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# The impact of the Pull of the Recent on the fossil record of tetrapods

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## ABSTRACT

**Question:** Why has there been an apparently exponential rise in the global diversity of life on land in the past 120 million years?

**Hypothesis:** Most of the apparent rise in diversity is an artefact of improved sampling towards the present day. A particular bias, the Pull of the Recent (POR), affects those fossil taxa with living representatives, by artificially inflating their numbers.

**Organisms:** The fossil record of tetrapods (amphibians, reptiles, mammals, and birds).

**Methods:** Compare lists of extant families and genera with totals and proportions that do, and do not, have fossil records in the Plio-Pleistocene.

**Results:** The POR extends its influence back to the early Eocene, accounting for at most 6.1% of the increase in tetrapod family diversity and 1.3% of generic diversity. Small animals, insectivores, and birds are most affected by the POR, perhaps because of their delicate skeletons.

**Conclusion:** The POR does not significantly distort the pattern of diversification, suggesting that the massive expansion of tetrapod biodiversity in the past 120 million years is largely a real biological pattern.

*Keywords*: biodiversity, diversity, fossil record, Pull of the Recent, tetrapods, vertebrates.

## INTRODUCTION

A key question in evolutionary biology concerns the origin of modern biodiversity: whether its current high richness was achieved 400–500 million years ago (Ma) and has remained steady ever since, or whether diversity expanded explosively in the past 100–150 million years (Myr). This divergence of opinion was highlighted 50 years ago, when Valentine (1968) argued that the empirical fossil record diversity data were reliable and showed continuing diversity increases since the Cambrian, and a four-fold expansion of marine generic diversity in the past 120 Myr, whereas Raup (1972) counter-argued that these rises were indications of biased sampling and that the number of marine families had remained more or less constant since the early Palaeozoic. These two viewpoints lead to profound differences in perception of macroevolution, Valentine's view allowing for continuing expansion and opportunism

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(Harmon and Harrison, 2015), and Raup's indicating a long-term, 400 Myr equilibrium in family diversity (Rabosky and Hurlbert, 2015). A key element of these discussions concerns the last 120 Myr, from the late Early Cretaceous and through the Cenozoic, the time when most of the increase is purported to have occurred; this is our focus here.

The empirical, or literalist, viewpoint is that the fossil record of all life, or all marine life, at global scale and at relatively high taxonomic level (e.g. families) shows a reliable pattern. Incomplete sampling and bias exist of course, but these are randomly scattered and overwhelmed or minimized by the scale of study. According to this view (Sepkoski *et al.*, 1981; Sepkoski, 1984; Benton, 1995; Benton *et al.*, 2000; Stanley, 2007), the diversity of marine families doubled and the diversity of marine genera quadrupled, and on land, raw terrestrial family diversity quadrupled (Benton, 1995; Sahney *et al.*, 2010). Taking account of scaling between levels in the taxonomic hierarchy, these increases might equate to multiplication of species numbers by five or ten times (Raup, 1975). Explosive radiation among vertebrates has also been identified in the interval from 150 to 100 Ma, based on analysis of evolutionary rates across synoptic molecular phylogenetic trees (e.g. Alfaro *et al.*, 2009; Meredith *et al.*, 2011; Rabosky *et al.*, 2013). These dramatic expansions in biodiversity are explained by major events in evolution, including the Mesozoic Marine Revolution [MMR (Vermeij, 1977)], a time in the sea when predatory behaviour and defences escalated, and the Cretaceous Terrestrial Revolution on land [KTR (Lloyd *et al.*, 2008; Vermeij and Grosberg, 2010; Meredith *et al.*, 2011)], when flowering plants diversified, followed by plant-eating, pollinating, and social insects and insect-eating lizards, birds, and mammals (Fig. 1). The MMR and KTR are identified at locality and regional scale, based on the replacement of particular clades and feeding modes by new clades with innovative feeding strategies, and so do not depend on the observation, or assumption, of explosive diversification from fossil-based data.

The alternative, bias, view (Raup, 1972; Alroy *et al.*, 2001, 2008; Alroy, 2010a, 2010b) is that all or most of these explosive expansions of raw palaeodiversity are a consequence of bias, the expectation that older rocks and fossils are less well preserved and sampled than more recent ones. In this view, biodiversity experienced its most dramatic expansions some 400–500 Ma in the sea, and subsequent rises are artefacts of improved preservation and improved sampling. Macroevolutionary phenomena such as the MMR and KTR are seen as important, but were accommodated generally within a steady total global diversity by the one-for-one, equilibrial replacement of taxa. Global biodiversity rebounded, but generally did not exceed, this equilibrium level following mass extinctions (Sepkoski, 1984; Alroy, 2010b). The apparent rises in biodiversity in the past 120 Myr are explained as a result of biased preservation, biased sampling, and the Pull of the Recent, a combination of factors that cause palaeontologists to overestimate diversity towards the present day (Raup, 1972).

The widespread finding of exponential patterns of increase for all terrestrial life (e.g. Benton, 1995; Eble, 1999; Kalmar and Currie, 2010), for angiosperms (Magallón and Castillo, 2009; Bell *et al.*, 2010), for insects (e.g. Nicholson *et al.*, 2014), and for tetrapods (e.g. Benton, 1995, 2001; Sahney *et al.*, 2010), especially in the past 120 Myr, could indicate a major difference between global diversification patterns on land and in the sea. Perhaps there is a cap to global carrying capacity in the oceans, but any such cap on land has yet to be reached (e.g. Eble, 1999; Benton, 2001). Equally, the huge expansion of teleosts, and teleost subclades (Alfaro *et al.*, 2009; Friedman and Sallan, 2012), as well as some other marine clades, might suggest that there has been no plateau to total marine diversity in the past 100–200 Myr.

A widely accepted view from the palaeontological side is that life has not diversified in the sea in the past 120 Myr (Alroy *et al.*, 2001, 2008; Alroy, 2010a, 2010b), and this position has

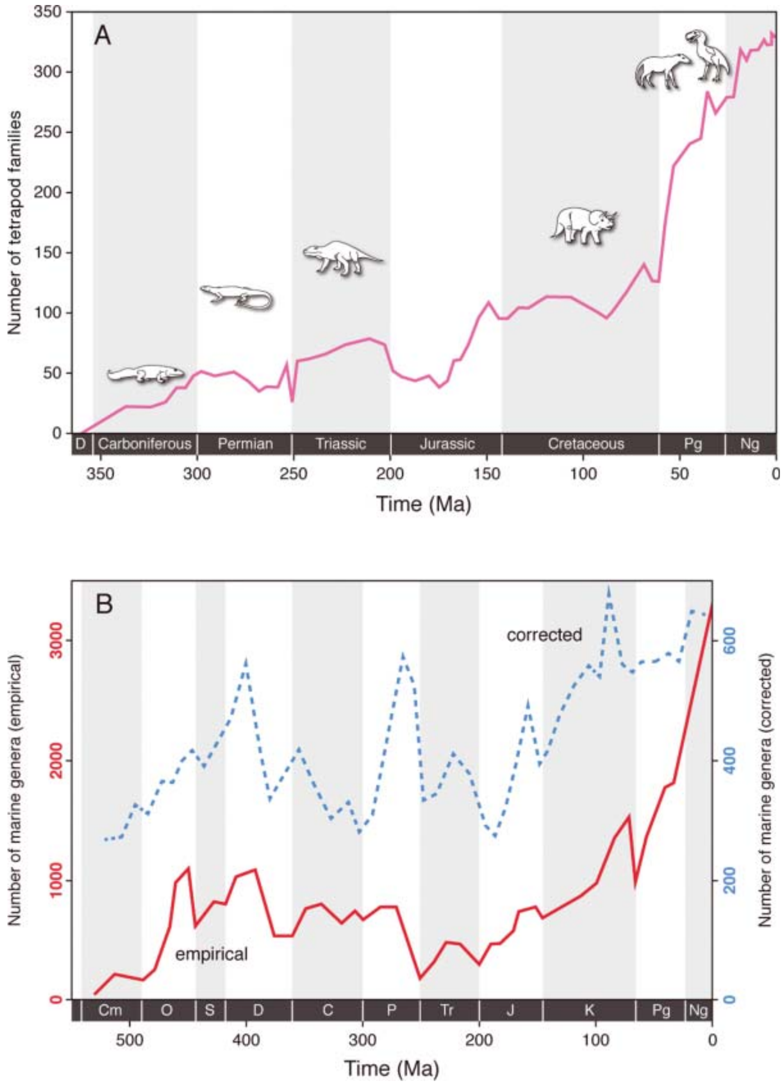

**Fig. 1.** Pattern of diversification through time for tetrapod families. The plot shows empirical data and sketch outlines of typical fossil taxa, highlighting the apparent four-fold increase in familial diversity in the past 100 Myr. *Abbreviations*: D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene. Based on Sahney *et al.* (2010).

been generalized to all life, including life on land. In the latter case, an equilibrial view can be sustained by positing breakthroughs and multiple logistic models to account for innovations and major diversity increases (e.g. Sepkoski, 1984; Alroy, 2010a). Phylogenomic data, on the other hand, show massive diversifications of some clades, additions of thousands of new species, without evident loss of competitors in order to maintain equilibrium. The past 120 Myr of global diversification, then, is important in seeking to discriminate between these very different world-views.

Here, we do not address the question of density-dependence and equilibrium models for global diversity (Sepkoski, 1984; Alroy, 2010a; Rabosky, 2013; Rabosky and Hurlbert, 2015) or the alternative, non-density-dependent, non-equilibrial view (Benton and Emerson, 2007; Stanley, 2007; Quental and Marshall, 2013; Harmon and Harrison, 2015). Our concern is whether the apparent diversity expansion of the past 120 Myr is real or not, and we focus on the bias and sampling arguments that it is not.

## BIAS AND THE PULL OF THE RECENT

Improved sampling includes geological and human aspects, such as preservation of aragonitic fossils and fossils in unlithified sediments (Alroy *et al.*, 2008; Sessa *et al.*, 2009) and more thorough sampling and more worldwide coverage of samples in the Cenozoic, and especially the Neogene, the past 23 Myr (Alroy *et al.*, 2008; Alroy, 2010a). In the case of the fossil tetrapods, considered here, questions of aragonitic fossils and lithified versus unlithified sediments are probably of little importance. On the other hand, there has doubtless been very variable sampling by age and location.

The 'Pull of the Recent' (POR) phenomenon (Raup, 1979) encompasses all the factors that improve our knowledge and counts of species towards the present day. It is to be distinguished from the 'Pull of the Present' (POP), which is a purely theoretical phenomenon, a property of the standard birth–death model of diversification, that gives rise to an apparently enhanced diversification rate towards the present (Etienne and Rosindell, 2012). The POR includes several aspects, but a key element concerns the use of range-through assessments of diversity (Fig. 2). Because the present day acts as an over-sampled horizon, it can artificially extend fossil range data backwards across unsampled intervals (gaps). In other words, if fossils of a particular species or genus are rare, the recorded stratigraphic range may be too short; if, however, the rare fossil taxon has living representatives, the range can be extended across the intervening gap, however long that gap might be (Raup, 1972, 1979; Jablonski *et al.*, 2003). An extreme case would be, for example, the Family Latimeriidae, for which the last fossil is *Macropoma* from the Late Cretaceous; the chance survival of the living coelacanth *Latimeria* allows the gap of 70 Myr to be bridged. *Latimeria* occurs in limited locations and so might be unlikely to be fossilized or to be found as a fossil, and so this case shows an extreme example of the gap-bridging bias.

Apart from this range-through, gap-bridging bias, the POR also involves a subsidiary aspect, that palaeobiologists may be biased by comparisons of Neogene fossils with extant taxa, and so could over-split the fossil species in line with those living taxa, rather than adopting a more conservative approach to species numbers. On the other hand, in some cases, palaeobiologists might be biased in under-emphasizing Neogene biodiversity by attempting to shoehorn fossil taxa into living species; this would artificially extend their stratigraphic ranges back in time, but at the same time could reduce estimated species counts.

Palaeontologists have used various means to counter these aspects of the POR. For example, Sepkoski (1984) and Alroy *et al.* (2001, 2008) excluded all living taxa and all fossil representatives of living taxa from their diversity plots. This certainly avoids the influence of living taxa on range extensions and on taxonomic practice, but the procedure itself biases counts of species and genera by removing a large sector of Neogene biodiversity without compensation, and so is guaranteed to remove much of any rise in diversity, whether the adjustment is justified or not.

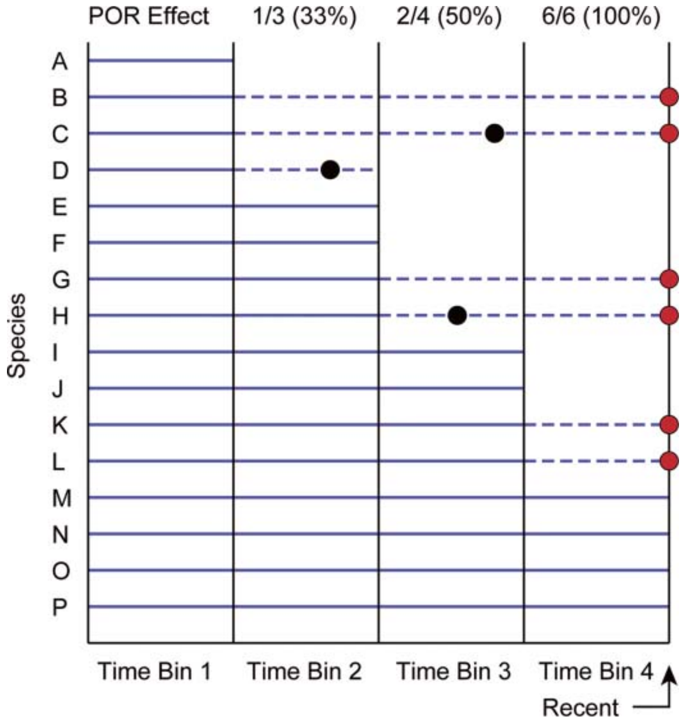

**Fig. 2.** Illustration of the Pull of the Recent effect. Here we have 21 hypothetical species (A to P), showing their stratigraphic ranges through four time bins. The known fossil records are shown by solid lines, inferred fossil records by dashed lines. Isolated fossils are scattered through time bins 2 to 4, but those in time bin 4 represent the present day. Isolated fossils confirm the presence of three of the inferred lineages, whereas modern individuals confirm six in total. The POR effect is enumerated along the top, as the number of lineages inferred from fossils alone/number inferred from extant taxa. If the POR effect is substantial, there should be many lineage extensions to the present day inferred solely from modern representatives (such as species B, G, K, L). If the POR effect is modest, those spans to the present day ought to include one or more fossils (such as species C, D, H).

The range-through POR problem is easier to explore (Jablonski *et al.*, 2003). One solution (Alroy, 2010a) is to use sampled-in-bin counts only. Diversity then reflects exact counts of what has been found in a time bin and makes no assumptions about any taxa that might span the time bin. Raup (1972) noted this distinction, and argued that the use of range-through taxa would mask times of poor sampling. However, in attempting to understand patterns of diversity change through time, excluding data removes signal. Furthermore, as often noted (e.g. Fara, 2001; Smith, 2007), range-through counts provide positive evidence of missing data by identifying Lazarus taxa, and so can correct for short-term poor sampling, such as when one time bin among many is massively undersampled.

Perhaps the POR has been overestimated, and previous data manipulations to escape its effects (e.g. Sepkoski, 1984; Alroy *et al.*, 2001, 2008) have removed real signal at the same time. The key question is: how many fossil taxa with living representatives exhibit the POR effect? Jablonski *et al.* (2003) found that the POR accounts for 5% of the Cenozoic increase in bivalve diversity. Here we explore the family and genus-level richness of the Tetrapoda, a clade of around 30,000 living species. Tetrapods are ideal candidates for identifying the potential bias of the POR, since they have a well-studied fossil record, the present-day diversity of the group is well known, and the palaeodiversity trend through the Phanerozoic is an exponential rise, a pattern that could indicate POR bias.

## MATERIALS AND METHODS

We evaluate the effect of the POR on tetrapods by identifying taxa that have both living and extinct representatives, then finding the youngest fossil occurrences of each taxon and seeing how many of these taxa leapfrog recent geological stages to the present. The aim is to test how often the occurrence of living relatives of fossil forms would artificially plug gaps in the fossil record. We examined multiple databases and compilations of extinct and extant taxa (www.evolutionary-ecology.com/data/3004Appendix.pdf), and surveyed primary literature to determine which living tetrapod families and genera lack fossil occurrences in the Plio-Pleistocene (the past 5.3 Myr), following previous methods used in a study of the impact of the POR on the fossil record of bivalves (Jablonski *et al.*, 2003). We considered both families and genera because tetrapod taxa had shorter durations than bivalves, and the two may behave differently: families are likely to contain more sampled specimens than genera, but genera are shorter-lived than families. We did not run the analysis at species level because there is considerable debate about the validity of many Neogene species of tetrapods compared with extant forms, and we wished to avoid such uncertainties. In addition, the majority of published diversity-through-time studies based on the fossil record have been conducted at family or genus, and not species, level.

The impact of the POR varies across hierarchical taxonomic levels in proportion to their mean temporal duration. Families of tetrapods in general have had longer durations than genera, and genera longer durations than species. This means that temporal ranges of families may encompass longer gaps than those of genera, and especially of species. Equally, short-lived taxa such as species may not be found at all if sampling is poor. Furthermore, following Jablonski *et al.* (2003), we use the Plio-Pleistocene, the past 5.3 Myr, as our POR sampling interval, and few species would span that interval.

The familial and generic taxonomic levels have advantages over species in several ways: (1) a large number of tetrapod workers have carried out repeated revisions of families and higher clades in the context of cladistic phylogeny, so there is a greater consensus on the nature of these categories and counts, hence families are subject to fewer errors and controversy than lower taxonomic levels, especially species; (2) independent analyses of tetrapod relationships using molecular data suggest that our broad understanding of the fossil record is reasonably complete (Benton, 1990; Patterson *et al.*, 1993; Benton *et al.*, 2000); (3) the family and generic records are more complete than the species records and new discoveries tend to enhance our understanding of the diversity of life, not change it radically (Benton and Storrs, 1994); (4) families and genera are less susceptible to irregular and biased sampling than species, so evolutionary signal is better maintained at this level; (5) families and genera have longer records and are typically widespread (species are short-lived and often confined to a single stage of geologic time); and (6) using families and genera allows less robust or questionable entities to be removed from analysis (e.g. monotypic species, species based on limited material).

A total of 1034 extinct and extant tetrapod families were initially tabulated. One-third of these families (355) are extant and 46 are only recorded in the present day. The remaining

309 extant families have a fossil record (Table 1). The 33,091 living species of tetrapods are divided into 5030 genera, of which only 757 have a fossil record (Table 2), according to the Paleobiology Database (PaleoDB). Thus 309 tetrapod families and 757 tetrapod genera form the database for this study.

Families and genera that generate a POR effect were identified by first consulting the PaleoDB, and then the wider literature. Raw data were extracted from the PaleoDB, and POR taxa were identified by checking the PaleoDB fossil families and genera against standard lists of extant tetrapods and noting those fossil forms with extant representatives (3004Appendix). Then, knowing that the PaleoDB does not yet report all fossil data, we pursued primary literature for each tentative POR taxon, and determined whether there truly was a Plio-Pleistocene gap or not. The geological time scale employed was Gradstein *et al.* (2012). Full details of the data are given in 3004Appendix.

The PaleoDB, which was the initial reference source for data, represents current knowledge to varying degrees: it is especially good for Cenozoic mammals, largely thanks to the work of John Alroy, Mark Uhen and others, but representation of other tetrapod groups (birds, crocodilians, lepidosaurs, turtles, lissamphibians) is incomplete. It cannot be estimated what proportion of the fossil records of these groups is represented by current records in the PaleoDB. Nonetheless, there is no reason to assume that the PaleoDB would under- or over-sample Plio-Pleistocene records compared with other Neogene or Cenozoic publications.

## Family-level database

The stratigraphic distribution of fossil mammals was initially taken from the *Fossil Record 2* (Benton, 1993) and narrowed to a database of tetrapod families with extinct and extant representatives. The PaleoDB (Alroy, 1998–2015) and primary literature were checked for

**Table 1.** Differences between modern and fossil record estimates of tetrapod biodiversity, assessed at the family level

| Clade | Mammalia | Aves | Reptilia | Amphibia | Total |
|---|---|---|---|---|---|
| Number of living families | 128 | 146 | 45 | 36 | 355 |
| Number of fossil families | 331 | 214 | 323 | 109 | 987 |
| Number of living families with a fossil record | 120 | 127 | 41 | 21 | 309 |
| Number of living families with a Plio-Pleistocene fossil record | 118 | 114 | 37 | 21 | 290 |
| Number of POR families[a] | 2 | 13 | 4 | 0 | 19 |
| % POR families[a] | 1.7 | 10.2 | 9.8 | 0 | 6.1 |
| Kendall's tau[b] | 0.9758 | 0.9490 | 0.4484 | 0.9835 | 0.9313 |
| Two-sided *P*-value | 0.0000 | 0.0000 | 0.0196 | 0.0000 | 0.0000 |

[a] POR = Pull of Recent; these are families that have a Cenozoic fossil record, but lack fossil representatives in the past 5 Myr (Pliocene; Pleistocene), and so potentially show the POR bias, namely the advantage of living taxa in indicating missing data.

[b] Kendall's tau measures the likelihood that the palaeodiversity curves with and without POR taxa are the same, possibly different or definitely different; here all are highly similar with the exception of reptiles ($P < 0.0001$). The impact on reptiles is greater because their fossil record has plateaued since the Aquitanian, with a net increase of just two families.

**Table 2.** Differences between modern and fossil record estimates of tetrapod biodiversity, assessed at the generic level

| Clade | Mammalia (31, 32) | Aves (16) | Crocodylia (17) | Lepidosauria (17) | Testudines (17) | Lissamphibia (18) | Total |
|---|---|---|---|---|---|---|---|
| Number of living species | 5416 | 10426 | 23 | 9766 | 328 | 7132 | 33091 |
| Number of living genera | 1229 | 2229 | 8 | 960 | 94 | 510 | 5030 |
| Number of fossil genera[a] | 3960 | 515 | 39 | 121 | 170 | 95 | 4900 |
| Number of living genera with a fossil record[b] | 440 | 168 | 6 | 64 | 44 | 35 | 757 |
| Number of POR genera from PaleoDB[c] | 20 | 5 | 0 | 13 | 8 | 1 | 47 |
| % POR genera from PaleoDB[c] | 4.5 | 3.0 | 0 | 203 | 18.2 | 2.9 | 6.2 |
| Number of POR genera, actual | 5 | 1 | 0 | 2 | 2 | 0 | 10 |
| % POR genera, actual | 1.1 | 0.6 | 0 | 3.1 | 4.5 | 0 | 1.3 |
| Kendall's tau[d] | 0.999 | 1.000 | 1.000 | 1.000 | 0.999 | 1.000 | 1.000 |
| Two-sided $P$-value | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 |

[a] Fossil genera: numbers of fossil genera from the Cenozoic (last 66 Myr) only, as listed in the PaleoDB.

[b] These are based only on the PaleoDB, with minimal correction (omitted Plio-Pleistocene taxa), and there may be many more extant taxa with a fossil record not yet included in the PaleoDB.

[c] POR = Pull of Recent; these are genera that have a Cenozoic fossil record, but lack fossil representatives in the past 5 Myr (Pliocene; Pleistocene), and so potentially show the POR bias, namely the advantage of living taxa in indicating missing data.

[d] Kendall's tau measures the likelihood that the palaeodiversity curves with and without POR taxa are the same, possibly different or definitely different; here all are identical at very high significance ($P < 0.0001$).

Plio-Pleistocene occurrences of these families, narrowing down the list of tentative POR taxa to 24 in 2011 and 19 when updated in 2013. A full listing of primary literature can be found at: http:palaeo.gly.bris.ac.uk/data/tetrapodsPOR.html. Furthermore, experts on these families were consulted to confirm whether there was indeed a Plio-Pleistocene gap. The families affected by the POR are listed below together with their last known fossil occurrence.

## Mammalian generic-level database

The stratigraphic distribution of fossil mammalian genera was downloaded from the PaleoDB (Alroy, 1998–2015) on 30 May 2013, showing stratigraphic distributions of 3960 genera with a fossil record to epoch level (including Early and Late Pliocene, and Early, Middle, and Late Pleistocene). These genera were checked against the complete listing of extant mammal species in Wilson and Reeder (2005) and PanTHERIA (Jones *et al.*, 2009) to identify those genera with living representatives. Twenty of the 440 living genera with a fossil record

(4.5%) had distributions that apparently leapfrogged the Pliocene–Pleistocene interval, occurring typically in the late Miocene, then the present day (including sometimes, the Holocene), but with no intervening fossil record. These taxa could contribute to the POR bias. However, on checking the standard database on fossil and modern mammals (McKenna and Bell, 1997), 15 of those 20 POR taxa turn out to have Pliocene or Pleistocene fossil records, which have not yet been included in the PaleoDB.

Five true POR mammalian genera are extant with fossil records extending up to the end of the Miocene, but not in the Plio-Pleistocene. These are the rodents *Anomalurus*, *Platacanthomys*, *Ratufa*, and *Zenkerella*, and the primate *Tarsius*. The remaining 15 genera were apparently POR taxa, but have a Plio-Pleistocene fossil record that is not entered in the PaleoDB. They are the marsupials *Chironectes*, *Hypsiprymnodon*, and *Pseudochirops*, the insectivore *Scaptonyx*, the bats *Asellia*, *Macroderma*, *Noctilio*, and *Scotophilus*, the rodents *Calmoyscus*, *Dremomys*, *Hylomys*, *Hylopetes*, and *Tamiops*, the artiodactyl *Catagonus*, and the carnivore *Hydrurga*.

## Avian generic-level database

Avian phylogeny was checked using Aves (Boyd, 2008–2009) and the stratigraphic distribution of fossil birds was downloaded from the PaleoDB (Alroy, 1998–2015) on 30 May 2013, showing stratigraphic distributions of all 515 included genera with a fossil record to epoch level (including Early and Late Pliocene, and Early, Middle, and Late Pleistocene). These genera were checked against lists of fossil (Olson, 1963–1978; Ruhe, 1993–2002; Brodkorb, 1995–2013; Public Authorship, 2006–2013) and extant bird species (Gill and Wright, 1991–2013; Lepage, 2003–2013) (2229 genera; 10,426 species) to identify those genera with living representatives. Five of the 168 living genera with fossil records (3.0%) had distributions that apparently leapfrogged the Pliocene–Pleistocene interval, occurring typically in the Late Miocene, then the present day, but with no intervening fossil record. These taxa could contribute to the POR bias. However, on checking the primary literature, four of those five POR taxa turn out to have Pliocene or Pleistocene fossil records that have not yet been included in the PaleoDB.

The single true POR avian genus is the crane (gruiform) *Balearica*. The remaining four genera were apparently POR taxa, but have a Plio-Pleistocene fossil record that is not entered in the PaleoDB. They are the heron (ciconiiform) *Ardeola*, the procellariiforms (gulls) *Diomedea* and *Oceanodroma*, and the accipitriform (eagle) *Geranoaetus*.

## Crocodylian generic-level database

Of the 23 living species and eight living genera of crocodilians, two genera (*Paleosuchus* and *Melanosuchus*) lack a fossil record and the remaining six all have Plio-Pleistocene occurrences recorded in the PaleoDB, hence there are no POR genera.

## Lepidosaurian generic-level database

The stratigraphic distribution of fossil lepidosaurs (snakes, lizards, rhynchocephalians) was downloaded from the PaleoDB (Alroy, 1998–2015) on 30 May 2013, showing stratigraphic distributions of 121 genera with a fossil record to epoch level (including Early and Late Pliocene, and Early, Middle, and Late Pleistocene). These genera were checked against the complete listing of extant lepidosaur species in The Reptile Database (Uetz *et al.*, 1995–2013)

(960 genera; 9766 species) to identify those genera with living representatives. The 9766 species of living lepidosaurs include 5796 species and 470 genera of lizards (Sauria), 184 species and 24 genera of amphisbaenians (Amphisbaenia), 3432 species and 489 genera of snakes (Serpentes), and one species and one genus of sphenodontid (Rhynchocephalia).

Thirteen of the 64 living genera with a fossil record (25%) had distributions that apparently leapfrogged the Pliocene–Pleistocene interval, occurring typically in the Late Miocene, then the present day, but with no intervening fossil record. These taxa could contribute to the POR. However, on checking the primary literature, 11 of those 13 POR taxa turn out to have Pliocene or Pleistocene fossil records, which have not yet been included in the PaleoDB.

The two true POR lepidosaurian genera are the iguanian lizard *Polychrus*, which has a middle Eocene fossil record and the extant boid snake *Eunectes*, which has a late Miocene fossil record. The 11 genera that were apparently POR taxa, but have a Plio-Pleistocene fossil record that is not entered in the PaleoDB are the chamaeleonid *Chamaeleo*, the agamid *Uromastyx*, the boids *Boa*, *Epicrates*, and *Eryx*, the filesnake *Acrochordus*, the vipers *Trimesurus* and *Tropidoclonion*, the blind snake *Typhlops*, and the colubrid *Telescopus*.

## Testudine generic-level database

The stratigraphic distribution of fossil turtles was downloaded from the PaleoDB (Alroy, 1998–2015) on 30 May 2013, showing stratigraphic distributions of 170 genera with a fossil record to epoch level (including Early and Late Pliocene, and Early, Middle, and Late Pleistocene). These genera were checked against the complete listing of extant turtle species in The Reptile Database (Uetz *et al.*, 1995–2013) (94 genera; 328 species) to identify those genera with living representatives.

Eight of the 44 living genera with a fossil record (18.2%) had distributions that apparently leapfrogged the Pliocene–Pleistocene interval, occurring typically in the Late Miocene, then the present day, but with no intervening fossil record. These taxa could contribute to the POR bias. However, on checking the primary literature, 13 of those 15 POR taxa turn out to have Pliocene or Pleistocene fossil records that have not yet been included in the PaleoDB.

The two true POR turtle genera are *Aspideretes* and *Dermatemys*. The eight genera that were apparently POR taxa, but have a Plio-Pleistocene fossil record that is not entered in the PaleoDB are *Chelus*, *Cuora*, *Cycloderma*, *Dermochelys*, *Lissemys*, *Ocadia*, *Phrynops*, and *Rhinoclemmys*.

## Lissamphibian generic-level database

The stratigraphic distribution of fossil lissamphibians was downloaded from the PaleoDB (Alroy, 1998–2015) on 30 May 2013, showing stratigraphic distributions of all 95 included genera with a fossil record to epoch level (including Early and Late Pliocene, and Early, Middle, and Late Pleistocene). These genera were checked against the complete listing of extant lissamphibian species in AmphibiaWeb (Hero, 2000–2013) (510 genera; 7132 species) to identify those genera with living representatives. The 7132 species of living amphibians include 6292 species (466 genera) of anurans (frogs and toads), 648 species (68 genera) of caudatans (salamanders), and 192 species (35 genera) of gymnophionans (caecilians).

Only one of the 35 living genera with a fossil record (2.9%) had a distribution that apparently leapfrogged the Pliocene–Pleistocene interval, and so could contribute to the POR bias. This taxon, *Lechriodus*, indeed has a Pliocene or Pleistocene fossil record, which has not yet been included in the PaleoDB.

## RESULTS

Among extant tetrapod families, 309 have a fossil record (21 amphibians, 41 reptiles, 120 mammals, and 127 birds). Of these 309 families, 290 have fossil occurrences in the Pliocene or Pleistocene. The POR thus affects 19 extant tetrapod families with a fossil record (6.1%), specifically 0% of amphibians, 9.8% of reptiles, 1.7% of mammals, and 10.2% of birds (Table 1). Hence, the POR has only a small influence on the observed rise in tetrapod biodiversity, especially through the Cenozoic (Fig. 3).

The effect of the POR at generic level is even more modest (Fig. 4; Table 2). Although the PaleoDB indicated 47 POR taxa in all (6.2% of 757 genera), checking of current literature (3004Appendix) reduced this to 10 POR taxa (1.3%), with small numbers distributed over mammals, birds, lepidosaurs and turtles, and none for crocodilians and lissamphibians. In a cumulative plot for all tetrapods through the Cenozoic (Fig. 4A), Plio-Pleistocene mammals are particularly well documented in the PaleoDB. Comparison of the totals for all data and data without the POR bias for all tetrapods (Fig. 4B) and for mammals only (Fig. 4C) shows a negligible statistical effect.

## DISCUSSION

It is probable that the POR bias diminishes with detailed study. For example, the POR was believed to distort the shape of marine invertebrate palaeodiversity significantly, with almost half of genera affected (Sepkoski, 1997). However, further exploration of the data, for bivalves at least, showed that this was mostly the result of errors and unresolved taxonomies in the original database; when these were corrected, the effect of the POR dwindled to 9%, and then to 5% when more recently discovered taxa were added (Jablonski *et al.*, 2003).

In the case of tetrapods, a similarly small number of taxa are affected, and the POR does not extend deep in time. At family level, the POR extends back to the Ypresian; it affects 1.6% of families in the Eocene, 0.3% of families in the Oligocene, and 4.2% of families in the Miocene (Fig. 3). Overall, the POR does not significantly affect the shape of the synoptic tetrapod familial diversity curve, and importantly, the peaks and troughs are not removed. Similarly, the POR affects tetrapod genera only in the Cenozoic, also back to the Ypresian, but predominantly in the Miocene, and the effect is small, impacting on 1.3% of fossil genera (Figs. 4B, C). As expected, the POR affects families more because in general a family has a longer stratigraphic range than a genus, and thus is more likely to extend deeper in time. With a patchy fossil record, a long-spanning family is more likely to include a 5 Myr gap in its record than a shorter-lived genus. Another observation is that the POR effect increases towards the present (Fig. 4); this is expected because late fossil occurrences will pull early time ranges forward whereas the reverse is not true.

Since only 19 families and 10 genera of tetrapods are affected by the POR, statistical analysis of biases against particular ecomorphs defined by habitat, diet, and body size cannot be conducted, but some general patterns are observed. The familial data indicate that birds are most affected by the POR (10%), perhaps because of their delicate skeletons

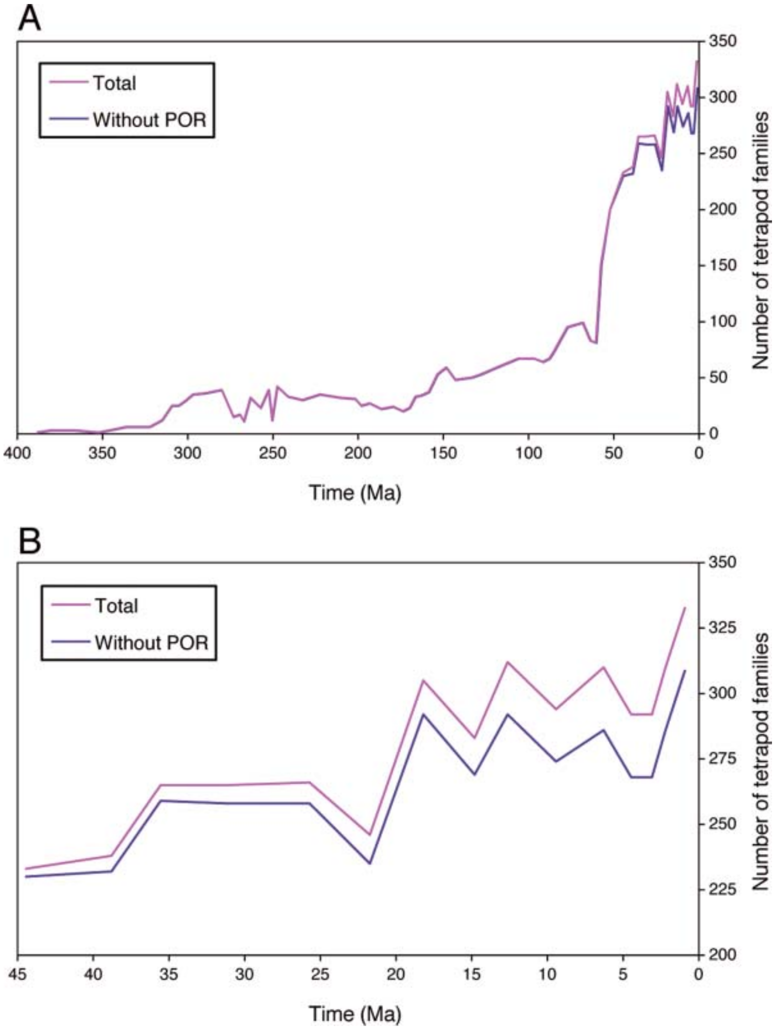

**Fig. 3.** Biodiversity of tetrapod families with and without the Pull of the Recent (POR) through the Phanerozoic (A) and the Cenozoic (B). The POR has affected tetrapod biodiversity since the Lutetian, 45 Ma. Data are summarized and statistical comparisons of curves are given in Table 1. Full data and the references used to compile the family-level data can be found in 3004Appendix.

and their recognized patchy fossil record (Fountaine *et al.*, 2005; Brocklehurst *et al.*, 2012). All affected taxa are small to medium in size (snout–vent length < 150 cm), except the family Sagittariidae and the boid snake genus *Eunectes*. Sagittariidae is represented today by the large Secretary bird and by much smaller fossils from the Oligocene and Miocene of France (Mourer-Chauviré and Cheneval, 1983), but nothing in between. Size is a bias of the POR for marine bivalves (Jablonski *et al.*, 2003) and for completeness of the fossil record in general (Cooper *et al.*, 2006): future discoveries of new Pliocene and Pleistocene fossils may be predominantly animals with small, fragile skeletons. Half of affected families are insectivores, and only two taxa are carnivores (Sagittariidae, *Eunectes*), although the diets of their ancestors are

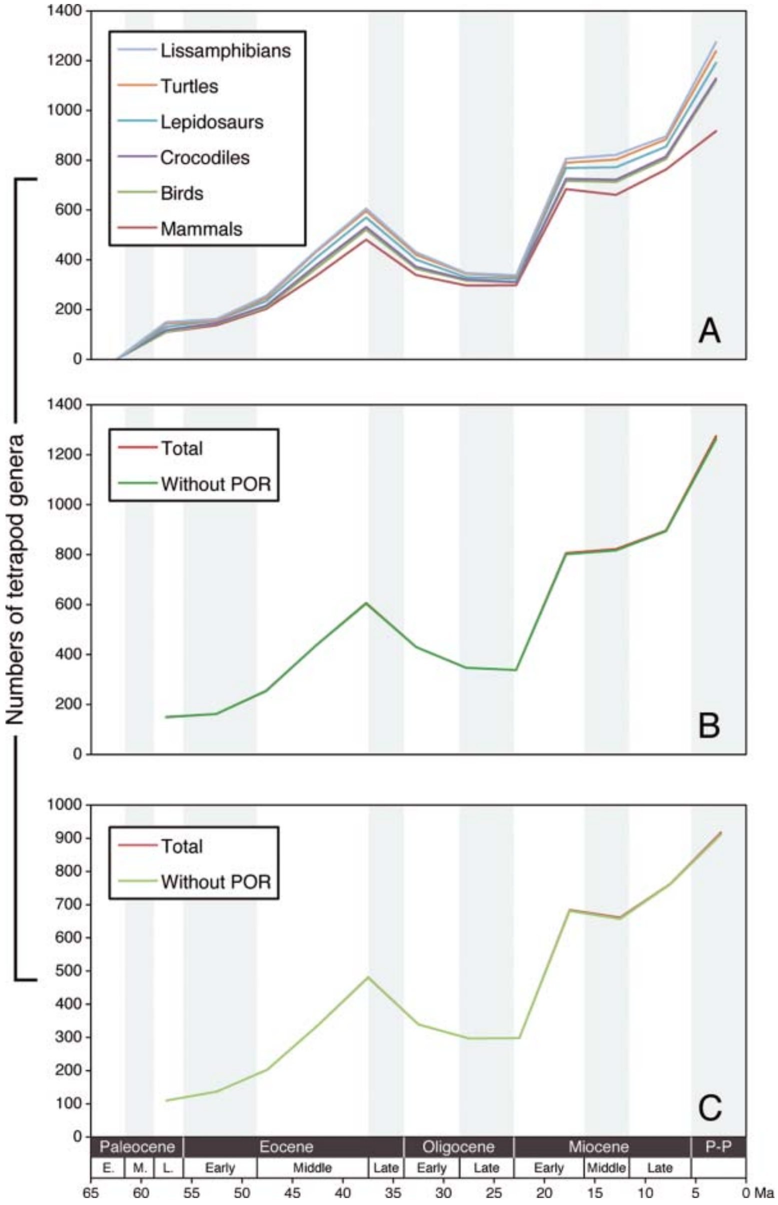

**Fig. 4.** Genus-level diversity of tetrapod genera through the Cenozoic. The plots show cumulative empirical measures from the PaleoDB for the major clades (A), and palaeodiversity with and without the Pull of the Recent (POR) for all tetrapods (B) and for mammals only (C), since only mammals are substantially documented in the PaleoDB. Full data and statistical comparisons of curves are given in Table 2. In (B) and (C), the differences between data with and without POR taxa are so small as to be invisible.

uncertain (Mourer-Chauviré and Cheneval, 1983). Most carnivores are medium to large animals and so likely to be preserved in the fossil record, whereas most insect-eating tetrapods are small, so the POR bias by diet may be the same as the size bias.

This does not mean that the massive explosion of terrestrial, and tetrapod, biodiversity in the past 100–150 Myr is now demonstrated to be real. The other potential biasing factors, such as improved fossil preservation and improved fossil discovery (sampling) have not been assessed independently. Indeed, it is hard to evaluate the influence of improved sampling on empirical palaeodiversity measures through time because there is no independent yardstick against which to compare the rock and fossil records (Smith, 2007; Benton *et al.*, 2011; Dunhill *et al.*, 2014; Benton, 2015). As the numbers of fossil samples, fossiliferous localities, and geological formations increase towards the present, so too do the raw measures of palaeodiversity (Benton, 2015). For example, treating the formation count as an independent metric of sampling (e.g. Peters and Foote, 2001; Barrett *et al.*, 2009) ignores the fact that palaeodiversity and formation counts are massively redundant for sparsely occurring taxa such as dinosaurs: the two metrics are closely linked as fossils accrue through research time, so they are highly correlated, but that is not proof that sampling drives palaeodiversity (Benton *et al.*, 2011, 2013; Benton, 2015). This problem with formation counts had been noted before (e.g. Crampton *et al.*, 2003; Smith, 2007), and these authors also highlighted the extreme variability of formation definitions, which are dependent on rock heterogeneity, fossil abundance, and regional customs. Map outcrop areas might be a better measure of sampling opportunity (Crampton *et al.*, 2003; Smith and McGowan, 2007; Wall *et al.*, 2009; Dunhill *et al.*, 2014), although map areas do not always indicate areas of available rock exposure (Dunhill, 2011, 2012). In any case, sampling is scalar: thousands of new specimens from a geological time bin may increase species or generic diversity by only modest amounts.

Covariation between fossil and rock time series, even if the two metrics are not redundant with one another, need not indicate bias. Indeed, rock volume and area do not increase through the past 120 Myr (Smith, 2007), and cannot explain the massive rises in palaeodiversity (Smith and McGowan, 2007). Furthermore, for the marine fossil record at least, rises in outcrop areas and palaeodiversity are plausibly explained by the common cause model (Peters, 2005; Hannisdal and Peters, 2011), a kind of species–area effect that links increases and reductions in marine shelf area with rises and falls in diversity. Under this interpretation, both the rock record and fossil record are treated as reasonably reliable, at least for large-scale inferences.

Undoubtedly there are gaps in the fossil record, especially at low taxic levels, but it has yet to be demonstrated that bias and sampling distort the fossil record of skeletonized organisms in a substantial way. There is no reason to believe that the POR has significantly influenced the shape of synoptic palaeodiversity patterns tabulated from the tetrapod fossil record. This conclusion provides support for the suggestion that the massive expansion of the diversity of tetrapods in the past 120 Myr is reasonably accurate (Benton and Storrs, 1994; Benton *et al.*, 2000, 2011; Kalmar and Currie, 2010) and that the effect of the Pull of the Recent is modest and cannot be used as evidence that the rise is artificial.

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