		36	8
Llanvirn, early	3	8			1							2	89	7
Nammalian					3					1			12	5
Pliensbachian	2	2		1	6	1		1		2			31	18
Thanetian	5	1				2			2	1		2	115	26
Turonian			2									1	32	14
Valanginian				3	3	1			3		4		27	8
Changxingian	14	9	11		7		2	2	6	21	7	6	2	265
Dorogomilovskian					1			2				2	1	10
Famennian	2	2	13		8		1		2	2		2	39	76
Frasnian	1								1				33	72
Kungurian	1			3	2								12	50
Llandeilo, late	1				6	1	2		3	5			11	33
Longtanian	3			2	6								1	15
Onnian		3	3		5	3	4			9	5	14	1	71
Spathian				2		3		1	2	1		2	17	45
Telychian		2	3		4	2				6	3	3	10	29
Toarcian	1					4		1	1	2			35	54
Yeadonian	4				2								1	5

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Table 3. List of quiescent stages classified into origination half-cycles.

Total numbers of families are indicated for extinctions and originations.

stratigraphic stage	originations	extinctions
Actonian	0	1
Aeronian	2	0
Arundinian	1	2
Asbian	8	4
Cautleyan	0	1
Chamovnicheskian	0	1
Kashirskian	4	5
Middle Llandeilo	0	0
Marshbrookian	0	0

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Table 4. List of the 27 habitat-specific fossil metrics. The number of half-cycles (n) and the number of half-cycles with 0 families are indicated. Zero number of families indicate either the absence of families in half-cycles (total richness metrics) or the lack of variation in family numbers (extinction and origination metrics). We did not run statistical comparisons for metrics with a very large number of zeros, i.e. the fresh water and terrestrial metrics of the Lower Paleozoic.

stratigraphic segment	metric	n	zeros
Lower Paleozoic	originations of marine families	22	0
	originations of fresh water families	22	18*
	originations of terrestrial families	22	20*
	extinctions of marine families	22	0
	extinctions of fresh water families	22	18*
	extinctions of terrestrial families	22	21*
	richness of marine families	22	0
	richness of fresh water families	22	14*
	richness of terrestrial families	22	20*
Upper Paleozoic	originations of marine families	22	5
	originations of fresh water families	22	7
	originations of terrestrial families	22	4
	extinctions of marine families	22	0
	extinctions of fresh water families	22	12
	extinctions of terrestrial families	22	7
	richness of marine families	22	0
	richness of fresh water families	22	0
	richness of terrestrial families	22	0
Mesozoic	originations of marine families	20	2
	originations of fresh water families	20	6
	originations of terrestrial families	20	4
	extinctions of marine families	20	2
	extinctions of fresh water families	20	12
	extinctions of terrestrial families	20	6
	richness of marine families	20	0
	richness of fresh water families	20	0
	richness of terrestrial families	20	0

\* Excluded from habitat-specific statistical analyses

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Table 5. Comparison between pairwise Pearson correlations of absolute and fractional habitat-specific fossil metrics. Abbreviations: LP: Lower Paleozoic. UP: Upper Paleozoic. MS: Mesozoic. N=22 (LP-UP), 20 (UP-MS, LP-MS).

	habitat	comparison	r (absolute)	r (fractional)
originations	marine	LP-UP	0.53	0.49
	marine	UP-MS	0.32	0.36
	marine	LP-MS	0.46	0.42
	fresh water	UP-MS	0.56	0.45
	terrestrial	UP-MS	0.61	0.30
extinctions	marine	LP-UP	0.88	0.65
	marine	UP-MS	0.63	0.46
	marine	LP-MS	0.65	0.23
	fresh water	UP-MS	0.46	0.07
	terrestrial	UP-MS	0.54	0.11
total richness	marine	LP-UP	0.62	-
	marine	UP-MS	0.45	-
	marine	LP-MS	0.47	-
	fresh water	UP-MS	0.40	-
	terrestrial	UP-MS	0.91	-

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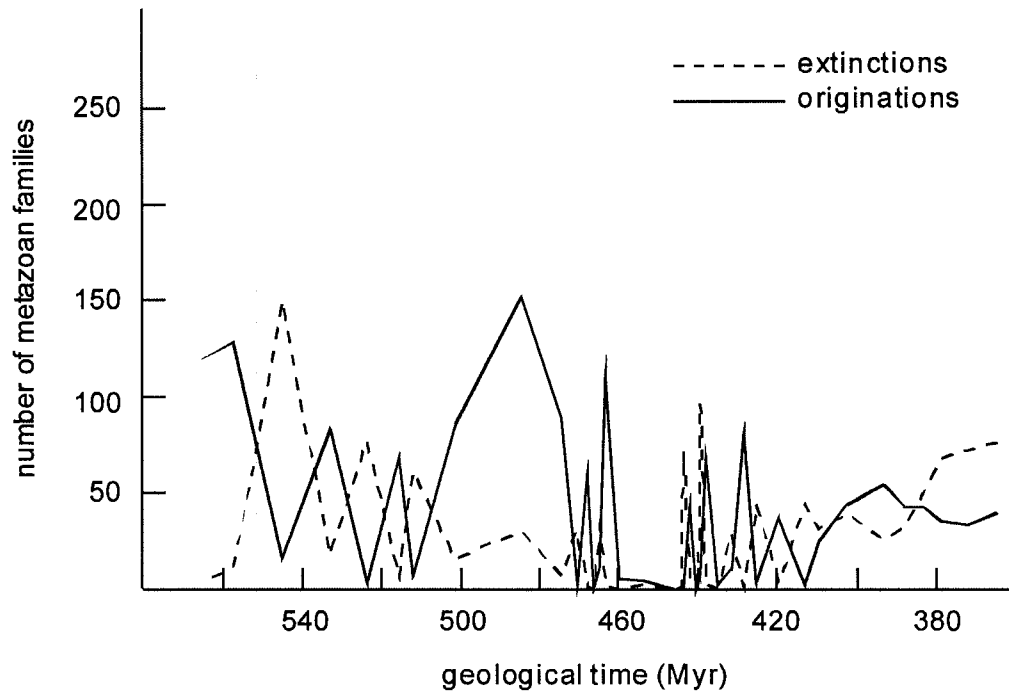


Figure 1a. Extinctions and originations of metazoan families per stratigraphic stage over the Lower Paleozoic. Geologic time is based on the Harland time scale (Harland et al. 1990). Data from Benton (1993).

See 1b (Upper Paleozoic), 1c (Mesozoic) and 1d (Cenozoic) on the following pages.

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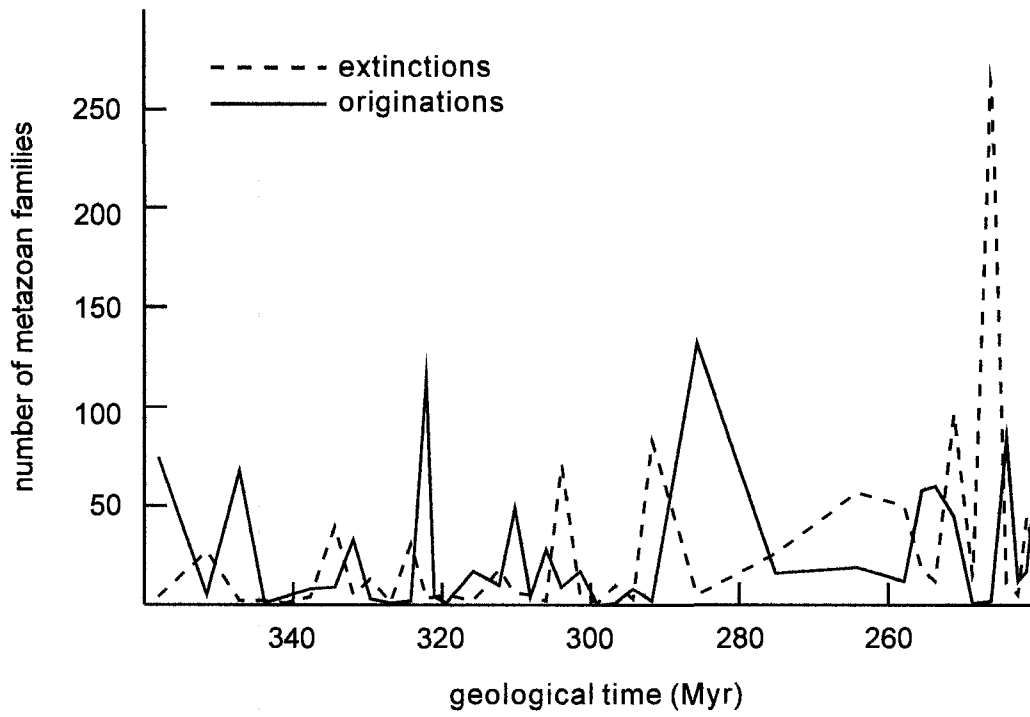


Figure 1b. Extinctions and originations of metazoan families per stratigraphic stage over the Upper Paleozoic.

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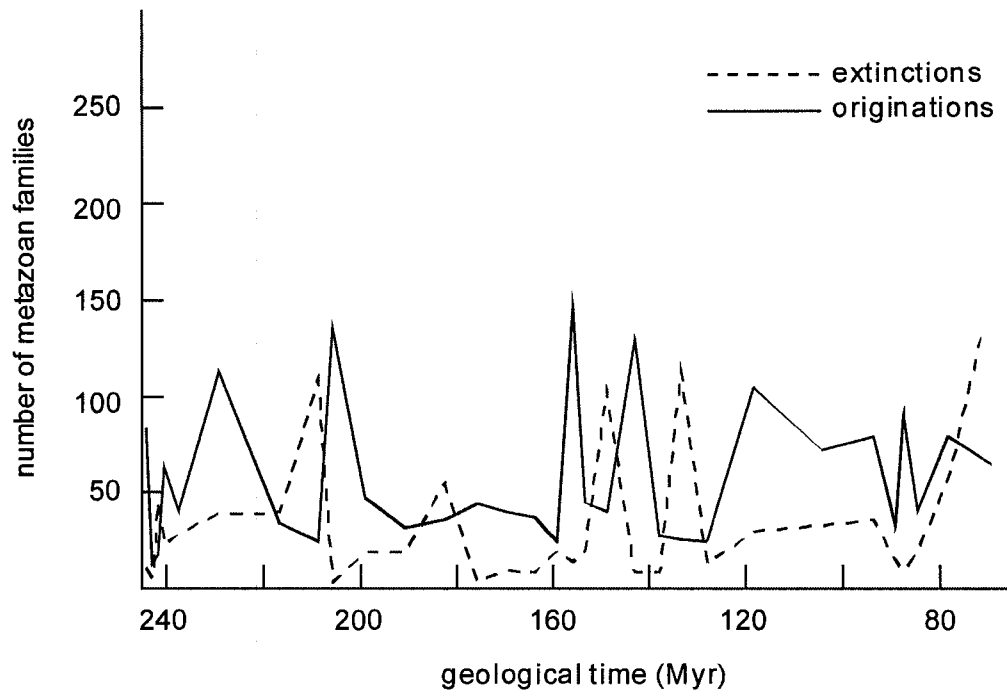


Figure 1c. Extinctions and originations of metazoan families per stratigraphic stage over the Mesozoic.

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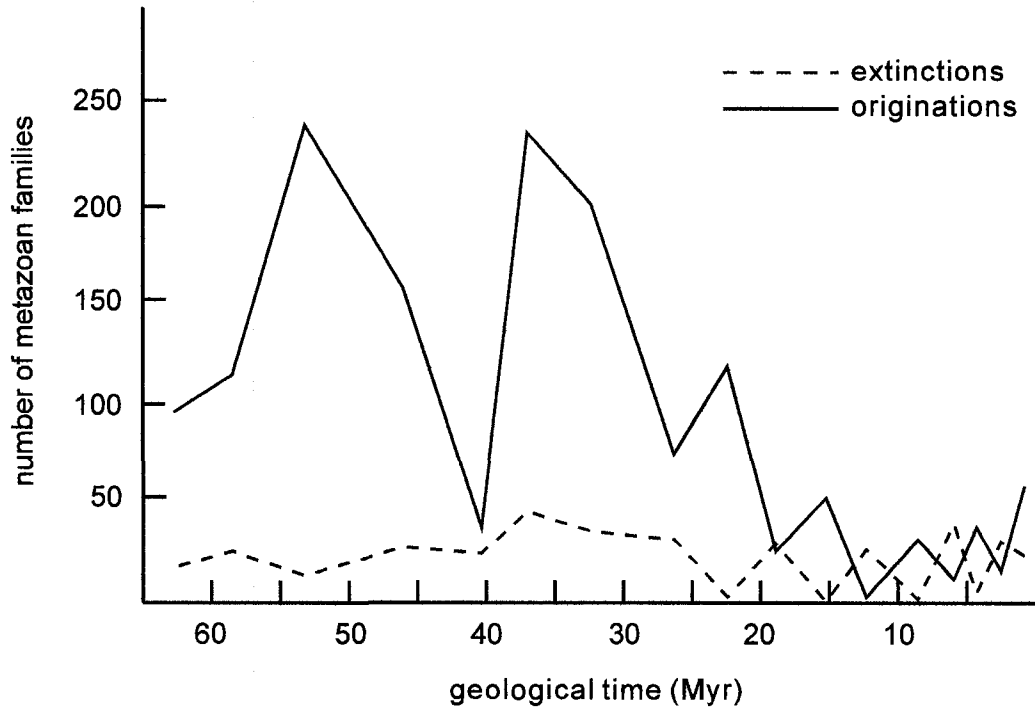


Figure 1d. Extinctions and originations of metazoan families per stratigraphic stage over the Cenozoic.

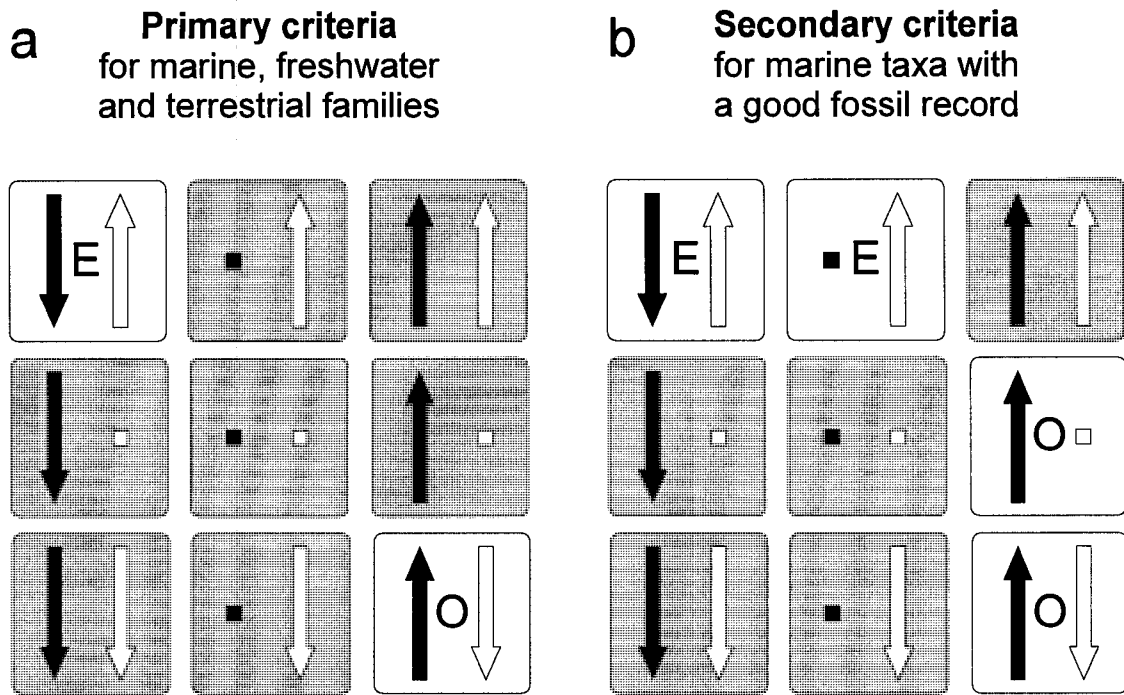


Figure 2. Classification scheme of Phanerozoic stages into origination (O) and extinction (E) half-cycles. Our primary and secondary stage classification criteria are based on stage to stage variation in family-level originations (black symbols) and extinctions (white symbols). Upward pointing arrow: increase in number of families. Downward pointing arrow: decrease in number of families. Dash: no change, i.e. same number of families as in preceding stage. Out of the 9 possible combinations of stage-to-stage variation in originations and extinctions, we considered two as primary stage classification criteria (highlighted squares of panel a), and four as secondary stage classification criteria (highlighted squares of panel b).

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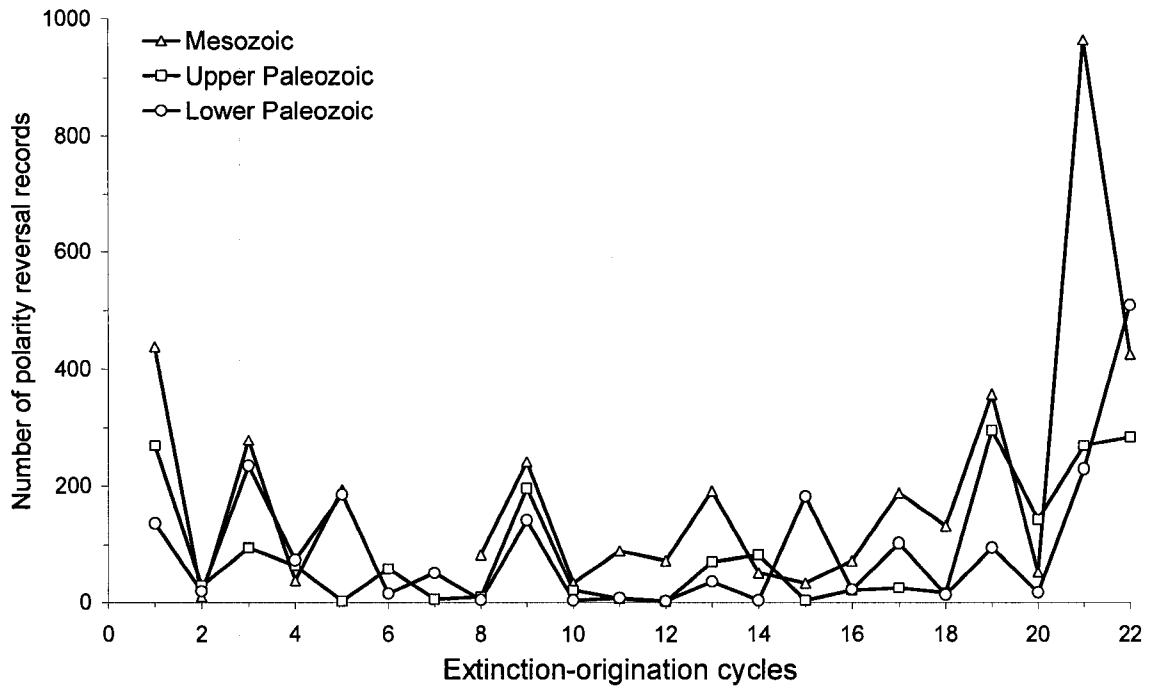


Figure 3. Number of magnetic polarity reversal records per half-cycle over 11 cycles (22 half-cycles) of three synchronized sections of the geologic column. The break in the Mesozoic is due to the Norian stage which is unresolved on the cyclic scale because it likely spans over both an extinction and an origination half-cycle.

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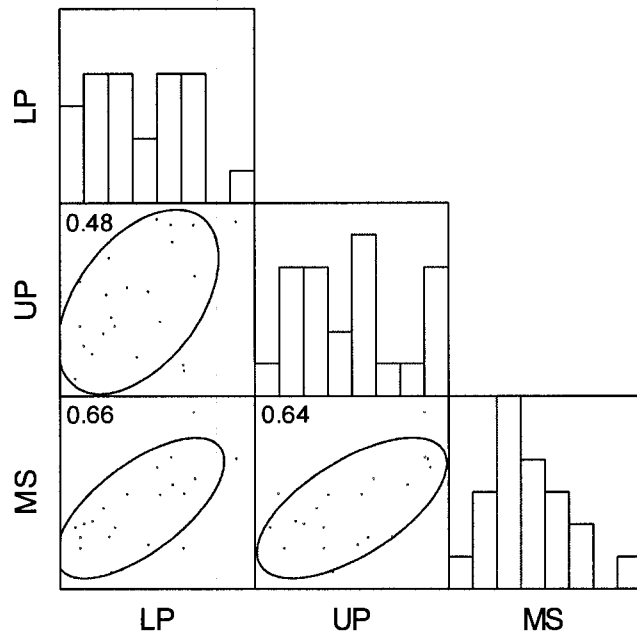


Figure 4. Correlations of number of magnetic polarity reversal records per half-cycle, raised to the power of 0.3, among synchronized segments of the Lower Paleozoic (LP), the Upper Paleozoic (UP) and the Mesozoic (MS). N=22 (LP-UP), 21 (LP-MS and UP-MS). Correlations stronger than  $r=0.42$  are significant at  $p<0.05$ .

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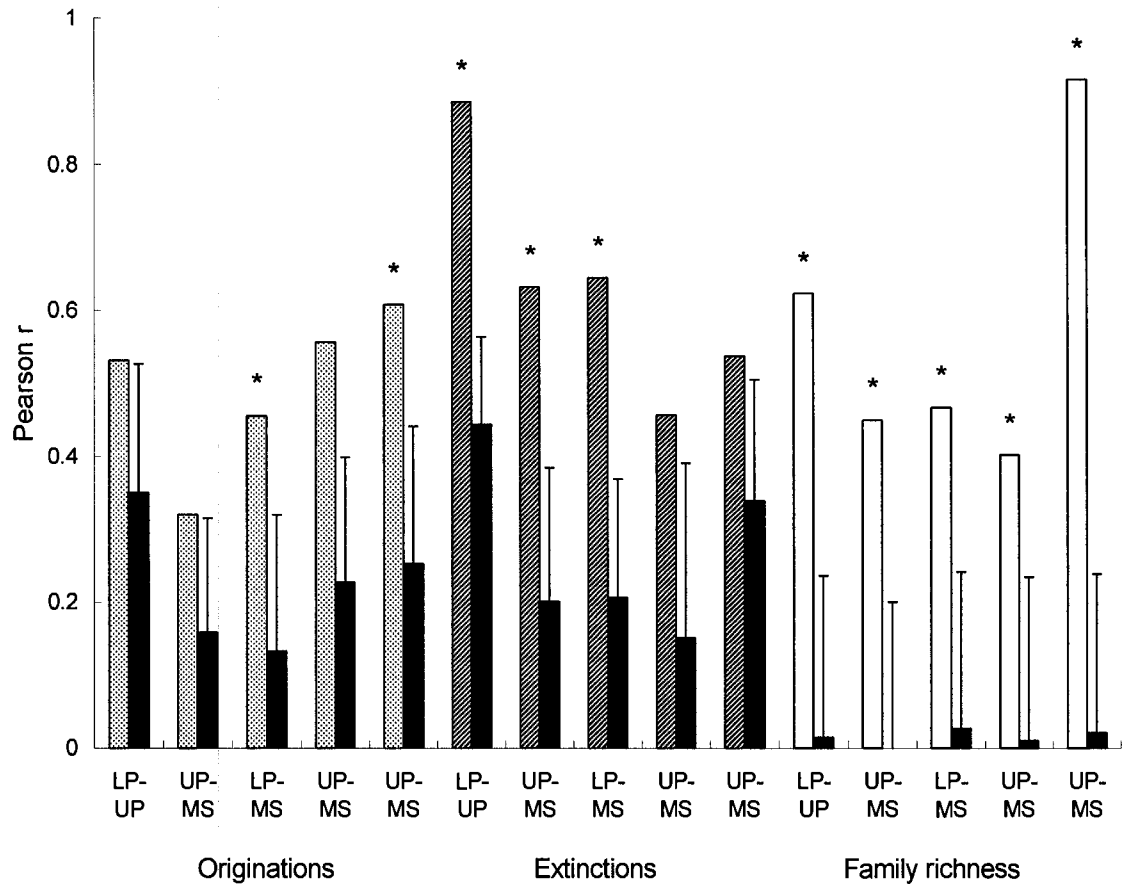


Figure 5. Comparison between observed and randomized total Pearson correlations for habitat-specific, absolute fossil metrics among the Lower Paleozoic (LP), the Upper Paleozoic (UP), and the Mesozoic (MS). The first three comparisons of originations, extinctions and richness are for marine families. The fourth is for fresh water and the fifth for terrestrial families, respectively, as listed in Table 5. The randomized mean values (black bars) represent the expected correlation introduced by our stage classification. Error: SD, based on 100 random trials. Significantly higher observed values are marked by asterisk (one sample t-test,  $p < 0.05$ ).

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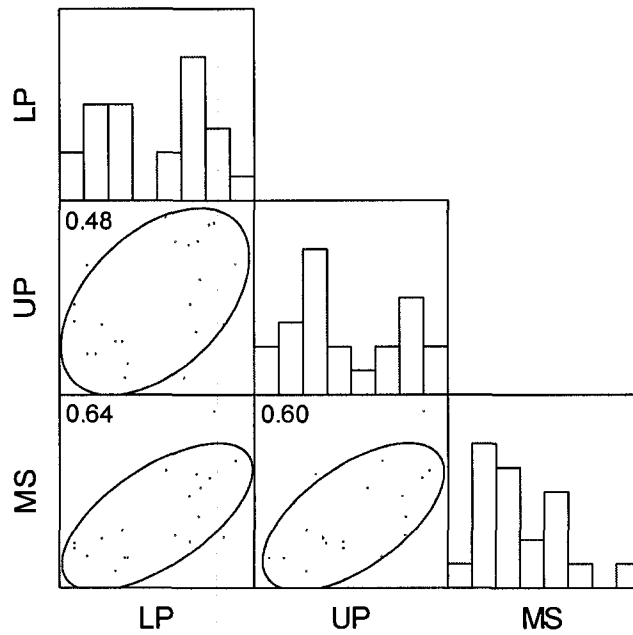


Figure 6a. Correlations of total numbers of originations per half-cycle, raised to the power of 0.2, among synchronized segments of the Lower Paleozoic (LP), the Upper Paleozoic (UP) and the Mesozoic (MS). N=22 (LP-UP), 20 (LP-MS and UP-MS).

*Phanerozoic supercycle*

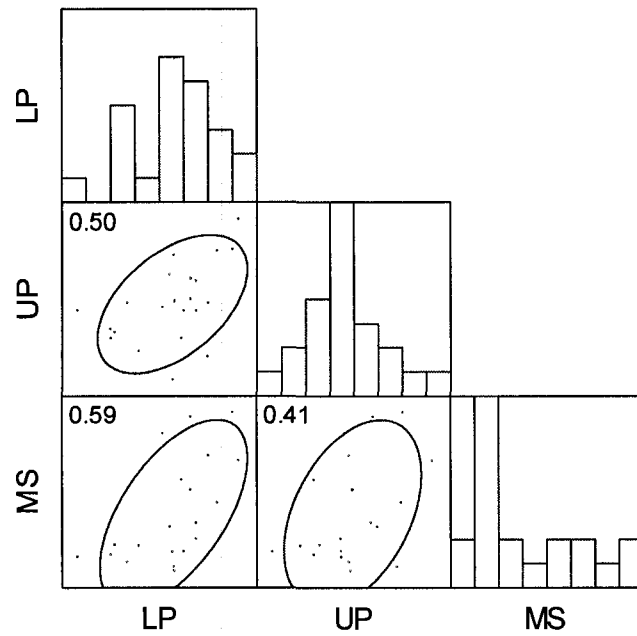


Figure 6b. Correlations of log-transformed fractional origination rates per half-cycle among synchronized segments of the Lower Paleozoic (LP), the Upper Paleozoic (UP) and the Mesozoic (MS). N=22 (LP-UP), 20 (LP-MS and UP-MS).

*Phanerozoic supercycle*

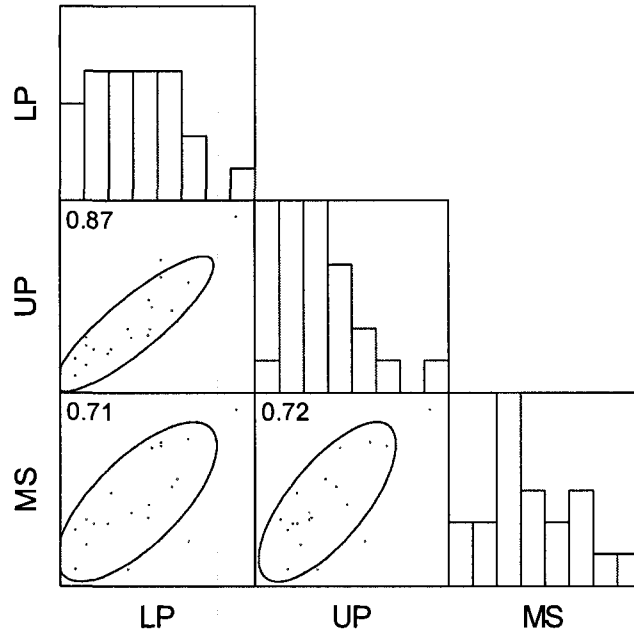


Figure 7a. Correlations of total numbers of extinctions per half-cycle, raised to the power of 0.2, among synchronized segments of the Lower Paleozoic (LP), the Upper Paleozoic (UP) and the Mesozoic (MS). N=22 (LP-UP), 20 (LP-MS and UP-MS).

*Phanerozoic supercycle*

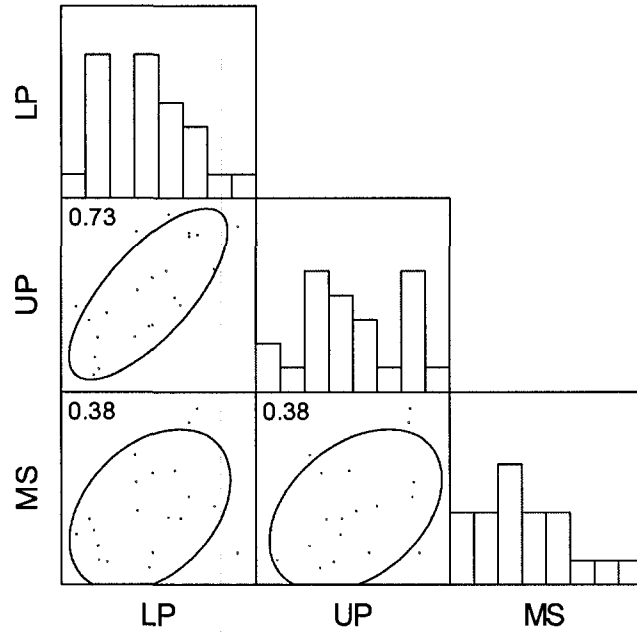


Figure 7b. Correlations of log-transformed fractional extinction rates per half-cycle among synchronized segments of the Lower Paleozoic (LP), the Upper Paleozoic (UP) and the Mesozoic (MS). N=22 (LP-UP), 20 (LP-MS and UP-MS).

*Phanerozoic supercycle*

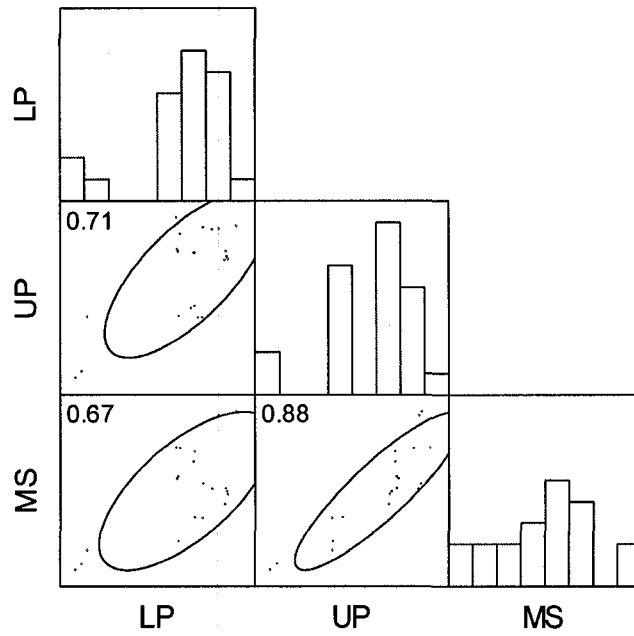


Figure 8. Correlations of family richness per half-cycle, raised to the power of 0.2, among synchronized segments of the Lower Paleozoic (LP), the Upper Paleozoic (UP) and the Mesozoic (MS). N=22 (LP-UP), 20 (LP-MS and UP-MS).

*Phanerozoic supercycle*

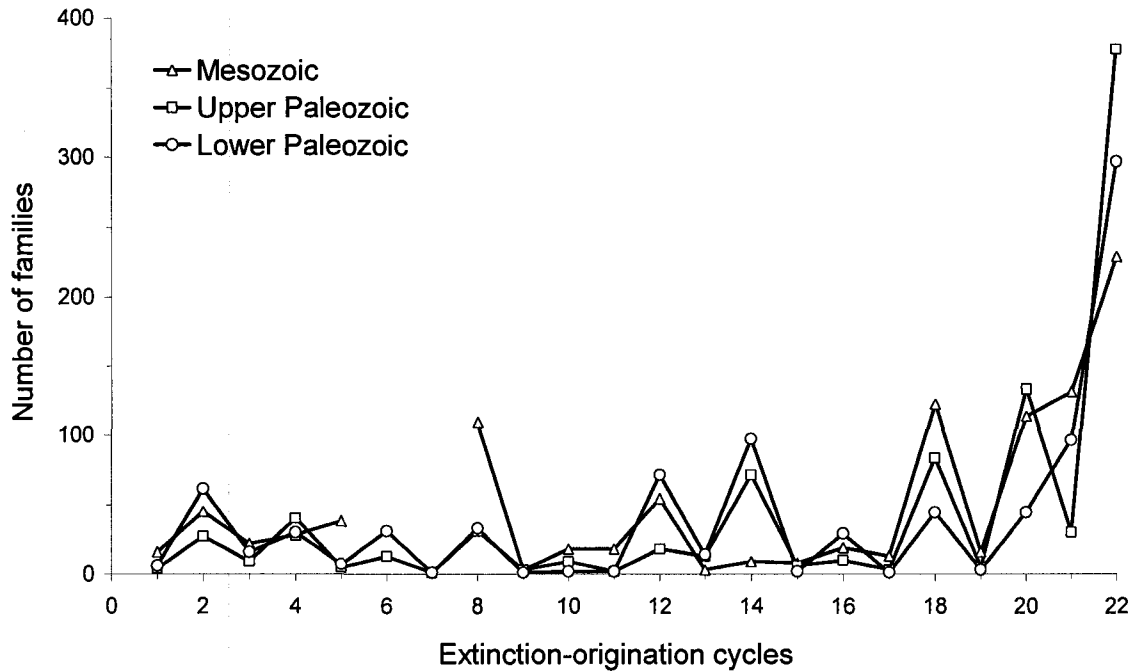


Figure 9. Family-level extinctions (marine, fresh water and terrestrial habitats combined) over 11 cycles (22 half-cycles) of three synchronized sections of the geologic column. The break in the Mesozoic is due to the Norian stage which is unresolved on the cyclic scale because it likely spans over both an extinction and an origination half-cycle.

*Phanerozoic supercycle*

Hirnantian	<b>14</b>	Hirnantian
Rawtheyan	<b>13</b>	unnamed
Cautleyan		
Pusgillian		
Onnian	<b>12</b>	unnamed
Actonian	<b>11</b>	
Marshbrookian		
Longvillian		
Soudleyan	<b>10</b>	unnamed
Harnagian		
Costonian	<b>9</b>	Darriwili an
Late Llandeilo	<b>8</b>	
Middle Llandeilo	<b>7</b>	
Early Llandeilo		
Late Llanvirn	<b>6</b>	unnamed
Early Llanvirn	<b>5</b>	
Arenig	<b>4</b>	unnamed
Tremadoc	<b>3</b>	Tremadocian
Dolgellian	<b>2</b>	unnamed
Maentwrogian	<b>1</b>	Paibian
Menevian		Middle Cambrian
Solvan		
Lenian		Early Cambrian
Atdabanian		
Tommotian		

Figure 10a. Comparison of the cyclic scale of the PTSC with Lower Paleozoic stages of the Harland time scale (Harland et al. 1990, on the left), and of the new ICS time scale (Gradstein et al. 2004, on the right). Numbered are the origination and extinction half-cycles (alternating black and white units in the central column) we used for statistical comparisons in this study.

*Phanerozoic supercycle*

Noginskian	<b>18</b>	Gzelian
Klazminskian	<b>17</b>	
Dorogomilovskian	<b>16</b>	Kasimovian
Chamovnicheskian	<b>15</b>	
Krevyakinskian	<b>14</b>	Moskovian
Myachkovskian	<b>13</b>	
Podolskian	<b>12</b>	
Kashirskian	<b>11</b>	
Vereiskian	<b>10</b>	
Melekesskian	<b>9</b>	Bashkirian
Cheremshanskian	<b>8</b>	
Yeadonian	<b>7</b>	
Marsdenian	<b>6</b>	
Kinderscoutian	<b>5</b>	
Alportian	<b>4</b>	
Chokierian	<b>3</b>	Serpukhovian
Arnsbergian	<b>2</b>	
Pendleian	<b>1</b>	
Brigantian		Visean
Asbian		
Holkerian		
Arunagian		
Chadian		
Ivorian		Tournasian
Hastarian		

Figure 10b. Comparison of the cyclic scale of the PTSC with Carboniferous stages of the Harland time scale (Harland et al. 1990, on the left), and of the new ICS time scale (Gradstein et al. 2004, on the right). Numbered are the origination and extinction half-cycles (alternating black and white units in the central column) we used for statistical comparisons in this study.

## *Phanerozoic supercycle*

### Appendix I

#### List of stratigraphic stages and classification criteria used

The following is an alphabetical list of the 123 stages of the Harland time scale (Harland et al. 1990). Stage order is from oldest (1 for Tommotian at the base of the Cambrian) to youngest (123 for the Holocene). The total number of originations and extinctions per stage (number of first and last appearing metazoan families), and change in originations and extinctions relative to the preceding stage (marine, fresh water and terrestrial families combined) are indicated. Primary stage classification criteria are indicated in the PTSC itself. For secondary criteria see Table 2.

Stage	System	stage order	total orig.	total ext.	change in orig.	change in ext.	classification	category
Aalenian	Jurassic	87	43	3	+8	-51	primary	origination
Actonian	Ordovician	20	0	1	0	+1	quiescent	origination
Aeronian	Silurian	27	2	0	-66	-2	quiescent	origination
Albian	Cretaceous	99	72	32	-32	+3	secondary	origination
Alportian	Mississippian	51	2	31	+1	+30	primary	extinction
Anisian	Triassic	78	63	22	+46	-23	primary	origination
Aptian	Cretaceous	98	104	29	+80	+17	secondary	origination
Aquitainian	Cenozoic	114	119	3	+44	-29	primary	origination
Arenig	Ordovician	9	151	30	+66	+14	uncertain	extinction
Arnsbergian	Mississippian	49	3	13	-30	+8	primary	extinction
Artinskian	Permian	68	19	57	+3	+31	primary	extinction
Arundian	Mississippian	44	1	2	-67	0	quiescent	origination
Asbian	Mississippian	46	8	4	+4	+3	quiescent	origination
Asselian	Permian	66	132	5	+130	-78	primary	origination
Atdabanian	Cambrian	2	128	12	+9	+9	secondary	origination
Bajocian	Jurassic	88	39	9	-4	+6	primary	extinction
Barremian	Cretaceous	97	24	12	-1	-101	primary	origination
Bartonian	Cenozoic	110	38	25	-121	-3	primary	extinction
Bathonian	Jurassic	89	36	8	-3	-1	secondary	origination
Berriasian	Cretaceous	94	129	8	+90	-95	primary	origination
Brigantian	Mississippian	47	9	40	+1	+36	primary	extinction
Burdigalian	Cenozoic	115	26	30	-93	+27	primary	extinction
Callovian	Jurassic	90	24	19	-12	+11	primary	extinction
Campanian	Cretaceous	104	79	56	+39	+38	uncertain	extinction
Capitanian	Permian	72	45	97	-15	+85	primary	extinction
Carnian	Triassic	80	113	38	+73	+10	primary	origination

## *Phanerozoic supercycle*

Cautleyan	Ordovician	23	0	1	-43	-3	quiescent	origination
Cenomanian	Cretaceous	100	79	35	+7	+3	primary	origination
Chadian	Mississippian	43	68	2	+63	-25	primary	origination
Chamovnicheskian	Pennsylvanian	62	0	1	-17	-4	quiescent	origination
Changxingian	Permian	74	2	265	+1	+250	secondary	extinction
Chattian	Cenozoic	113	75	32	-126	-4	primary	extinction
Cheremshanskian	Pennsylvanian	55	17	2	+16	-3	primary	origination
Chokierian	Mississippian	50	1	1	-2	-12	uncertain	origination
Coniacian	Cretaceous	102	90	9	+58	-5	primary	origination
Costonian	Ordovician	15	110	1	+99	-32	primary	origination
Danian	Cenozoic	106	96	18	+32	-136	primary	origination
Dolgellian	Cambrian	7	7	61	-61	+55	primary	extinction
Dorogomilovskian	Pennsylvanian	63	1	10	+1	+9	secondary	extinction
Eifelian	Devonian	37	43	49	0	+17	primary	extinction
Emsian	Devonian	36	43	32	-11	+6	primary	extinction
Famennian	Devonian	40	39	76	+6	+4	secondary	extinction
Frasnian	Devonian	39	33	72	-2	+5	secondary	extinction
Givetian	Devonian	38	35	67	-8	+18	primary	extinction
Gorstian	Silurian	31	37	3	+34	-41	primary	origination
Griesbachian	Triassic	75	84	11	+82	-254	primary	origination
Harnagian	Ordovician	16	5	0	-105	-1	uncertain	extinction
Hastarian	Mississippian	41	75	4	+36	-72	primary	origination
Hauterivian	Cretaceous	96	25	113	-2	+105	primary	extinction
Hettangian	Jurassic	83	136	3	+112	-106	primary	origination
Hirnantian	Ordovician	25	4	97	-1	+88	primary	extinction
Holkerian	Mississippian	45	4	1	+3	-1	primary	origination
Holocene	Cenozoic	123	-	-	-	-	none	unclassified
Homerian	Silurian	30	3	44	-78	+43	primary	extinction
Ivorian	Mississippian	42	5	27	-70	+23	primary	extinction
Kashirskian	Pennsylvanian	58	4	5	-45	-1	quiescent	origination
Kimmeridgian	Jurassic	92	44	19	-102	+6	primary	extinction
Kinderscoutian	Pennsylvanian	52	114	3	+112	-28	primary	origination
Klazminskian	Pennsylvanian	64	8	3	+7	-7	primary	origination
Krevyakinskian	Pennsylvanian	61	17	5	+8	-66	primary	origination
Kungurian	Permian	69	12	50	-7	-7	secondary	extinction
Ladinian	Triassic	79	40	28	-23	+6	primary	extinction
Langhian	Cenozoic	116	53	1	+27	-29	primary	origination
Lenian	Cambrian	3	16	149	-112	+137	primary	extinction
Llandeilo, early	Ordovician	12	60	1	+58	-30	primary	origination
Llandeilo, late	Ordovician	14	11	33	+11	+33	secondary	extinction
Llandeilo, middle	Ordovician	13	0	0	-60	-1	quiescent	origination
Llanvirn, late	Ordovician	11	2	31	-87	+24	primary	extinction
Llanvirn, early	Ordovician	10	89	7	-62	-23	secondary	origination
Lochkovian	Devonian	34	44	39	+19	+8	primary	origination
Longtanian	Permian	73	1	15	-44	-82	secondary	extinction
Longvillian	Ordovician	18	1	1	-3	-1	uncertain	origination
Ludfordian	Silurian	32	2	44	-35	+41	primary	extinction
Lutetian	Cenozoic	109	159	28	-82	+14	primary	extinction
Maastrichtian	Cretaceous	105	64	154	-15	+98	primary	extinction
Maentwrogian	Cambrian	6	68	6	+65	-71	primary	origination

## *Phanerozoic supercycle*

Marsdenian	Pennsylvanian	53	4	4	-110	+1	primary	extinction
Marshbrookian	Ordovician	19	0	0	-1	-1	quiescent	origination
Melekesskian	Pennsylvanian	56	10	18	-7	+16	primary	extinction
Menevian	Cambrian	5	3	77	-80	+59	primary	extinction
Messinian	Cenozoic	119	12	40	-20	+38	primary	extinction
Myachkovskian	Pennsylvanian	60	9	71	-19	+69	primary	extinction
Nammalian	Triassic	76	12	5	-72	-6	secondary	origination
Noginskian	Pennsylvanian	65	2	83	-6	+80	primary	extinction
Norian	Triassic	81	33	39	-80	+1	none	unclassified
Onnian	Ordovician	21	1	71	+1	+70	secondary	extinction
Oxfordian	Jurassic	91	146	13	+122	-6	primary	origination
Pendleian	Mississippian	48	33	5	+24	-35	primary	origination
Piacenzian	Cenozoic	121	16	31	-22	+26	primary	extinction
Pleistocene	Cenozoic	122	59	24	+43	-7	none	unclassified
Pliensbachian	Jurassic	85	31	18	-16	0	secondary	origination
Podolskian	Pennsylvanian	59	28	2	+24	-3	primary	origination
Pragian	Devonian	35	54	26	+10	-13	primary	origination
Priabonian	Cenozoic	111	237	46	+199	+21	uncertain	extinction
Pridoli	Silurian	33	25	31	+23	-13	primary	origination
Pusgillian	Ordovician	22	43	4	+42	-67	primary	origination
Rawtheyan	Ordovician	24	5	9	+5	+8	uncertain	origination
Rhaetian	Triassic	82	24	109	-9	+70	primary	extinction
Rhuddanian	Silurian	26	68	2	+64	-95	primary	origination
Rupelian	Cenozoic	112	201	36	-36	-10	primary	origination
Sakmarian	Permian	67	16	26	-116	+21	primary	extinction
Santonian	Cretaceous	103	40	18	-50	+9	uncertain	extinction
Serravallian	Cenozoic	117	3	27	-50	+26	primary	extinction
Sheinwoodian	Silurian	29	81	1	+71	-28	primary	origination
Sinemurian	Jurassic	84	47	18	-89	+15	primary	extinction
Solvan	Cambrian	4	83	18	+67	-131	primary	origination
Soudleyan	Ordovician	17	4	2	-1	+2	uncertain	extinction
Spathian	Triassic	77	17	45	+5	+40	secondary	extinction
Telychian	Silurian	28	10	29	+8	+29	secondary	extinction
Thanetian	Cenozoic	107	115	26	+19	+8	secondary	origination
Tithonian	Jurassic	93	39	103	-5	+84	primary	extinction
Toarcian	Jurassic	86	35	54	+4	+36	secondary	extinction
Tommotian	Cambrian	1	119	3	+119	+3	primary	origination
Tortonian	Cenozoic	118	32	2	+29	-25	primary	origination
Tremadoc	Ordovician	8	85	16	+78	-45	primary	origination
Turonian	Cretaceous	101	32	14	-47	-21	secondary	origination
Ufimian	Permian	70	58	18	+46	-32	primary	origination
Valanginian	Cretaceous	95	27	8	-102	0	secondary	origination
Vereiskian	Pennsylvanian	57	49	6	+39	-12	primary	origination
Wordian	Permian	71	60	12	+2	-6	primary	origination
Yeadonian	Pennsylvanian	54	1	5	-3	+1	secondary	extinction
Ypresian	Cenozoic	108	241	14	+126	-12	primary	origination
Zancian	Cenozoic	120	38	5	+26	-35	primary	origination

Appendix II

Half-cycle category as a predictor in multiple regressions

Multiple regression models predicting stage-level change in number of metazoan families, extinction and origination rates, using half-cycle category as a predictor variable alongside with the continuous variables of Table 3a of Chapter 4.

Standardized coefficients of terms, retained both by forward selection and by backward elimination, are shown ( $p < 0.05$ ). Note that magnetic polarity reversal intensity and half-cycle category are the only variables retained both by forward selection and by backward elimination in all models. Dependent variables are transformed as indicated in Table 1 of Chapter 4.  $N=120$  (marine and combined metrics), 95 (continental metrics). The Norian and the Pleistocene, stages unresolved on the cyclic scale are excluded.  $R^2$  values without half-cycle category are from the models of Table 3a of Chapter 4.

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	change			originations			extinctions		
	marine	contin.	all	marine	contin.	all	marine	contin.	all
reversal intensity <sup>0.33</sup>	0.635	0.306	0.635	0.454	0.206	0.575	0.435	0.535	0.576
cratering <sup>0.2</sup>									
log(CO <sub>2</sub> )	0.291	-0.268		0.218					
mid-point age		0.385			0.506				
stage duration <sup>0.2</sup>				0.315					
carbonate*		-0.205							-0.177
carbonate and clast.*	0.348	0.460	0.245		0.178		0.260		0.292
marine clastic*						0.225			
terrestrial clastic*	-0.189								
total amount of rock*									
Half-cycle category**	0.160	0.291	0.223	0.175	0.295	0.198	0.266	0.196	0.249
R <sup>2</sup> (no half-cycle cat.)	0.575	0.343	0.583	0.508	0.416	0.480	0.344	0.338	0.499
R <sup>2</sup> with half-cycle cat.	0.626	0.575	0.633	0.545	0.488	0.553	0.409	0.366	0.549

\* (10<sup>3</sup>km<sup>3</sup>)<sup>0.2</sup>

\*\* categorical variable with two levels, describing whether a stratigraphic stage is part of an extinction or an origination half-cycle in the PTSC

## Chapter 6

# An astronomical model of the variation in paleodiversity

Preface

Originally part of an appendix, the material presented in this chapter was not reviewed by the thesis examining committee. Highly speculative, this chapter solely represents the personal views and current understanding of the thesis candidate.

The goal of this short essay is to emphasize the need to develop multidisciplinary, mechanistic models to explain cyclic variation in fossil diversity over the Phanerozoic. We also propose that such a model take into consideration certain features of the Sun and our solar system which are difficult to explain for a single star system.

### *An astronomical model of the variation in paleodiversity*

"Single-star systems are not very common, perhaps even rare, compared to binary-star systems, which constitute the majority of observable stars. Even triple-stellar associations are frequently observed."

(Taylor, 1992, p.38)

#### A multidisciplinary binary model

Variation in fossil richness and paleodiversity have been related to a great variety of factors. These include isostatic cycles, sea level change and anoxia (extinctions: Hallam 1994), cyclic patterns in glaciations (Milankovitch cycles), bolide impacts (extinctions: Raup and Sepkoski 1984; Raup 1994) and magnetic polarity reversals (Chapter 4). We are unaware of any specific model that would predict such a wide variety of relationships. What follows is the sketch of a general mechanistic model, according to which the ultimate driving forces for cyclic bio- and geo-events on our planet are astronomical phenomena.

The binary star model we present can be regarded as a variation of the *Distant Solar Companion or Nemesis Theory* (Davis and Muller 1984; Whitmire and Jackson 1984; Raup 1999; Muller 2002). According to this theory, the periodic passages of a relatively small and cool companion star of the Sun causes periodic comet showers on Earth. The theory was originally proposed to explain periodicity in mass extinctions (Raup and Sepkoski 1984). Its main weakness is that the hypothetical distant solar companion would require a highly eccentric and unstable orbit to match the ca. 26-32 Myr periodicity proposed for mass extinctions (e.g. Raup and Sepkoski 1984; Tiwari and Rao 1999).

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There is, however, mounting astronomical evidence to support the existence of a distant solar companion. This includes the low angular momentum of the Sun (Taylor 1992, p.37), the sheer edge of the solar system (Allen and Bernstein 2001), accelerating precession (Cruttenden 2003), the recent discovery of the distant planetoid Sedna, etc. For example, in observable single star systems most of the angular momentum is carried by the star itself. In our solar system, however, most of the angular momentum is carried by the Jovian planets, Jupiter in particular. This is difficult to explain within the framework of the current single star model of the solar system.

### Cyclicality at multiple scales

An early observation we made during our paleodiversity study was that physical conditions on our planet appear to vary cyclically, alternating between two modes. We will refer to these as mode A and mode B environmental conditions. Mode A is characterized by low lying continents, shallow and widespread seas, uniformly mild climate, high degree of humidity and thick cloud cover. Mode B conditions can be described as hot and dry in subtropical zones. High seasonality and extreme weather conditions dominate. Continents are high and a polar ice cap is present. Thus, contemporary environmental conditions correspond to mode B. We propose that cyclicality between mode A and mode B occur at multiple scales throughout Phanerozoic history (Fig. 1). We also propose that three distinct astronomical phenomena are responsible for this multi-scale cyclicality.

## *An astronomical model of the variation in paleodiversity*

First, consider the hypothesis that our Sun is, like the great majority of stars, part of a binary system. We propose that the periodic passages of the distant solar companion cause asteroid showers, intense cosmic radiation, magnetic polarity reversals and other geologic and climatic phenomena on our planet. These geologic events are the direct causes of cyclicity in bio-events and fossil preservation as well. We also propose that the magnitude of bio-events vary due to the precession of Earth's position during successive stellar oppositions, or at times when wave(s) of asteroids reach the inner solar system. This primary signal is at the scale of systems in the geologic column (Fig. 1a). It has long been known that the beginning of Phanerozoic systems generally correspond to mode A geologic and climatic conditions, while their end is characterized by mode B conditions (Fenton and Fenton 1958, pp.26-27).

Secondary oscillations (Fig. 1b) would be caused by a proposed 9:2 orbital resonance of the two stars in our binary system, explaining the alternating spectra of extinction and origination half-cycles throughout Phanerozoic history (PTSC chart, pp. 211-212). Due to the 9:2 orbital resonance, stars would be at opposition at every second passage of the companion star only. We hypothesize that extinction half-cycles culminate by the periodic passages of the companion star, triggering the environmental phenomena already associated with extinction events in the scientific literature (e.g. bolide events: Davis and Muller, 1984; Raup 1985, 1999; sea-level change and anoxia: Hallam, 1994, 1996). Subsequently, origination half-cycles begin with a rapid melting of the polar ice cups which is followed by a gradual accentuation of mode A isostatic

and climatic conditions. We propose that the end of origination half-cycles is marked by rapid transgression and smaller scale bolide events due to gravitational interactions between the outer solar system (Kuiper Belt and Oort Cloud) and the outer rim of the planetary system of the companion star (sheer edge effect).

The impacts of the periodic passages of the companion star and these sheer edge effects would differ greatly because geologic and climatic conditions on Earth are very different when they happen (Fig. 2a-b). In particular, coastal areas are highly vulnerable to flooding when mode A isostatic conditions culminate. At the other extreme, rapid melting of the polar ice cups may trigger an isostatic chain reaction of subsidence at a moment when continents are the highest. This is because continents in temperate and tropical regions are uplifted and upheld by the pressure of ice in polar regions. Hence, the impacts of these two types of astronomical events will register with a lag=+2 autocorrelation in the fossil record, corresponding to the alternating spectra of origination and extinction half-cycles on the PTSC (pp. 211-212). While mode A environmental conditions are ultimately triggered by astronomical phenomena, the gradual return of mode B environmental conditions can be regarded as a spontaneous, endogenous process during extinction half-cycles, just like the return to normal magnetic polarity from reversed polarity in the course of origination half-cycles. Sea-level fall toward the end of origination half-cycle can be the result of continued isostatic readjustment, i.e. the combined effect of shallow seas and low lying continents (Thesis conclusion: Fig. 3).

## *An astronomical model of the variation in paleodiversity*

Finally, at the smallest scale, the orbital motion of the Sun and the Earth produces a third-order or climatic oscillation (Fig. 1c) at the scale of the Sun's orbital period around the common center of mass of the binary system. We propose that, in accordance with Kepler's second law, the Sun's orbital velocity varies considerably due to the eccentricity of its orbit in the proposed binary model. It is this variation in the Sun's orbital velocity what causes the axial tilt of the Earth and the eccentricity of Earth's orbit to increase when the Sun's orbital velocity is increasing (Fig. 2b). Increase in axial tilt and orbital eccentricity will accentuate mode B climatic conditions on Earth. The opposite happens when the Sun's orbital velocity decreases: the tilt of the Earth's axis and Earth's orbital eccentricity decrease, entailing mode A climatic conditions.

### Proposed orbital periods and their implications

In contrast to earlier theories about a distant solar companion, we propose a binary model based on realistic and stable orbital periods for the Sun and the distant solar companion. Orbital periods of known binary stars span from less than a day to tens of thousands of years. Binaries with a separation >20 000 years are very rare, possibly because of encounters with giant molecular clouds (Whitmire and Jackson 1984).

Based on anthropological evidence and historical records on climatic conditions, we propose an orbital period of approximately 1260 years for the Sun and 5670 years for the distant solar companion. The exact orbital periods we propose are also integers of Jovian years:

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$$T_{\text{Sun}} = 15 \text{ years of Uranus}$$

$$T_{\text{Companion Star}} = 478 \text{ years of Jupiter}$$

According to this scenario, global warming during the 20th century can be (partly) attributed to the Sun having past periapsis, corresponding to its maximal orbital velocity, in the early 20th century. The Little Ice Age (13-19 centuries) could be interpreted as a result of gradual increase in Earth's axial tilt and in the eccentricity of Earth's orbit, due to the accelerating orbital velocity of the Sun. The 1260 year orbital period for the Sun would also imply the accentuation of mode A climatic conditions coinciding with the Medieval Warm Period (800-1300 AD). Further back in time, mode A isostatic conditions would coincide with the beginning of the Nippurian calendar (3760 BC) and the beginning of the Holocene would be marked by the previous passage of the companion star. Finally, we propose that the five most recent passages of the companion star may be detectable in Vostok ice core data, explaining the sharp increases in temperature (Fig. 3).

A potentially testable prediction of the above described precise astronomical model could relate the magnitude of the largest scale environmental perturbations (Fig. 1a) and changes in paleodiversity to the precession of Earth's position during successive stellar oppositions (ca. 0.1316 Earth years). Thus, the greatest mass extinction events in Phanerozoic history ought to coincide with Earth being in a similar position on its orbit. This test, however, may require an extensive re-examination of several commonly accepted ideas in science (e.g. Chapter 5: supercyclicity vs. contemporaneity hypotheses; the underlying

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assumptions of radioactive dating; rates of evolution and the duration of the Phanerozoic; etc). This is beyond the scope of the present essay.

To illustrate these difficulties, let us consider the apparent difference in scale between the orbital periods of our binary model and stage-level cyclicality in the fossil record. At the present, geologic time "measured" from radioactive decay is based on the assumption that radioactive decay products accumulate with an unchanging rate. This implies that millions of years are needed to produce substantial amounts of daughter atoms. We propose, however, that decay rates are not constant, and that most daughter atoms are produced in short intervals of time during exposure to cosmic radiation. Thus, the amount of radioactive decay products found in rocks would be essentially a function of the number of exposures, i.e. the number of passages of the companion star in the past. This is analogous to the punctuated equilibrium theory of evolutionary biology (Eldredge and Gould, 1972). It has been proposed that rates of speciation are not constant, but punctuated by sudden burst in rates of mutations which can be induced by exposure to cosmic radiation. Similarly, cosmic ray bombardment is known to cause nuclear spallation in radioactive isotopes (e.g. Geyh and Schleicher 1990). This concept could reconcile the apparent scale difference between a realistic binary model and periodicity in the fossil record at the scale of stratigraphic stages.

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Tables and figures

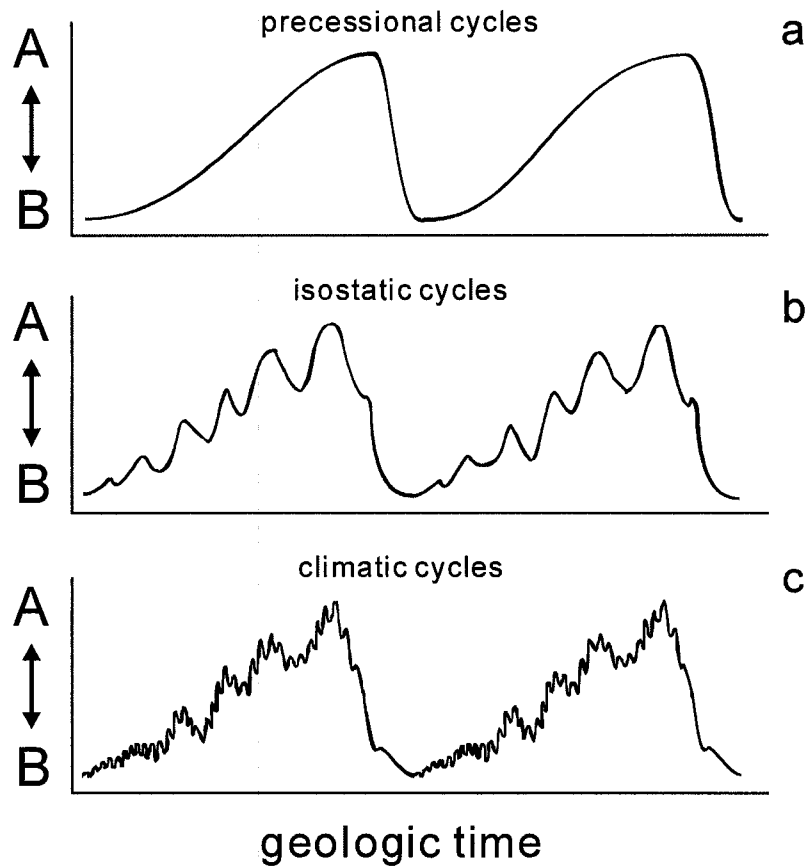


Figure 1. Schematic patterns of first, second and third order fluctuations in global environmental conditions. Mode A: uniformly mild climate, shallow seas and low continents. Mode B: high seasonality, mountain buildup and polar ice caps. Age increases from left to right on X axis.

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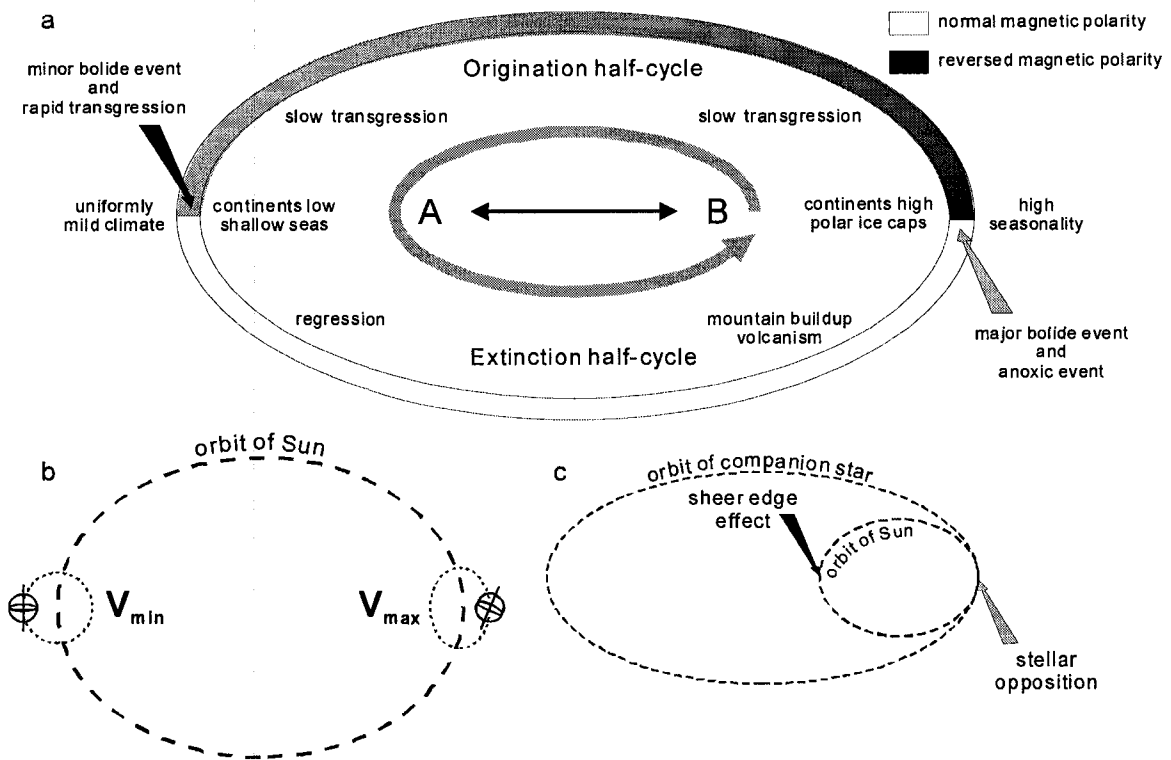


Figure 2. A general mechanistic model of cyclic environmental phenomena driving extinctions and originations over Phanerozoic times.

2a: Isostatic, eustatic and climatic cycles, magnetic polarity reversals and bolide impact events in relation to alternating extinction and origination half-cycles.

2b: Variation in Earth's axial tilt and Earth's orbital eccentricity as a function of the Sun's orbital velocity ( $V$ ).

2c: Stellar orbits of our proposed binary model, with an orbital resonance of 9:2 for the Sun and the hypothetical distant solar companion. The positions of the Solar system, corresponding to the beginnings of extinction and origination half-cycles are indicated by arrows with reference to 2a. Note that extinction and origination events occur only at every four and a half revolution of the Sun, due to the 9:2 orbital resonance.

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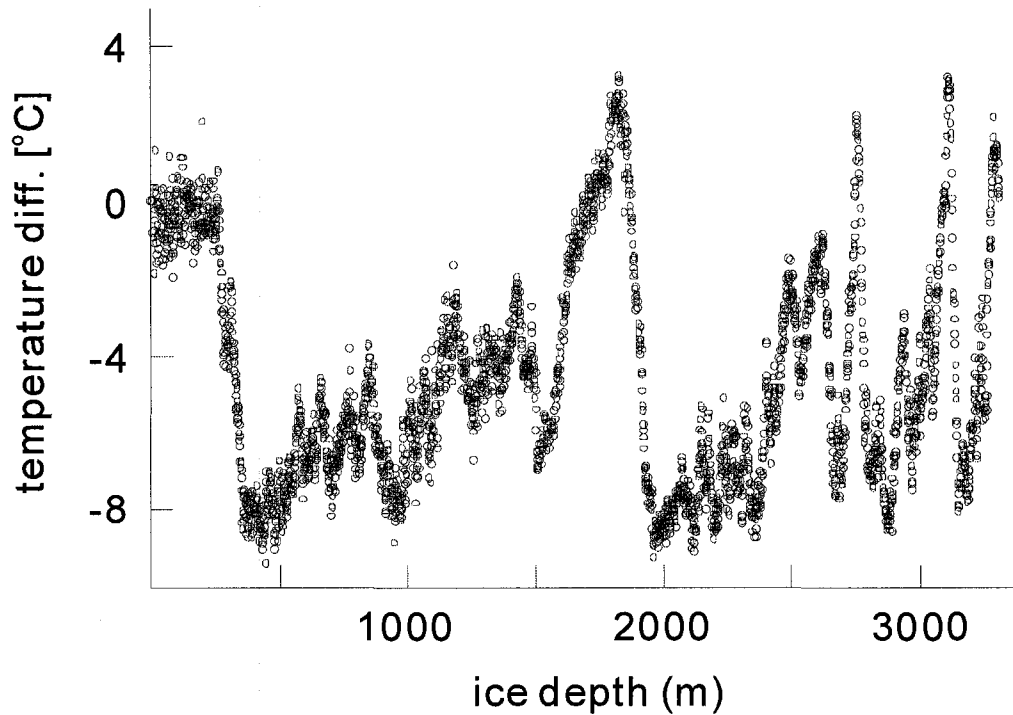


Figure 3. Historical variation in temperature as a function of depth, based on Vostok ice core data from Petit et al. (2001). Past temperature estimates are based on difference from the recent -438 ‰ mean deuterium value. Note that the signal is squeezed due to the compaction of ice at greater depths. N=3316.

# Conclusion

This section summarizes the findings of the thesis in the form of theoretical relationships and models derived from our studies of contemporary and past diversity.

## The effects of interactions on avian richness

The major findings of our contemporary avian diversity study can be resumed as: (1) Global patterns of richness are not idiosyncratic and can be modeled as a function of contemporary abiotic environmental predictors. (2) Patterns of continental and insular diversity are commensurable. (3) The effects of area and isolation on richness are additive. (4) Richness depends strongly on interactions between various environmental predictors, area and climate in particular. Note that most of these points are either directly or indirectly related to interactions or to the lack of interaction between abiotic predictors.

The two-way interactions we identified conform to a few generalized patterns. The three dimensional, theoretical surfaces of these interactions become smooth and regular when we control for other factors exerting a major influence on richness. For example, the area-precipitation interaction presents a relatively uniform surface if we control for the effects of temperature, isolation and elevation. The distance to continent-neighbor effect interaction presents a smooth surface if we control for the effects of area, climate and elevation. All together, we identified five such, biologically important interactions:

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1. Area X Precipitation (Fig. 1a)
2. Area X Temperature (Fig. 1a)
3. Temperature X Elevation (Fig. 1b)
4. Temperature X Precipitation (Fig. 1c)
5. Distance to continent X Neighbor effect (Fig. 1d)

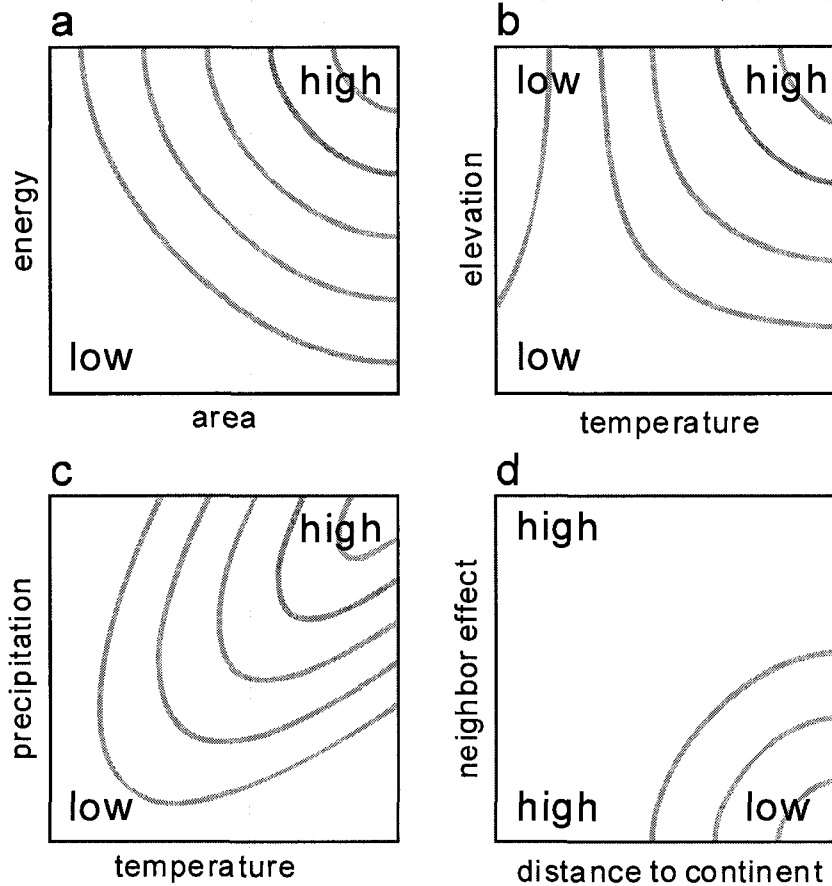


Figure 1. Theoretical surfaces of two-way interactions between various abiotic predictors of avian richness. Low and high refer to bird species numbers (Z axis). 1a: Area and energy (temperature and/or precipitation) are both severely limiting factors, i.e. both can limit avian richness on our planet effectively to zero. 1b: Elevation is not a severely limiting factor, and its effect is negative in colder regions. 1c: Ridge effect caused by water deficit (lower right) and ice cover (upper left). 1d: The importance of neighboring islands, in reducing isolation, increases with distance to the continent.

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The above described interactions are intuitive to a great extent. For example, it is clear that richness will not increase with area in totally dry or extremely cold regions. Conversely, richness will not increase with energy among islands which are too small to sustain any species. Note however, that we could apply the same logic to support the notion of an area-isolation interaction as well. In this case, richness is not expected to increase with area on completely isolated islands. Conversely, richness should not decrease with isolation on islands which are too small to support any species (Fig. 2).

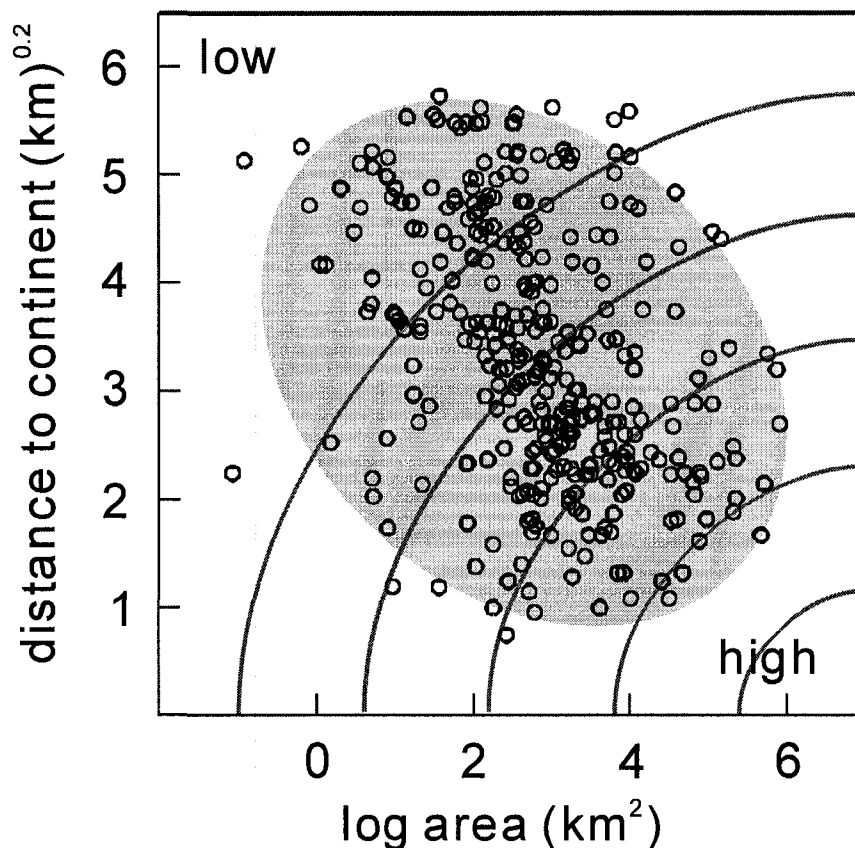


Figure 2. Theoretical surface of a hypothetical area-isolation interaction. Low and high refer to bird species numbers (Z axis). The grey area in the center shows general sample availability. The small circles indicate the actual data in our island study (Chapter 1). Note that data from the zones in the lower left and upper right would be critical to detect an area-isolation interaction effect.

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The lack of an area-isolation interaction is probably the most intriguing finding of our avian diversity study. In Chapter 2 we have explained how earlier studies might have come to the conclusion that the richness-area slope depends on isolation. Here we like to explain why we did not find such an interaction.

In our opinion, patterns of global geography and sampling bias limit the testability of a hypothetical area-isolation interaction. Despite our explicit efforts to collect critical data, we were unable to fill the gaps shown in figure 2. On one hand, there is a correlation between island size and distance to continent ( $r=-0.37$ ,  $n=346$ ,  $p<10^{-12}$ ). This is because large islands far from continental mainlands are very rare on our planet. On the other hand, small coastal islands exist in large numbers, but there are no published checklists for their avifaunas. We see two main reasons for this: (1) These islands do not have endemic species or sub-species to attract bird watchers. Their avifauna is generally unremarkable, a mere subset of the species found on the mainland or on nearby larger islands. (2) These islands tend to be smaller than minimal species ranges needed to support permanent breeding populations. As a consequence, regular vagrants, visitors, non-breeding residents, and especially, irregular breeding species make the compilation of checklists problematic.

In conclusion, the results of our avian diversity study may be pointing toward a new paradigm in the field of island biogeography. Nevertheless, our main finding, that species-area slopes do not depend on isolation, needs to be verified using richness data from less mobile taxa. Conversely, data formerly used to demonstrate differences in SAR slopes, and implicitly supportive of the ETIB, may

## *Conclusion*

need to be reanalyzed to assess the effects of climate, log transformation and correlation between island size and isolation on SAR slopes.

### A multivariate approach to model fossil diversity

Marine diversification over the Phanerozoic is complex in comparison to the monotonic increase we have seen in continental diversity (Chapter 3, Figs. 5, 7-9). While a simple ranking of stratigraphic stages in temporal order can explain about 92% of the variation in continental family richness since the Devonian (Chapter 3), geologic time can statistically explain only about 11% of the variation in marine family richness<sup>0.2</sup> prior to the Cenozoic, and 43% including the Cenozoic. A multiple regression approach to model marine richness may well worth the effort in the future.

Environmental descriptors analogous to those controlling contemporary richness patterns can statistically explain more than >70% of the variation in marine family richness over the Phanerozoic (Table 1). This illustrates the future potentials of a multivariate approach to model marine fossil richness. In our opinion, it is just a matter of time until high resolution sea-level and climate data, covering the entire Phanerozoic, will be available. We hope that as our knowledge about past environmental conditions and paleodiversity increases, we will also witness increasing exchange of ideas and methods between ecologists and paleontologists.

In summary, our study of Phanerozoic diversity offers the view of an outsider to the field of paleontology, with its advantages and disadvantages. We

## Conclusion

propose the inclusion of continental taxa into global diversity studies. We advocate a multivariate approach to model fossil richness and variation in fossil richness. We also present a strong case for the link between magnetic polarity reversals and variation in fossil richness. We hope that these results may present some useful contribution to the study of paleodiversity.

Table 1. A multiple regression model explaining variation in family richness<sup>0.2</sup> of marine metazoans over the Phanerozoic.  $R^2=0.724$ .  $N=122$  stratigraphic stages.

	std. coeff.	tolerance	p
carbonate and clastic sediments [ $10^3\text{km}^2$ ] <sup>0.2</sup>	-0.519	0.587	$<10^{-12}$
terrestrial clastic sediments [ $10^3\text{km}^2$ ] <sup>0.2</sup>	0.540	0.558	$<10^{-12}$
log(RCO <sub>2</sub> )	-0.315	0.299	0.001
relative change in sea level*	0.523	0.516	$<10^{-11}$
marine provinciality index**	0.210	0.365	0.011

\* Based on Vail et al. (1977)

\*\* Number of high and low diversity provinces, based on Valentine et. al. (1978)

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### The Phanerozoic signature

The implications of our Phanerozoic time synchronization chart are potentially far reaching. We propose a formal distinction between "origination" and "extinction" stages and their regrouping into half-cycles to improve the chances of detecting (super)cyclic and periodic phenomena over the Phanerozoic. We have shown that this distinction is highly significant from a statistical point of view (Chapter 5, Appendix II). More importantly, however, the cyclic time scale can play a key role in the formulation of a general, multidisciplinary theory explaining the mechanics and the history of our biosphere. In chapter 6 we present the outlines of such a general theory in the framework of an astronomical model, guided by the Popperian view, that one can learn more from a precise theory, even if it be erroneous, than from a carefully vague one.

Here we like to present a stand-alone version of our view of Phanerozoic dynamics without reference to the binary model (Fig. 3). While probably imperfect and incomplete in some details, this schema aims to emphasize regularity and repetitiveness over noise and bias in paleontological data. We hope our efforts will stimulate interest in this concept we can term: the "Phanerozoic signature".

## Conclusion

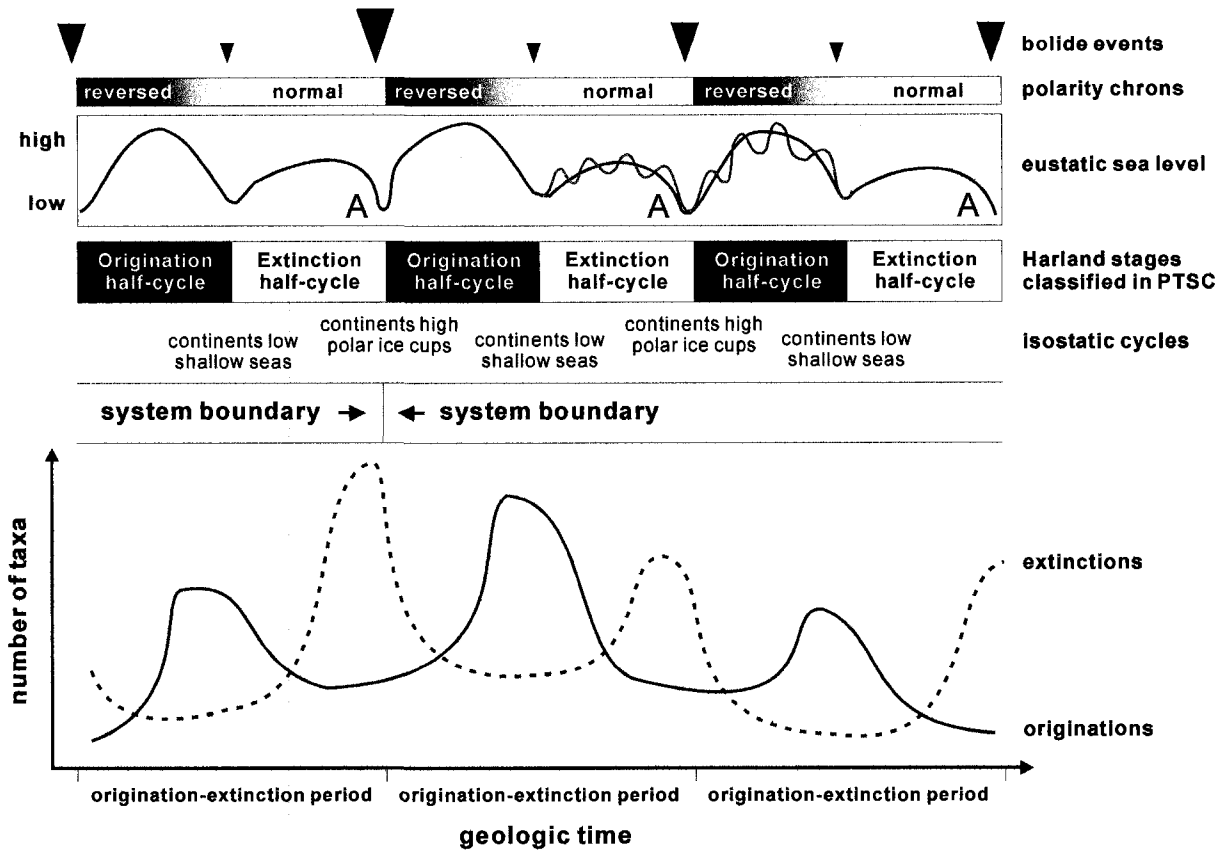


Figure 3. Schematized pattern of variation in fossil richness and geologic phenomena over the Phanerozoic based on results of Chapter 4 and 5.

The main eustatic sea level curve is based on Hallam (1996, Fig. 2). The blue curve shown over part of the eustatic sea level curve indicates fourth order cycles. A: anoxic event.

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# Glossary

**AIC.** Akaike Information Criterion. A measure of the goodness of fit of a statistical model. Models with lower AIC values are preferred.

**Anoxic event.** Relatively rapid oxygen depletion in the Earth's oceans, often coinciding with or causing marine mass extinctions. The mechanism(s) of anoxic events are still poorly understood.

**Big Five mass extinctions.** Refers to the five largest Phanerozoic extinction events: End Ordovician, Late Devonian (Frasnian-Famennian stage boundary), End Permian, End Triassic and End Cretaceous.

**Bolide.** A large meteor, visible in the sky as it (partially) burns up in the atmosphere during its descent.

**Change in number of families.** Fossil metric we use in Chapter 4. It is the total number of fossil families for a given stratigraphic stage with a different distribution status (absence or presence) with respect to the previous stage. We did not consider gaps (intermittent stages in stratigraphic distribution) for calculating this metric.

**Chondrite.** A common type of stony meteorite.

**Chron.** Geologic time corresponding to a world-wide body of rock strata of specified primary magnetic polarity.

**Cratering.** Abiotic metric we use in Chapter 4 to predict variation in fossil richness. A measure of the frequency and magnitude of bolide impacts.

**Eustatic.** Related to global sea level change.

**Fourth order cycle.** Small scale fluctuation in eustatic sea level; thought to be the result of alternating glacial-interglacial cycles or alternating wet and dry (global) climatic conditions driven by variation in Earth's orbital geometry.

**Fullerenes.** Plural of fullerene. A family of carbon allotropes, also called buckyballs.

**Geodynamo.** Generation and regeneration of the Earth's magnetic field via convection of the liquid iron alloy in the outer core and a coriolis effect due to planetary rotation.

**Half-cycle.** According to our interpretation of coupled extinction and origination

## Glossary

intervals during the Phanerozoic, an extinction-origination cycle consists of an origination half-cycle and an extinction half-cycle. Typically, a half-cycle corresponds to one or more stratigraphic stages of the Harland time scale.

**ICS.** International Commission on Stratigraphy.

**Isolation.** The net effect of barriers to dispersal to a given area. Operationally, isolation has often been measured as the shortest distance over an uncolonizable intervening area (e.g., sea).

**Isostatic cycles.** Vertical, flotation movements among segments of the lithosphere.

**Jovian planets.** The four gas giants: Jupiter, Saturn, Neptune and Uranus.

**Kuiper Belt.** A zone of the Solar system extending from the orbit of Neptune (at 30 au) to a distance of 50 astronomical units from the Sun.

**Milankovitch cycles.** Cyclicity in glacial and interglacial ages, explained by variation in insolation via the wobbling of Earth's axis of rotation, shifting of the tilt of Earth's axis of rotation and variation in the eccentricity of Earth's orbit around the Sun.

**Neighbor index.** Metric we use to quantify the combined isolation-reducing effects of neighboring islands. High values indicate reduced isolation.

**Oort Cloud.** A postulated spherical cloud of comets beyond 50 astronomical units from the Sun.

**Orbital resonance.** Stable orbital resonance: the orbital periods of two or more celestial bodies are related by a ratio of integers.

**Period.** Major subdivision of geologic time. Its equivalent chronostratigraphic unit is a *system*.

**PTSC.** Acronym for the Phanerozoic time synchronization chart we present in Chapter 5 (pp. 211-212).

**RCO<sub>2</sub>.** Past/present ratio of atmospheric carbon dioxide.

**Regression.** Geologic event during which sea level falls, exposing sea bottom in shallow zones.

**SAR.** Species-area relationship.

**Series.** A chronostratigraphic unit of intermediate rank. Systems are

## Glossary

subdivided into series, and series are subdivided into stages. The temporal equivalent of a series is an *epoch*.

**Species richness.** The number of distinct species that occur in a defined area.

**Stage.** A chronostratigraphic unit of smaller scope. Phanerozoic systems are subdivided into series, and series are subdivided into stages. The temporal equivalent of a stage is an *age*.

**Superchron.** A long interval of geologic time ( $10^7$ - $10^8$  yrs), during which Earth's magnetic field apparently did not reverse.

**System.** Major chronostratigraphic subdivision. Its equivalent time unit is a *period*.

**Taphonomic.** Related to fossil preservation.

**Taxic.** Taxonomic.

**Transgression.** Geologic event during which sea level rises, flooding coastal areas.

**Transgressive-regressive sequences.** Stratigraphic pattern produced by cyclic rise and fall in sea-level, i.e. eustatic cycles

**Unconformity.** Gap in a stratigraphic sequence, caused by a temporal break in deposition, erosion or uplift.