University of Reading

The evolutionary paths to diversity

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This thesis is dedicated to the ancestors of my own lineage

To Charles Sharp - with whom I would have loved to discuss all this – and to his wife Anne-Marie, their daughter Leonie Lazarus and grand-daughter Corinne O'Donovan. To Margaret 'Peggy' O'Donovan – who prayed for so many years - and to her husband John and their son Bryan O'Donovan.

The apple never falls far from the tree

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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Abstract

At the heart of diversity lies evolution, a continually acting process that has shaped and honed the enormous variety of life forms on Earth. To study evolutionary tempos and modes at a high resolution this thesis uses ancestral state reconstruction. This powerful, statistical method works within the framework of a novel, phylogenetic model which flexibly embraces the temporal and taxonomic complexity of the evolutionary process. Consistently across geographical and morphological data covering a wide range of species from dinosaurs to angiosperms to fish, evolutionary mode is broadly characterised by an overwhelming majority of negligible and small sized changes, interspersed with comparatively rare, exceptionally large ones. However, importantly, evolution is shown to work on a continuous scale without such categorical distinction. At a finer level, the magnitude of evolution's steps differs depending on the direction of change being selected for, organisms' biological history and the environment an organism evolves in. Changes to morphology of an exceptional magnitude have contributed to the process of undergoing major evolutionary transitions such as those seen in cetaceans and bats. These exceptional changes also differentially affect speciation and body size evolution depending on the nature of an organism's environment. The signatures of evolutionary and ecological processes through time are revealed, for the first time showing that global scale movement across a famous evolutionary radiation universally follows an early burst pattern, moderated by speciation. On a larger temporal and taxonomic scale evolutionary changes increase in magnitude constantly through time suggesting that despite physical space filling up, there is no limit to evolutionary potential or to the diversity it creates. Current results spanning varying scales are viewed in the light of historical concepts of adaptive landscapes with leaps between and within peaks and zones, and are reconciled within the framework of this complex biological paradigm.

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"*It doesn't matter how you get from A to B, so long as you get there!*"
Chris Venditti, (2014)[1]

Without doubt my first thanks go to Chris Venditti without whom I would not have attempted a PhD, less, completed one. He has worked patiently and tirelessly to teach me how to conduct new and exciting research. Chris has listened to talks being practiced, viewed posters, convinced me to face the worlds of statistics and learning R and has stood by me throughout, even on the hardest of days. He has been committed to me as a student and has been a truly wonderful supervisor and friend, both of which must have been challenging at times. He has nurtured my interests, both allowing and facilitating work that I could never have been more captivated by. Through his hard work primarily, I have become a scientist and I feel grateful, honoured and lucky to have been able to spend the last four years working so closely with him.

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[1] Venditti, C. (2014). *Personal communication.*

means least George Butler. These people have been important and wonderful figures both within and outside of the office environment.

The last four years has encompassed a whole spectrum of life ranging from the extremes of happiness to those of being less so. Throughout all of this my family and friends have surrounded me with support and encouragement, reminding me that it will all be okay in the end. They have repeatedly forgiven my long absences both physical and emotional and continue to stand by me, cushioning my falls and championing my successes. My parents, grandmother and godmother have been unflappable constants, offering unbounded measures of love, kindness and help, all of which I have called upon and could not have done without. They have talked me down from hysteria and guided me through times when things felt insurmountable. Making these four incredible family members proud has been a major source of motivation. Mention must specifically also go to Pri and Charlotte – better friends than anyone could dream of. Late night conversations, daily messages, visits and prosecco drinking, they too have been constant figures in my life with the last few years being no exception. I am so grateful to them for their warmth and love, for always being there, always helping and always knowing what to say to make things better. They have never failed to bring laughter, comfort and pure happiness to my life. I feel honoured and lucky to have a support network that has the strength of steel and which has made me feel encircled by friends, some of whom need to be named are Tilly, Rachel, Jo R, Sue, Anna, Emily, Shef, Frankie, Sally and Margery. These friends have protected me, anchored me and reminded me of who I am during times when I was lost, or at least felt that way. They have sent words of support and motivation along with crazy photos and videos that always make me laugh; collectively and individually they are my home.

Over the last four years I have adapted and evolved in wonderful and unexpected ways and certainly more resemble an animal suited to the academic environment now than four years ago. I have been spoilt with the knowledge and expertise that have surrounded me. In addition to this, I have learnt my own strength and resilience in the face of personal and academic adversity. These years provide my foundation as an adult and as a scientist who can move forward and stand on the shoulders of giants. To the eleven year old girl who wanted to be 'a scientist' when she grew up, with the help of everyone mentioned and more, we have done it!

Contents

Introduction

"*From so simple a beginning endless forms most beautiful and most wonderful have been and are being evolved.*"
Charles Darwin, (1859)[1]

The diversity of nature

Life began in a 'primordial soup' (Oparin, 1924; Haldane, 1929; Miller, 1953) approximately four billion years ago (Betts *et al.*, 2018) and from this simple existence, a vast diversity of varying forms has arisen. Purple bacteria with tails and green glowing fungi, intricate leafy sea dragons, enormous oak trees, miniscule leaf chameleons, flying dinosaurs (birds) and giant insects; the natural world is, and always has been, an immense collection of shapes, sizes and colours. Vertebrates alone, which make up but a small fraction of the tree of life show variation in their body size which spans an astonishing five orders of magnitude; from the minute frog species *Paedophryne amauensis* at 7.9mm long (Rittmeyer *et al.*, 2012) up to the blue whale *Balaenoptera musculus* which on average grows to a length of 25.8m (Branch *et al.*, 2007). Delving deeper, beyond just visual diversity, there is variation in other features of nature given that morphologies are underlain by a wealth of behaviours, physiologies and ultimately genetic variation. At a larger scale too, ever since life arose, there has been variation in features of nature such as how many species there are and which species go extinct. It is exactly this bewildering amount of variation which piques the interests of biologists and results in questions being formulated and tested such as, why are there hundreds of thousands of beetle species but fewer than five species of elephant? Why did the dinosaurs finally go extinct after the impact of the Chicxulub asteroid and yet the mammals did not? To answer questions such as these raises others, perhaps more complex to test and answer, such as what is a species? None of these questions however are new. Biologists and natural historians have been asking similar ones for hundreds of years. Ultimately, they all boil down to the same, fundamental question, of how has the diversity that surrounds us been created?

Qualitatively, biological variation arises as a function of the nuanced roles that each organism plays: its life history, interactions with the environment and its

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[1] Darwin, C. (1859). On the origin of species by means of natural selection. London, UK: John Murray

interactions with other organisms. This, however is a simplistic view of nature. These roles and interactions are not fixed once established, rather they are dynamic, such that each organism's morphology, physiology and genetic material are constantly under pressure to exist and thrive in a world of continuously moving targets (Van Valen, 1973). After all, "*adaptive zones, not only the animals occupying them, evolve"* (Simpson, 1944). In the face of this idea, that taxonomic idiosyncrasies are being formed and honed by an ever changing environment, it seems that biologists' ultimate quest to understand the routes to diversity will be, or is, as complex as that which it seeks knowledge of.

Historical ideas about evolution

To understand the natural world and its diversity is to understand the full breadth of the evolutionary process through deep time both in isolation and as a function of its interplay with ecology. Two characteristics of evolution commonly studied are its tempos and modes. These terms in the context of evolution are used to describe variation in the rate, or speed, of evolution (tempo) and the distribution or culmination of these rates over time (mode) (Simpson, 1944; Simpson, 1953). It is the combination of tempos and modes acting across portions of the tree of life through deep time that has shaped modern diversity and that seen in the fossil record.

For Darwin, evolution was a process that happened in many, small steps, each creating variation within a population, in heritable traits which differentially affect an organism's chances of survival (Darwin, 1859). Whilst Darwin acknowledged that the speed at which evolution altered traits may have differed across the tree of life and that 'saltations' may have occurred, overall, evolution was a steady, constantly labouring, gradualistic process (Table 1). Conversely, the lesser emphasised features of Darwin's ideas were the focus of Eldredge and Gould's hypothesis of punctuated equilibrium. They posited that gradualism is rare in nature and that rather, stasis, or "mild" change at most was the major state, with rapid and large changes occurring only at the time of speciation events (Gould and Eldredge, 1977; Table 1). That evolution can occur at extremely different rates through time is echoed and formalised in the ideas put forward by Simpson. He famously categorised varying rates of evolution and unlike those before him, reconciled these macroevolutionary ideas with both those of their genetic underpinning and those of the broad scale trends seen in the fossil record (Simpson, 1944; Simpson, 1953; Laporte, 1983). Simpson proposed that 'regular' evolutionary tempos fit within three different rate 'classes' or modes: horotely, bradytely and tachytely (standard, slow and fast rates respectively). These rates fall within the realms of ‘normal evolution’ however Simpson suggested another class, distinct from these called ‘quantum evolution’ which falls outside the bounds of regularity. Quantum evolution was deemed a controversial but important feature of evolution (Wright, 1945) describing the process whereby a shift or change large enough for a species to occupy a different adaptive zone occurs (Simpson, 1944; Simpson, 1953; Table 1). Simpson expanded his ideas in the context of adaptive radiations, a term coined almost half a century earlier by Osborn (1900; 1902) describing the process whereby organisms in a varied environment speciate rapidly to take advantage of ecological opportunities, thus increasing diversity. Simpsonian evolution works to explain how the differing types and rates of evolution therein can serve to underpin such a pattern of biological expansion.

Table 1 | Expectations of tempo, mode and magnitude of change in trait value from the historical theories underpinning modern evolutionary comparative methods

Author(s)	Hypothesis	Tempo	Mode	Changes in trait
Darwin	Gradualism	Constant	Slow, homogeneous	Small
Eldredge and Gould	Punctuated equilibrium	- Stasis - Rapid	Slow or static punctuated by rapid evolution	Big
Simpson	- Regular - Quantum	- Slow, medium, fast - Exceptionally fast	Varying rates through time and in different lineages	Exceptionally small through to exceptionally big

There have been many other works that have questioned how evolution has generated biological diversity, however those briefly summarised form the main framework of the paradigm within which we now consider evolution. These ideas have provided the foundation on which subsequent evolutionary biologists have worked to create statistical models that characterise the evolutionary process in a realistic way.

Modern models of evolution and ancestral state reconstruction

One important distinction in the way that modern biologists work in comparison to those such as Darwin is that we characterise biological processes statistically. In doing this we not only view such processes in a quantitative way but also then frame questions and form hypotheses quantitatively too. A major advance in modern evolutionary biology came from the development of phylogenetic tree inference and phylogenetic comparative methods. Phylogenies use genetic, morphological or a combination of the two types of data to show how a group of species are related to each other. In doing this they also highlight that much of a species' evolutionary past is shared with other, closely related species. This is the effect of common ancestry and it has an impact for how we can study data associated with the species in a tree. The variation we see in species' traits has arisen since those species have diverged from each other, but their starting state was the same given that they arose from a common ancestor (Felsenstein, 1973). For example, the chimpanzee (*Pan troglodytes*) and the human (*Homo sapiens*) shared billions of years of history. Approximately 7.9 million years ago however (7.3 – 8.4 million year ago; Dos Reis *et al.*, 2018), when the ancestral species gave rise to the chimpanzee and modern human lineages, they then evolved independently of each other. It is during this time that their respective body sizes have also diverged. The effect of shared history renders species' data statistically non-independent (Felsenstein, 1985; Harvey and Pagel, 1991). Using the example of the human and the chimp, we only wish to study the variation in traits that has accrued since the two species diverged. This forms the rationale of the independent contrasts method (Felsenstein, 1985) to account for shared ancestry which in turn has acted as the foundation for the suite of phylogenetic comparative methods that are now available.

Having first been introduced to account for the statistical non-independence of species data (Grafen, 1989; Martins and Hansen, 1997; Pagel, 1997; Pagel, 1999; Hadfield and Nakagawa, 2010), phylogenetic comparative methods have become the cornerstone for how we model biological evolution. Underpinning almost all statistical methods that seek to characterise historical processes of continuous trait evolution is the Brownian motion (BM) model. The BM model is a homogeneous, random walk or diffusion model where evolution proceeds with changes in trait value drawn from a normal distribution with a mean of zero and a single, unknown variance (σ^2) (Felsenstein, 1973; Felsenstein, 1985; Harvey and Pagel, 1991). This manifests as a process whereby at every instance of time a trait can change in either direction, unaffected by the nature of any previous changes and at the same instantaneous rate, with variation in a trait increasing gradually through time (Felsenstein, 1973). BM has been criticised however on the basis that many people have interpreted it as modelling purely neutral evolution, or that which occurs by genetic drift (Butler and King, 2004; Kutsukake and Innan, 2013; Elliot and Mooers, 2014). Counter to this however, random walks have also been suggested as being adaptive and still the product of selection (Pagel, 1994; Blomberg and Garland Jr, 2002; Baker *et al.*, 2015) which is important for a realistic model, given we know that selection occurs in nature (Butler and King, 2004; Kutsukake and Innan, 2013; Baker *et al.*, 2016). In addition, it has been stated that there is no explicit reason why we should expect changes to conform to a normal distribution (Felsenstein, 1985; Elliot and Mooers, 2014). Despite this, the BM model, owing to its mathematical tractability forms the basis of many other models and in small phylogenies performs very well (Freckleton and Harvey, 2006; Harmon *et al.*, 2010).

Given the improbability that evolution has acted at the same tempo and mode in every lineage across billions of years of history, modifications applied to whole phylogenies uniformly to detect deviations away from BM are commonly implemented. They are frequently achieved through transforming the branch lengths of the phylogeny (Pagel, 1997; Pagel, 1999) to reflect altering rates of evolution through time such as in the case of early and late burst models (Pagel, 1999; Blomberg *et al.*, 2003; Harmon *et al.*, 2010). In the case of the former, trait change occurs rapidly, early on in a clade's history and slows through time, as in a classic 'adaptive radiation' and regarding the latter, the rate of trait evolution begins slowly and increases through time. Others include trait change occurring as a direct product of speciation events (Pagel, 1997) linking directly to the theory of punctuated equilibrium (Gould and Eldredge, 1977) and understanding how much variation in a trait can be explained by the structure of the phylogeny (Pagel, 1999).

The Ornstein-Uhlenbeck (OU) model is another such extension of Brownian motion. Originally introduced to describe stabilising selection in populations of organisms (Lande, 1976) it has subsequently been applied to evolution at the species level (Hansen, 1997; Butler and King, 2004) however, interpretations that reconcile evolutionary mode at both scales is possible (Hansen, 2012 although see Cooper *et al.,* 2016). The OU model incorporates a stochastic, random drift element along with a deterministic element which exists owing to the presence of selection; without the latter, the model reduces to pure BM (Butler and King, 2004). The model therefore allows the existence of discrete trait optima to be tested (Beaulieu *et al.*, 2012) and if present can determine whether these optima differ across organisms occupying different ecological niches (e.g. Hansen, 1997; Butler and King, 2004; Davis *et al.,* 2014). The OU model characterises an adaptive landscape (Uyeda and Harmon, 2014) in the way that Simpson described it (Simpson, 1953). The landscape is made up of fitness peaks defined by trait optima that can apply to whole trees (in the case of a single optimum OU model), individual clades or individual lineages (in the case of multiple optima OU models) (Butler and King, 2004; Beaulieu *et al.*, 2012; Uyeda and Harmon, 2014; Puttick, 2018). Natural selection then works to draw species closer to their optimum, with the intensity of selection highest where the species' trait value is furthest from the optimum value, acting to cause directional trends in trait change. For example, imagine a frugivorous, arboreal, clade of primates in this theoretical landscape, existing within the realms of a frugivorous, arboreal niche, or, adaptive zone, to use Simpson's language. Selection would act to determine that the variance in traits such as body size, tooth size and gut length collectively reduced owing to all of the traits being pulled towards their particular optimum, maximising the fitness of each species in the clade. Given that niches too evolve (Simpson, 1944), the theoretical adaptive landscape changes its form through time. This means that trait optima change, resulting in organisms being said to shift between adaptive zones in response (Ingram and Mahler, 2013).

More complex expansions of the BM model have been developed in the light of the fact that evolution has been shown not only to act at varying speeds, or tempos through time, but also in different clades of a single phylogenetic tree (O'Meara *et al.*, 2006). This triggered the development of a swathe of models, broadly termed 'variable rates' models, which through different means allow for rates to vary through time and in subsets of a phylogeny (Eastman *et al.*, 2011; Venditti *et al.*, 2011; Revell *et al.*, 2012; Thomas and Freckleton, 2012; Rabosky *et al.*, 2013) or even on individual branches (Venditti *et al.*, 2011; Kutsukake and Innan, 2013; Landis *et al.*, 2013; Elliot and Mooers, 2014; Kratsch and McHardy, 2014; Duchen *et al.*, 2017). These models can be split into two categories based on their methodological approach – those that characterise evolution as a homogeneous process and those that characterise evolution as a heterogeneous process.

Homogeneous models parameterise the evolution of continuous traits using a single stochastic process, or underlying distribution, for all of the branches in a phylogeny. Elliot and Mooers, (2014) use a stable, or heavy tailed distribution, of which the normal distribution is a special case. Continuous trait evolution is modelled as a symmetrical, stochastic process, without assuming constant variance as in a BM model. The heavier the tails of the distribution, the more volatile the random walk required to explain the data at the tips of the phylogeny. This serves to increase the probability (compared to a normal distribution) that incremental changes in trait value have come from the tails of the distribution. Changes in these tails characterise large alterations to increase or decrease trait values by magnitudes outside the scope of possibility under a

BM model. Another special case of the stable distribution is the Lévy distribution which has also been used to model continuous trait evolution (Landis *et al.*, 2013; Duchen *et al.*, 2017). Unlike under a BM model, where by necessity changes in trait value must be similar to each other across a phylogeny, stable processes that deviate from the normal distribution allow for the possibility of 'jumps' in trait value where the changes along branches are not continuous with each other (Landis *et al.*, 2013). The behaviour of evolution inferred from these distributions is thus comparable and can be interpreted as small changes occurring most frequently (modal region of the underlying distribution), interspersed with potentially extremely large changes (from the tails of the distribution), the latter of which have been found to occur on the order of millions of years (Uyeda *et al.*, 2011). These models may stir ideas about punctuated evolution (not necessarily punctuated at speciation events as proposed by Gould and Eldredge, (1977)) however their homogeneous nature rather implies that there should not be a distinction between gradual and punctuated models at all (Duchen *et al.*, 2017).

Increases or decreases in the rate of evolution equate to very large or very small changes in trait value respectively relative to the amount of time that they took to occur. Heterogeneous models consider that rather than coming from the same underlying distribution as the 'regular' changes, that changes occurring at fast or slow rates must come from other, distinct distributions. This has the effect of creating a 'background rate' of evolution which acts broadly across the branches of a phylogeny as a whole, starting at the root of the tree. The background rate is characterised, as in BM, with a normal distribution, which is why these models can still be considered as extensions of a BM model. Where rates are detected that cannot be accommodated by this background rate, a rate shift occurs. Such deviations from the background rate manifest in the variance of traits in monophyletic clades increasing or decreasing which means they can be characterised by a normal distribution with an increased or decreased variance compared to that of the background rate. Given this, variable rates models commonly apply the new rate arising from a rate shift to all descendent branches within a monophyletic clade (Eastman *et al.*, 2011; Revell *et al.*, 2012; Thomas and Freckleton, 2012; Rabosky *et al.*, 2013). The method of Venditti *et al.*, (2011) differs from others by not only modelling variance increases or decreases in whole clades but further allows for shifts in the mean of a distribution describing a clade's trait values. Such a mean shift is applied to the single branch and node at the root of the clade in question, meaning that an increased or decreased rate is seen on that one branch in isolation and not on all of its descendent branches. Both branch (mean shift) and clade (variance difference) scalars are also used in other variable rates models, which are not based on Brownian motion

(Kutsukake and Innan, 2013; Kratsch and McHardy, 2014). Even when applied in a maximum likelihood framework (Thomas and Freckleton, 2012), owing to their complexity, variables rates models can easily become over-parameterized and as such, the provision of *a priori* information regarding the number of shifts or rate regimes is a common feature of their implementation (Eastman *et al.*, 2011; Rabosky *et al.*, 2013). In addition, or as an alternative to supplying prior information, models run in a Bayesian MCMC framework can use a reversible jump MCMC algorithm (Green, 1995) which allows for parameters to 'jump' in and out of the model as required as the MCMC chain proceeds (Eastman *et al.*, 2011; Venditti *et al.*, 2011; Rabosky *et al.*, 2013). All of these approaches attempt to model as best possible the same ideas visualised predominantly by Darwin, (1859) and Simpson, (1944; 1953). They characterise species evolving to maximise their fitness within a world of adaptive peaks and fitness valleys which they jump between and across as the landscape constantly changes its form around them.

As evolution proceeds it leaves signatures of its previous work such that past events are not lost. In addition, where ancestral species have not left fossil evidence, as is the case for the majority of lineages, it becomes impossible to directly measure features of extinct organisms. Ancestral state reconstruction (ASR) takes data at the tips of a phylogeny, along with the structure of the tree and a model of evolution and estimates the value of a given trait for every ancestor in the tree. This approach enables signatures of the way that evolution has worked to be used to fill in those gaps and inform on the traits of ancestral species in the absence of fossil evidence (Pagel, 1999). In addition, ASR allows us to reconstruct behavioural traits (e.g. Shultz *et al.,* 2011, Maor *et al.,* 2017, Cardinal *et al.,* 2018), soft tissue traits (e.g. Sauquet *et al.,* 2018; Tsai *et al.,* 2018) and even genetic traits (Organ *et al.*, 2007) that could never have been retrieved from fossils even if there was a perfect fossil record. It has been claimed that ASR is often misled when fossil data are not used in addition to extant data (Finarelli and Flynn, 2006; Slater *et al.*, 2012; Pant *et al.*, 2014; Mitchell, 2015). This implies that extant data may not be representative of the traits present in extinct lineages (Finarelli and Goswami, 2013) and that the inclusion of fossils may thus act to 'calibrate' the reconstruction process. However, in contrast it has also been argued that the model of evolution used is more important for accurate ASR than the inclusion of fossils which can have a limited, or completely lacking impact on reconstructed trait estimates (Puttick and Thomas, 2015). It has been shown that where a realistic, flexible model of evolution is used, it is possible to reconstruct evolutionary history from extant organisms alone and estimate ancestral trait values exactly in line with fossil evidence (Baker *et al.*, 2015).

Approaches to estimating the values of continuous traits at ancestral nodes can vary. In some cases ancestral states are implicit in the model of evolution which aims first and foremost to estimate evolutionary rates (Rabosky *et al.*, 2013). In such cases, the ancestral states can subsequently be inferred from the phylogeny which can be transformed by the rates of evolution acting on its branches (Baker *et al.*, 2015). Alternatively ASR may be an explicit part of inferring the model of evolution (Kutsukake and Innan, 2013; Kratsch and McHardy, 2014) and thus also contribute to the calculation of the likelihood, with the rates produced as a by-product of having inferred trait states at ancestral nodes (Elliot and Mooers, 2014). Regardless of how they may be obtained there is overarching evidence to suggest that where the underlying model of evolution is realistic - incorporating rate heterogeneity both temporally and taxonomically – the estimation of ancestral states provides us with an accurate and otherwise impossible view into the deep past.

The contributions of this thesis

There is abundant evidence to suggest that evolution is not a homogeneous process, rather, that it acts at varying speeds at different times and in different taxonomic lineages. When these complexities of the evolutionary process are taken into account, one can make accurate inferences about the tempos and modes of trait evolution and the nature of ancestral traits from across the tree of life. This thesis uses a modified version of the variable rates model of Venditti *et al.,* (2011; henceforth termed 'the variable rates model') which identifies varying rates of evolution which deviate significantly from the background rate of evolution, or Brownian expectation, on individual branches or in whole clades of a phylogeny without *a priori* knowledge of their taxonomic or temporal position. Where previously, ancestral traits were implicit in the model it is here developed further such that ASR is an explicit part of the model inference process[2].

This variable rates model is used over any of the other approaches available given its lack of requirement for *a priori* knowledge regarding the number or position of rate shifts in a tree and flexibility in not predefining the underlying distribution characterising the mode of evolution. This flexibility allows the signatures of past evolutionary events present in extant data to be detected only if they exist and not because a predefined

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[2] The modified model of Venditti *et al.,* (2011) is described in detail within the experimental chapters of this thesis

model is fitted to the data. Features of and interpretations about evolutionary processes from other approaches can still be identified from this new method. In cases where no varying rates, or rates of limited magnitude are detected, the model of evolution that best fits the data is likely to be a pure Brownian one; this can be tested using Bayes Factors given that the variable rates model is implemented as a complex form of Brownian motion. Where accelerated rates are detected concentrated early in a phylogeny as a whole or in an individual clade (a nuance overlooked by methods applying a global slow-down transform (Puttick, 2018) (e.g. Pagel, 1999), one can infer an early burst pattern of evolution (Pagel, 1999; Harmon *et al.*, 2010). This may be a pattern defining cases where organisms experienced ecological opportunities resulting in shifts in adaptive zones, subsequently setting the scene for an evolutionary radiation (Osborn, 1900; Schluter, 2000; Venditti *et al.*, 2011). Chapter 1 finds exactly this slow-down through time signature, having applied the variable rates model to dinosaurian geographical data whilst Chapter 2 finds the opposite signature of a late burst of evolution in the magnitude of morphological changes from across the tree of life. It is also possible to interpret OU-like processes where a mean shift, or jump to a different adaptive zone (Venditti *et al.*, 2011) occurs along a single branch and is then followed by a subsequent reduction in variance in the branches of the descendent clade. Thus, even without the 'optimum' and the 'strength of selection' parameters of the OU model, it is possible to detect the central concepts that are studied using the OU process – selection, shifts between adaptive zone and constraints - using the distribution of varying rates detected by the variable rates model. Ultimately, it is important to be able to link the statistical parameterisation of models used to processes acting at every scale of biology; reconciling evolution at the individual, population and species levels. In addition, to interpret parameters in the context of genetic mechanisms, types of selection and broadly acting phenomena at the macroevolutionary level. This reconciliation should work towards creating a more seamless view of evolution than has ever been possible and uncover how it has worked on the raw variation available in nature to create diversity. This seamless view must also embrace the vast complexities and nuances of the evolutionary process to truly reflect reality.

Chapter 1 of this thesis applies the variable rates model to geographical data in the form of longitudes and latitudes describing the locations of every known fossil of 596 species of dinosaurs. The dinosaurs represent a morphologically diverse and speciose clade of organisms that are well studied in terms of their phenotypic traits (e.g. Brusatte *et al.,* 2012; Benson and Choiniere, 2013; Benson *et al.,* 2014; Sullivan and Xu, 2017) although less so in terms of their speciation and extinction dynamics (Sakamoto *et al.*, 2016). They were also a clade that dominated terrestrial habitats across the globe for over 150 million years; with fossils known from every continent the dinosaurs had a cosmopolitan distribution but very little is known about how such a distribution evolved. In this chapter, a new biogeographical model is developed whereby the locations of the dinosaurian ancestors in a comprehensive phylogenetic tree (Benson *et al.*, 2014) are reconstructed in continuous, three dimensional space, whilst also simultaneously accounting for varying rates of movement through time and in different lineages and is implemented in a Bayesian, MCMC framework. Calculated from the estimated ancestral locations, the distance travelled and speed of movement along every branch of the phylogeny revealed the mode of dinosaur spread to be characterised by mostly small dispersal events interspersed with large, rare, long distance movements. The high resolution of the data allows previous ideas about large scale periods of endemism (Mannion *et al.*, 2012; Herman *et al.*, 2016; Longrich, 2016) to be refuted, given that there was regular movement of species between Gondwanan and Laurasian landmasses. All dinosaurs moved initially very rapidly but over time the movement of all clades of dinosaurs uniformly reduced demonstrating a typical 'early burst' pattern of evolution. This pattern is commonly identified as the signature of an adaptive, or evolutionary radiation, although previous examples of such a slow-down through time have never been shown in geographical data and most are also typically geographically restricted (Grant, 1981; Seehausen, 2006; Mahler *et al.,* 2010 although see Sakamoto *et al.,* 2016). The geographical signature of an evolutionary radiation is therefore shown in this work for the first time. The inclusion of a measure of net speciation enables these biogeographical results to also contribute to understanding the dynamics associated with speciation in allopatry and sympatry and the relative contributions that these modes of generating new species made to dinosaur diversity over their 170 million year history.

In Chapter 2, the evolutionary tempos and mode acting across the tree of life to generate the diversity of morphological traits in extant and extinct organisms are revealed. Similar to the approach taken in Chapter 1, ancestral body sizes, or body size proxies are estimated in 143 phylogenetic trees such that the magnitude and direction of trait change along every branch could be quantified. Combined into a single distribution the nature of morphological changes in organisms spanning the natural world, the product of billions of years of evolutionary history can be characterised. Just as was the case for the mode of geographical expansion in the dinosaurs (Chapter 1), evolution has created and modified morphologies in small, gradual steps the vast majority of the time. In some cases however, extraordinary leaps in trait values occur as the result of extreme episodes of selection (Baker *et al.*, 2016). Unlike those who have previously found morphological evolution to proceed in this way (Landis *et al.*, 2013; Elliot and Mooers, 2014; Cooney *et al.*, 2017; Duchen *et al.*, 2017; Landis and Schraiber, 2017; Chira *et al.*, 2018) this work studies the frequency and magnitude of changes to both increase and decrease trait size and the dynamics of morphological trait change through time. Relationships between the magnitude of morphological changes and ecology, metabolic strategy and varying levels of taxonomy are all quantified with the aim of understanding the roles of life history strategies, environment and evolutionary history in driving morphological change. Patterns of evolution are different depending on whether selection is driving body size to increase or decrease and counter to previous findings (e.g. Slater *et al.,* 2010; Derryberry *et al.,* 2011; Hughes *et al.,* 2013) including those in Chapter 1 based on the traditional view of adaptive radiations (Osborn, 1900; Simpson, 1944; Schluter, 2000; Losos, 2010), morphological changes increase in magnitude through time akin to a late burst model of evolution (Pagel, 1999; Blomberg *et al.*, 2003). This is considered in the context of both recent research regarding a lack of evidence for early bursts of morphological change (Cooper and Purvis, 2010; Harmon *et al.*, 2010; Venditti *et al.*, 2011; Puttick, 2018) and the traditional ideas concerning the interactions of morphological evolution with biogeography, ecology and speciation. Both the habitat organisms evolve in and their ancestry influence how large or small the incremental steps that evolution has taken to create extant and extinct organisms' morphological traits. Thus, large scale morphological evolution is discussed in terms of fundamental features of the natural world given that these provide the basis of evolution's landscape, its stage and set, in which the play and its characters have been carved out.

Finally, using the 'exceptional changes' data generated in Chapter 2 the role of exceptionally large evolutionary changes in generating diversity is considered. These sometimes extraordinarily large jumps in morphological traits are a rare feature of evolution in comparison to the overabundance of small, sometimes negligibly small changes that make up the bulk of evolution's work. Here, the distribution of these changes in three major vertebrate radiations (mammals, fish and birds) is studied using a measure of phylogenetic signal (Lynch, 1991) resulting in an understanding of how or if they are perpetuated through time and lineages. Both the ecological and evolutionary consequences of these jumps are tested and discussed in the context of both body size evolution and speciation. Ecological variation and the formation of new species are both frequent features of this thesis given its aim to reconcile historical concepts about evolution and the masterpieces it has created. It does this using powerful, cutting edge, statistical techniques which facilitate new views of the vastness of the natural world.

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Chapter 1 | Dinosaurs reveal the geographical signature of an evolutionary radiation

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"Great things are not done by impulse, but by a series of small things brought together."
Vincent Van Gough, (1882)[1]

ABSTRACT

Dinosaurs dominated terrestrial ecosystems across the globe for over 100 million years and provide a classic example of an evolutionary radiation. However, little is known about how these animals radiated geographically to become globally distributed. Here, we use a biogeographical model to reconstruct the dinosaurs' ancestral locations, revealing the spatial mechanisms that underpinned this 170-million-year-long radiation. We find that dinosaurs spread rapidly initially, followed by a significant continuous and gradual reduction in their speed of movement towards the Cretaceous/ Tertiary boundary (66 million years ago). This suggests that the dominant mode of dinosaur speciation changed through time with speciation originally largely driven by geographic isolation – when dinosaurs speciated more, they moved further. This was gradually replaced by increasing levels of sympatric speciation (species taking advantage of ecological opportunities within their existing environment) as terrestrial space became a limiting factor. Our results uncover the geographical signature of an evolutionary radiation.

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[1] Van Gough, V. (1882). Communication in a letter to his brother.

INTRODUCTION

From a single, modest ancestor that existed over 230 million years ago at the beginning of the Mesozoic era (which spans from 252 to 66 million years ago (Ma)), the dinosaurs evolved into a group that was morphologically and ecologically diverse as well as speciose (Brusatte *et al.*, 2008a; Brusatte *et al.*, 2008b; Sakamoto *et al.*, 2016). During this time, dinosaurs spread geographically and are now known for their dominance of terrestrial environments (Sereno, 1997) across the entire globe. Given that the earliest known dinosaur fossils are from rocks now in South America dating from the early Late Triassic period (Martinez *et al.*, 2011) (approximately 231 Ma) it is often assumed that this is where the ancestor of all dinosaurs existed (Brusatte *et al.*, 2010; Langer *et al.*, 2010). Despite there being thousands of later dinosaur fossils littered across the globe, the limited insight into the locations of intermediate species means that we cannot determine how dinosaurs came to be so far away from their origin. As a result, descriptions of raw fossil locations paint a limited picture of dinosaur biogeography. To uncover how the dinosaurs spread to every corner of the Earth, a different approach is needed.

We introduce a Bayesian statistical method to reconstruct the ancestral locations of the dinosaurs in a comprehensive phylogenetic tree (Benson *et al.*, 2014) to fill the gaps in the fossil record and uncover the dinosaurs' paths across the globe. We do this in continuous, three-dimensional space (Bouckaert, 2016) using all of the available fossil occurrence data describing the dinosaurs' locations – including multiple locations for individual taxa (see Methods). Our model allows us to detect significant increases or decreases in the speed of dinosaur movement without any prior information about the temporal or phylogenetic position of such shifts having based our geographical model on a previously published variable rates model (Venditti *et al.*, 2011). This means that unlike any previous biogeographical study, we can determine the distance moved (we use this term and its derivations to describe the movement of species rather than of individuals or populations) as well as the speed and direction of movement along each branch of the phylogenetic tree (see Methods).

RESULTS AND DISCUSSION

Using our estimates of ancestral locations, we can describe the intermediate steps that resulted in the dinosaur species for which we have fossil evidence, thus making our view of the dinosaur radiation more complete than was previously possible with fossil locations alone. Our reconstructions indicate that the ancestor of all dinosaurs originated within the landmass that is now South America, which corroborates the common assumption based on the early dinosaur fossil record (Brusatte *et al.*, 2010; Langer *et al.*, 2010).

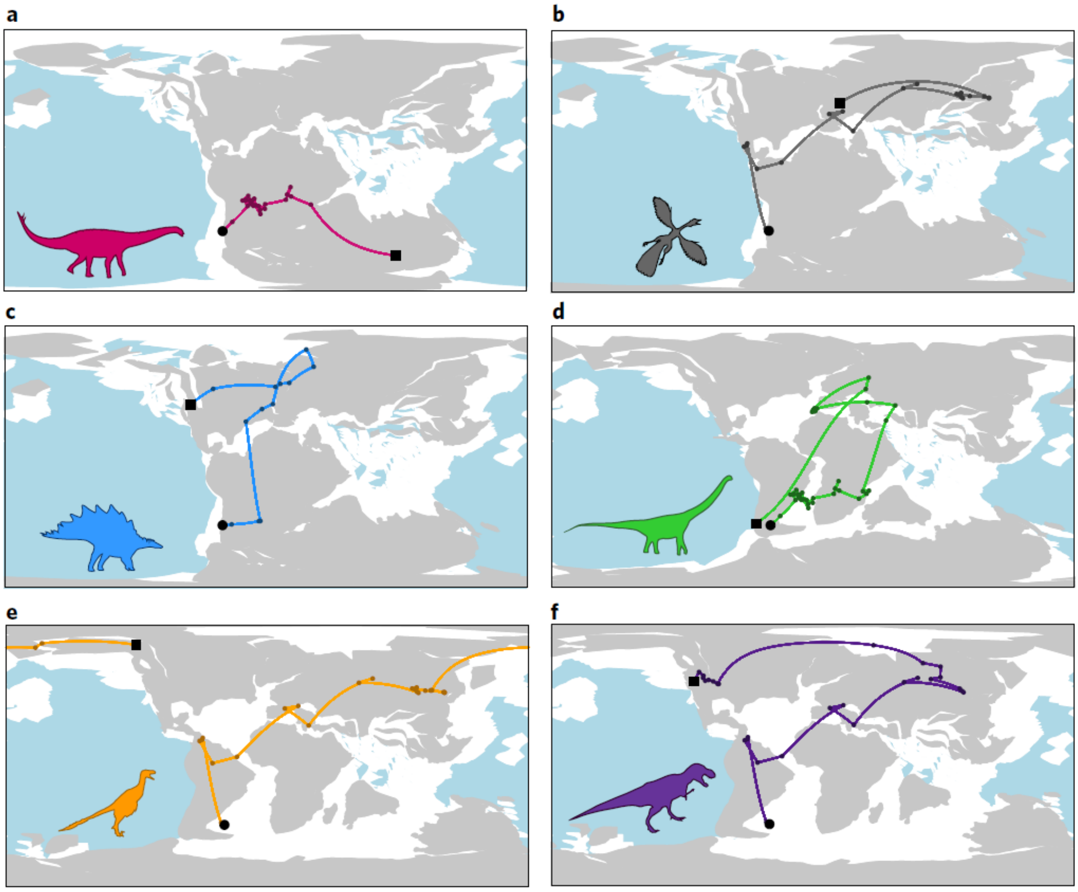


Figure 1 | Six reconstructed paths from the dinosaurian root node (black circle) to the fossilized species (black square). The coloured circles represent the centroids of the reconstructed ancestral locations (these are used for visualization purposes only and posterior distributions of estimated ancestral locations are used in all analyses). Paths are plotted onto geological age level palaeomaps from the time to which the fossil species is dated (grey) with all preceding age level palaeomap layers plotted in white (see Methods). **a** - The path of *Rhoetosaurus brownei* (silhouette of *Spinophorosaurus nigerensis*). **b** - The path of *Archaeopteryx lithographica*. **c** - The path of *Stegosaurus stenops*. **d** - The path of *Andesaurus delgadoi* (silhouette of *Wintonotitan wattsi*). **e** - The path of *Dromaeosaurus albertensis* (silhouette of *Dromaeosauroides bornholmensis*). **f** - The path of *Tyrannosaurus rex*. **a** - Credit: Zoonar GmbH/Alamy Stock Photo. **b** - Credit: YAY Media AS/Alamy Stock Photo. **c** - Credit: Corey Ford/Alamy Stock Photo. **d** - Credit: Nobumichi Tamura/Stocktrek Images/Getty. **e** - Credit: Stocktrek Images/Alamy Stock Photo. **f** - Credit: Universal Images Group North America LLC/Alamy Stock Photo.

A sample of dispersal paths taken by six species is shown in Figure 1. These illustrate the diversity of routes taken across the globe, even by dinosaurs that ended up in the same location (Figure 1c, f), and show a pattern whereby ancestral nodes mostly cluster together but with a descendant occasionally moving far away from its predecessors. This pattern of movement is universal among the dinosaurs, and hence their expansion can be said to be characterized by a mixture of mostly short-distance, local movements interspersed with long-distance dispersals. This characterization holds true throughout the course of the Mesozoic era (252 – 66 Ma) in each of the Triassic (252 – 201 Ma), Jurassic (201 – 145 Ma) and Cretaceous (145 – 66 Ma) periods, which is demonstrated by the bimodality of the distributions of distances travelled along each branch of the phylogeny (Figure 2a). The terminal branch leading to the flightless Mesozoic bird, *Patagopteryx*, represents the greatest distance associated with an individual branch in the phylogenetic tree. Over 52 million years, the ancestral populations of this species moved more than 19,000km, which equates to just under half the circumference of the Earth at the Equator. On average, however, ancestral populations moved a distance (± standard deviation (s.d.)) of 2,141 ± 20km before being classed as a new species (average branchwise distance), which is equal to the distance between London, UK, and Kiev, Ukraine.

Previous work based on inspection of the fossil record alone often implies that dinosaurs were in some way latitudinally restricted in their movement, or that areas of endemism are consistent with the idea of floral and faunal distributions occurring in latitudinal belts (McAllister Rees *et al.*, 2004; Ezcurra, 2010; Mannion *et al.*, 2012) owing to climate (Noto and Grossman, 2010; Brusatte, 2012; Herman *et al.*, 2016), geographical barriers (Longrich, 2016) or competition (Longrich, 2014). By considering the complete evolutionary history of each dinosaur species in the phylogeny (that is, movement from root to each terminal branch via estimated intermediate ancestral locations) rather than the fossils alone, we see no such restriction in the dinosaurs' movement through time, as dinosaur species routinely traverse between northern and southern landmasses (Figure 1). Considering a larger geographical and taxonomic scale than that of an individual species' path, we find that the dinosaurs expanded from South America in every possible direction (Figure 2b) to inhabit all available land. However, we find that there is some variation through time in the distance travelled in each direction (Figure 2a). In the Triassic period, the greatest distances covered were towards the north, northeast and east, which supports the notion that the dinosaurs radiated spatially over Pangea from the southwest of the landmass (Figure 2a, b). All migrations in the Triassic period occurred rapidly (Figures 2a and 3a, b) but those towards the south (given these dispersals only covered short distances) and northeast were fastest at an average speed (± s.d.) of 349 ± 1.32km per million years (Myr^{-1}). In the Jurassic period movement

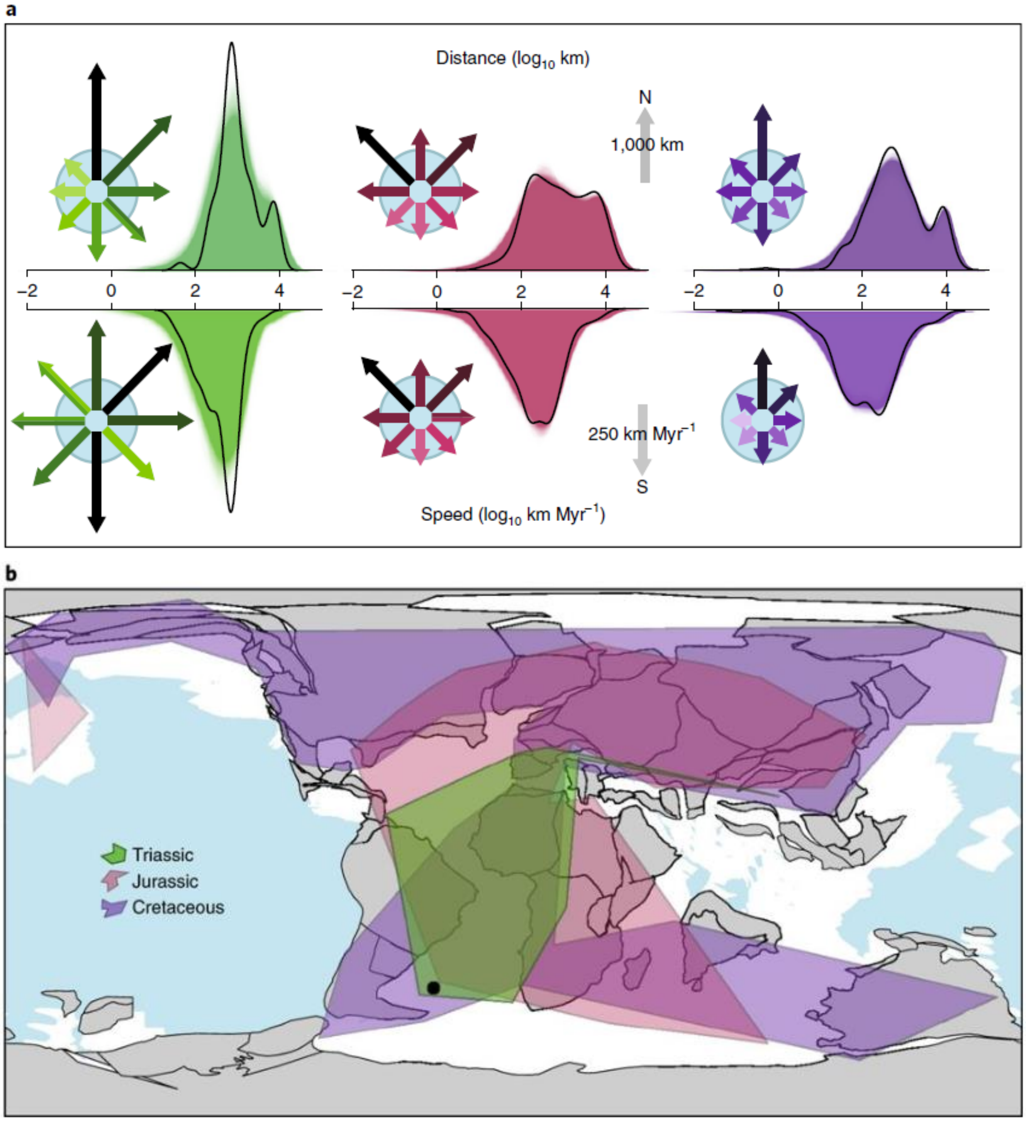


Figure 2 | The dinosaurs' distance, speed, direction and area covered through time. **a** - The distributions of log-transformed branchwise distances (top) and speeds (bottom) for each of the three periods of the Mesozoic era (green, Triassic; red, Jurassic; purple, Cretaceous). Next to each distribution is a 'globe' with arrows, the length and shade of colour of the arrows show the magnitude of distance or speed travelled in the given direction. Arrows in different shades indicate that the mean distance or speed travelled in that direction is significantly different from those travelled in the other directions. Conversely, arrows of the same shade indicate that the mean distances or speeds moved in those directions are not significantly different from one another. **b** - The areas covered by the dinosaurs, including both fossilized species' and reconstructed ancestral locations in the Triassic (green), Jurassic (red) and Cretaceous (purple) periods. The areas are plotted onto a map that spans from the beginning of the Triassic period to the end of the Cretaceous period (white), with the final map layer in grey and outlined in black (see Methods). The root node, or ancestor of all the dinosaurs, is plotted as a black circle.

towards the northwest was favoured, closely followed by dispersal to the northeast, west, north and east (Figure 2a), suggesting that during the time after their initial expansion the dinosaurs moved predominantly to cover longitudinal space. This is in contrast to the directions moved in the Cretaceous period, which again favour latitudinal radiation; species travelled an average of 1,000km towards the north while those moving in all other directions on average traversed less than half this distance. During the Cretaceous period, all movement was slow (Figures 2a and 3a, b), with even the fastest dispersals towards the north occurring 1.5 times slower than the fastest movement in the Triassic period. Without the ability to accurately estimate ancestral locations, such nuances of dinosaur biogeography have previously remained a mystery.

Our ancestral location reconstructions and branchwise distances travelled allow us to statistically test hypotheses about whether and how distance moved and speed of movement changed over millions of years of dinosaur evolution. In addition, as we know that speciation and spatial distribution are intimately linked (Wiens, 2011), we can also use this information to reveal how biogeography interacts with speciation and abiotic factors to provide a better understanding of the dinosaur radiation.

To this end, taking into account the uncertainty associated with our reconstructed ancestral locations we ran a series of 1,000 Bayesian Markov chain Monte Carlo (MCMC) phylogenetic generalized least-squares regressions with pathwise distance (distances travelled from the root node to each terminal branch) as the dependent variable and path length (time elapsed since the root, measured in millions of years) as the independent variable, enabling us to study the speed of movement through time (see Methods). We allowed the speed to vary over time (including a second-order polynomial term for path length) and assessed the impact of other biological variables including speciation rate (node count), diet, gait and taxonomic group (Ornithischia, Theropoda, Sauropodomorpha, Paraves and Aves), sampling biases such as formation count and valid count (Sakamoto *et al.*, 2016) and sea level (Haq *et al.*, 1987) as a proxy for land area. Our model reduction process (see Methods) resulted in a model in which dinosaur movement reduced and slowed over the course of the Mesozoic era. We determined parameters to be significant if they were significantly different from zero in > 95% of the regressions ($\%MCMC_{1,000} > 95$; see Methods). All groups of dinosaurs exhibited a universal relationship between distance moved and time (path length $\%MCMC_{1,000} = 100$, path length squared $\%MCMC_{1,000} = 100$). We also found that gait and diet had no effect on the pathwise distances moved by the dinosaurs, and neither did formation count, valid count or sea level.

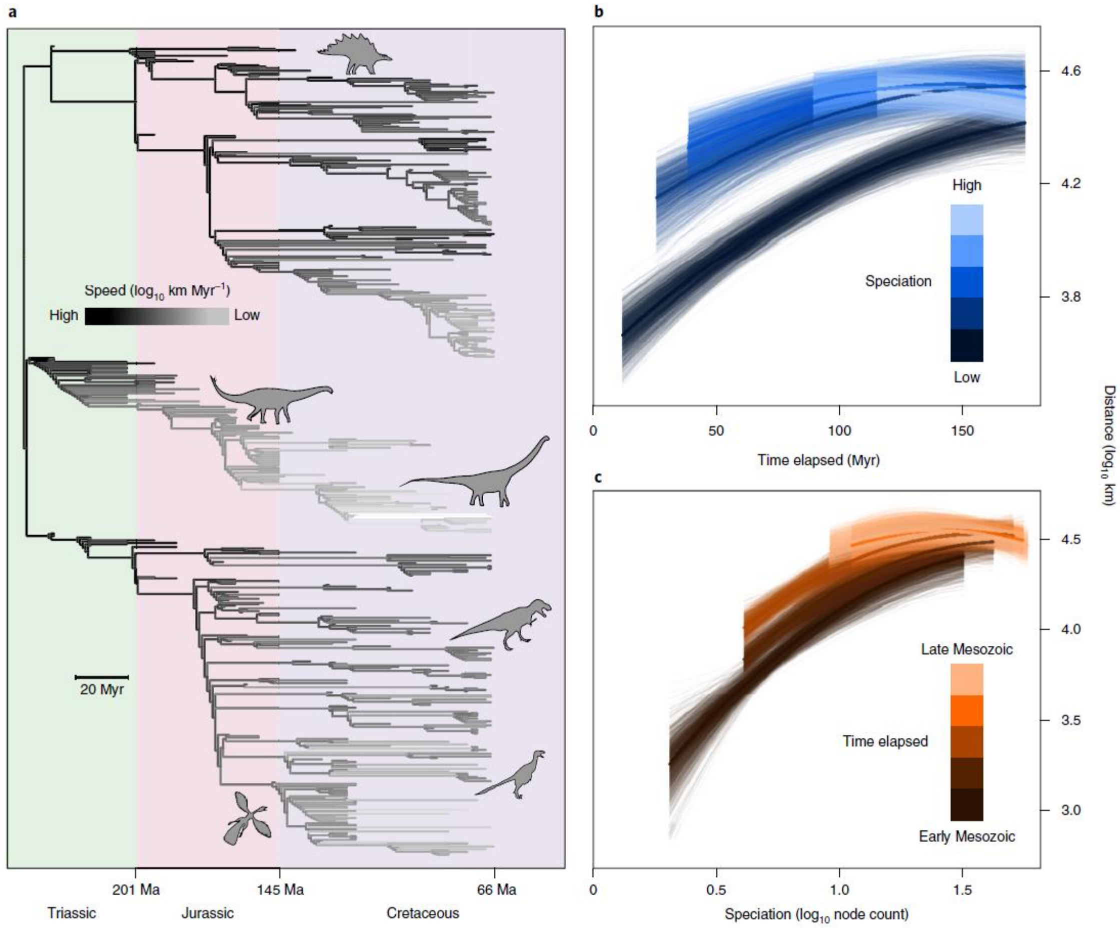


Figure 3 | The influence of speciation and time on dinosaur movement. **a** - The dinosaur phylogenetic tree with branch lengths measured in millions of years, and with each branch coloured to reflect the predicted speed of movement calculated from the mean branchwise distance, branch length and the number of preceding speciation events. Silhouettes as in Figure 1. **b** - Interaction plot of predicted distance moved over time at five different rates of speciation (values of log node count). Each regression line plotted is using the mean coefficients from a single Markov chain Monte Carlo (MCMC) regression. The line in bold represents the prediction made from the mean coefficients of all 1,000 regressions. **c** - Interaction plot of the effect of speciation (log node count) on predicted distance moved at five different times during the Mesozoic era (252–66 Ma). Each regression line plotted is using the mean coefficients from a single MCMC regression. The line in bold represents the prediction made from the mean coefficients of all 1,000 regressions.

It has previously been demonstrated (Sakamoto *et al.*, 2016) that speciation rate in dinosaurs declines through time, and so to allow for this we also tested the significance of the interaction between path length and speciation rate. As expected there is a strong interactive effect (%MCMC$_{1,000}$ = 100; Figure 3b, c), which means that the dinosaurs' speed of movement not only decreases over time, but is also further adjusted by speciation, which itself declines with time. As the Mesozoic era proceeded, and as more speciation occurred along a lineage, the resultant species moved more slowly across the Earth (Figure 3a – c). The variables in our final regression model explain just under half of the variation in distance moved (mean R^2 = 0.46, calculated from the mean R^2 of each of the posteriors for the 1,000 regressions). The parameters associated with speciation rate on average contributed approximately 50% of this R^2 value confirming the importance of speciation dynamics in determining faunal distributions.

Our results point to an interesting new view of biological radiations. Slowdowns in evolutionary rates through time, be they associated with morphology or speciation, have historically been recognised as representing a so-called adaptive radiation (Simpson, 1944; Schluter, 2000). The slowdown phenomenon has been widely reported and is often considered pervasive in nature (but see Venditti *et al.,* 2010), with famous examples ranging from cichlid fishes (Seehausen, 2006) to Anolis lizards (Mahler *et al.*, 2010), Darwin's finches (Grant, 1981) (although these examples are geographically restricted) and, more recently, dinosaurs (Sakamoto *et al.*, 2016) – yet the causes underpinning this type of radiation pattern remain unclear. Osborn, (1900), who first coined the term adaptive radiation, suggested that species emerge in response to adaptive or 'mechanical' changes associated with ecological opportunity (the number of open or underused niches within an environment). However, emphasis has since been placed on the role of physical barriers isolating populations and preventing gene flow as the trigger for speciation, this being considered to result in a non-adaptive radiation (Erwin, 1992; Losos and Miles, 2002; Abe and Lieberman, 2009; Rundell and Price, 2009; Simões *et al.*, 2016). It is almost certain that in reality, evolutionary radiations are initiated by and maintained via a complex mixture of both physical barriers and adaptation to new ecological opportunities. While we may never be able to identify all of the ingredients of this cocktail, an adaptive radiation cannot be truly identified or understood considering speciation or morphological change alone, but must be viewed in the light of spatial data. Therefore, our results provide the hitherto missing geographical link, by demonstrating that in dinosaurs at least, rates of movement through time show those characteristic patterns seen in rates of morphological change and speciation. As such, for the first time, we have revealed the geographical signature of an evolutionary radiation – some of which will have certainly been the product of adaptation.

Early dinosaurs moved and speciated rapidly, with both processes slowing through time. This pattern is consistent with the hypothesis that speciation was first driven by geographical isolation, but as space became limited the dinosaurs moved less and thus the pressure to become specialized and use resources present in the increasingly saturated environment resulted in sympatric speciation. Or perhaps both geographical and sympatric speciation were co-occurring early in the history of the dinosaurs and, as time went on, the balance shifted and sympatric speciation began to dominate. An example of this may have been the case of the paravians (or later avians) where, not being able to move into new environments to evade competition with other theropods, they adapted and specialized to occupy aerial space. This ability to overcome the limit on terrestrial space and take advantage of the unoccupied niches may well have laid the foundation for their survival of the end-Cretaceous mass extinction (which killed non-avian dinosaurs) and their subsequent diversification into one of the most successful vertebrate groups today. A further example is the duck-billed dinosaurs (Hadrosaurs), which were found to evade the late Cretaceous slowdown in speciation rate (Sakamoto *et al.*, 2016) and which we find to move particularly slowly (Figure 3a). The Hadrosaurs' cranial ornamentation has been hypothesized as being a product of sexual selection (Padian and Horner, 2011; Hone *et al.*, 2012), which is one of the proposed mechanisms for sympatric speciation (Higashi *et al.*, 1999; Servedio and Boughman, 2017). This adds credence to our hypothesis that this mode of speciation may have become more common as space became limited.

CONCLUSION

While the case of the dinosaurs provides a magnificent example of how we can study millions of years of complex biogeographical dynamics, it also allows us to address important and longstanding questions about how organisms evolve and why they exist where they do. Using data regarding movement through time has enabled us to discover that speciation and therefore dinosaur diversity was propagated by a combination of geographical isolation and *in situ* adaptation and divergence, the balance of which is dependent on the availability of physical space. This highlights that sympatric speciation does occur in nature and that this kind of speciation makes a real contribution to the diversity of life on Earth. By uncovering the links between speciation and movement, we have revealed that it is possible to detect an evolutionary radiation from data regarding movement in space and time. This means that we can now consider the pivotal spatial mechanisms underpinning famous evolutionary processes such as adaptive radiations without relying solely on patterns in morphological trait data. Using a combination of fossil data, phylogenetic trees and the most realistic biogeographical model so far, we can finally shine light on the evolution of diversity through deep time and understand the processes governing how life is distributed over the planet, even in organisms that became extinct over 66 million years ago.

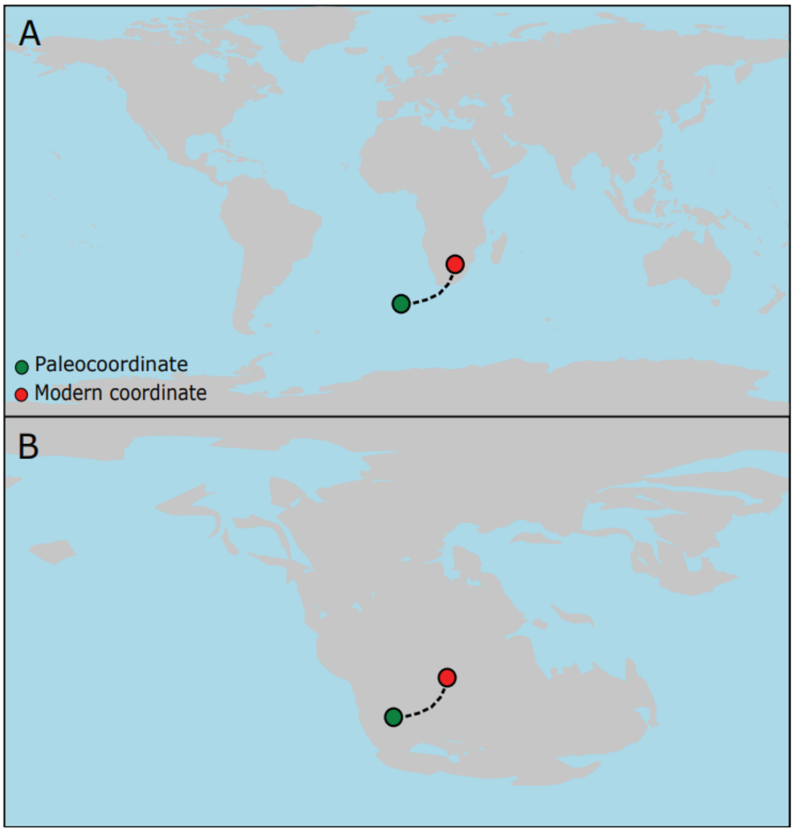
METHODS

Biogeographical data and phylogenies

We used geographical data downloaded from the PaleoBiology Database. Data were downloaded on 8 October 2014, using the group name 'Dinosauria' and the parameters latitude/ longitude (in decimal), paleolatitude/ paleolongitude (in decimal), period, stage, maximum age (Myr), minimum age (Myr) and midpoint age (Myr) via the Fossilworks portal (http://fossilworks.org) concerning the fossils of the Dinosauromorpha (which includes non-dinosaur dinosauromorphs and the Dinosauria). Specifically, the data regarding species' locations were paleocoordinate data that describe the longitudinal and latitudinal positions of the fossils at the time from which they were deposited (Methods Figure 1).

We sourced the paleomap reconstruction coordinates through the application programme interface (API) of the programme Macrostrat (https://macrostrat.org/), which uses the GPlates plate reconstruction model (EarthByte Project, 2015). We sourced a map for each of the 30 ages in the Mesozoic era and plotted them in base R (R Core Team, 2016).

To account for the fact that species' data are non-independent (Pagel, 1997), we study the spread of the dinosaurs using two previously constructed phylogenies (Benson *et al.*, 2014), which differ slightly in their topology. We time-calibrated the trees by scaling them using the mid-range value of the first appearance date (FAD) with the branch then extended to the mid-range value of the last appearance date (LAD) for each species. We used previously published age data (Benson *et al.*, 2014) to do this. We chose to use this method on the basis that the mid-range ages are good estimates of the FAD and LAD, and work within the given uncertainty that surrounds the dates. This method results in conservative estimates of the branch lengths (measured in millions of years) and thus also of the evolutionary rates. Our analyses are based on the assumption that these phylogenies provide a relatively reliable estimate of dinosaur evolutionary time scales. We used the 'mbl' method of the R package 'paleotree' (Bapst, 2012; R Core Team, 2016), enforcing a minimum branch length of 1Myr.

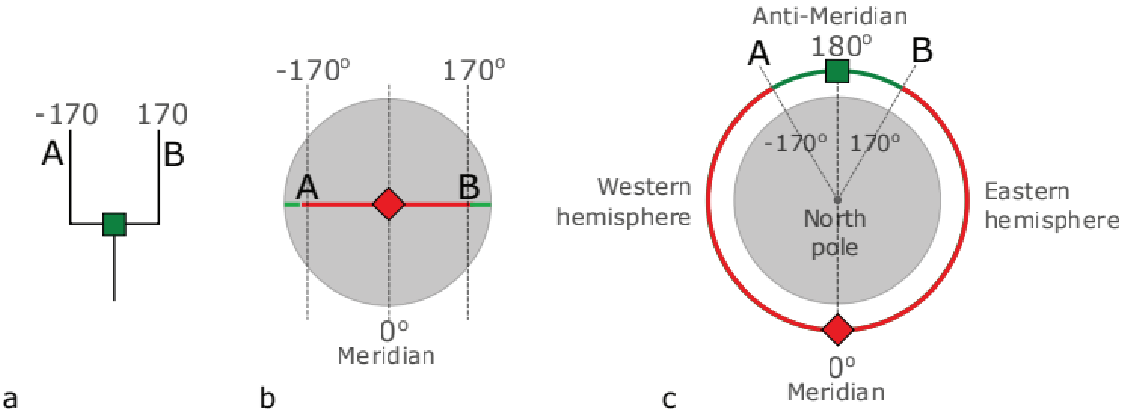


Methods Figure 1 | The importance of using coordinates that are in both the right geographic and temporal context. **a** - A modern map with a paleocoordinate (which occurs in the sea) plotted with its modern counterpart (which, correctly, occurs on land). **b** - The same coordinates as in **a** but plotted onto a paleomap representing the arrangement of the landmasses during the time period that the paleocoordinate comes from. Now in the correct temporal setting the green circle occurs on land as expected. This also demonstrates the importance of using paleocoordinates to understand past locations accurately; these points are 2,949km apart from each other.

Both trees contain 624 species of which we have data for 596 dinosaurs and 10 dinosauromorphs (which are included in the ancestral location reconstruction to aid in the estimation of the root location but subsequently removed from all other analyses). All analyses were run using both phylogenies to test the robustness of our method in the face of minor topological uncertainties. We present results from one of the two trees chosen arbitrarily owing to the fact that analyses from both trees yielded qualitatively the same results.

Ancestral location reconstruction

In previous studies of faunal biogeography, both actual and reconstructed biogeographical data were treated as discrete areas such as whole continents (for examples, see Lawing and Matzke, 2014; Walimbe *et al.,* 2014; Kaliszewska *et al.,* 2015; Fernando *et al.,* 2017; Wang *et al.,* 2017). This confines ancestral areas to the same finite locations as their descendant species at the tips of the phylogeny and limits the resolution of the information we can glean about a group's biogeographical history. We therefore build on more recent work reconstructing locations in continuous space (Lemmon and Lemmon, 2008; Lemey *et al.*, 2010; Walker and Ribeiro, 2011; Bouckaert *et al.*, 2012; Grollemund *et al.*, 2015) in three dimensions (Bouckaert, 2016). Our biogeographical model is implemented in the computer program BayesTraits (Pagel *et al.*, 2004).



Methods Figure 2 | The problem with using longitude (and latitude) in ancestral location reconstruction. **a** - A simple representation of a phylogenetic tree which shows how species A and B are related. The reconstruction of the location of their common ancestor (green square) demonstrates the problem with using longitude (and latitude) to describe locations on a sphere. **b** - The positions of species A and B on a 2D map of the Earth. When considered in a flat context, the two locations appear far apart (distance represented by the red line on the equator). The average of their longitudes is 0° which is where their ancestor's position would erroneously be reconstructed (red diamond). **c** - The two species' locations when considered on a 3D globe (represented by the grey circle as the Earth viewed from above) are very close. This is shown by the green line linking the species with the green square marking where the ancestor would be reconstructed. This green line represents the same green lines as in diagram **b**, which are severed as an artefact of projecting the 3D globe onto a flat map projection.

When using longitude and latitude as indicators of location over the entire Earth, the nature of the non-continuity of the longitude scale means that geographically close locations appear numerically far apart and thus, ancestral locations are reconstructed erroneously (Methods Figure 2). To study biogeographical spread we model the Earth as a more realistic sphere and therefore convert locations from longitude and latitude into coordinates in three-dimensional space (x, y and z) using the following formulae (Hofmann-Wellenhof, 1992; Jones, 1999):

Conversion to x, y, z:

$$x = (N + h) \cos\varphi \cos\lambda$$

$$y = (N + h) \cos\varphi \sin\lambda$$

$$z = ((b^2 / a^2) N + h) \sin\varphi$$

Conversion to longitude and latitude:

$$\varphi = \arctan((z + e'^2 b \sin^3 \theta) / (p - e^2 a \cos^3 \theta))$$

$$\lambda = \arctan(y / x)$$

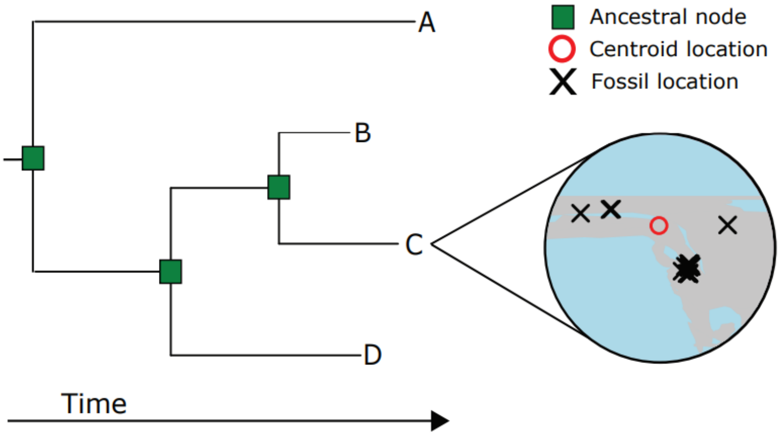
where x, y, z are the three-dimensional coordinates of the point in question, φ and λ represent the latitude and longitude, respectively, of the point, and h is the height of the point above the surface of the Earth. For simplicity h was kept at zero in our conversions. a and b are the lengths of the Earth's semi-major (6,384km) and semi-minor (6,353km) axes (radii), which we set as both equal to the mean of 6,371km given that we model the Earth as a perfect sphere. N is the curvature of the radius of the prime vertical (which describes the radius taken perpendicular to the point on the surface of the Earth until the polar axis is intersected) and is calculated by:

$$N = \frac{a^2}{\sqrt{a^2 \cos^2\varphi + b^2 \sin^2\varphi}}$$

e^2 is the eccentricity squared calculated by $(a^2 + b^2)/a^2$ and e'^2 is the second eccentricity squared and calculated by $(a^2 + b^2)/b^2$. An auxiliary quantity, θ, is calculated by (za/pb) and lastly p, which is equal to $\sqrt{x^2 + y^2}$.

To estimate ancestral locations we take advantage of the wealth of available dinosaur occurrence data and we sample these multiple tip locations in proportion to their probability (Methods Figure 3). This avoids using centroids, which are non-representative averages (Quintero *et al.*, 2015) of multiple geographical locations.

We estimate the ancestral positions, by first proposing a location that is an average of the longitude and latitude of its descendants. For each iteration of ancestral locations we move a certain distance (set by estimating the distance within which approximately 30% of suggested locations will be accepted) and random bearing away from this starting point. Subsequently proposed locations are made in three-dimensional space which are then converted into longitude and latitude, to confirm that the location is on the surface of the Earth, and then converted back to an *xyz* coordinate. This process continues as long as the MCMC chain proceeds with both tip and ancestral locations accepted in proportion to their probability.



Methods Figure 3 | The importance of including all of the available fossil occurrences as data at the tips of the phylogeny used to estimate ancestral locations (green squares). The red ring indicates the position of the centroid calculated given the fossil locations of the species *Dromaeosaurus albertensis* (black crosses). This location is likely to have been occupied by the species but given that no fossils have been found there we work on the basis of using precise locations of fossils that indicate definite presence at a location. Thus, we sample the distribution of locations given for each tip in the phylogeny according to their probability. We therefore incorporate realistic variation in the location of each species when estimating the ancestral locations.

Along with the tip and ancestral locations we simultaneously estimate the rates of evolution acting across the single phylogeny. We use a previously published variable rates model (Venditti *et al.*, 2011), which detects shifts away from the background rate of evolution (or expectation under a Brownian motion model of evolution) in whole clades of the phylogeny or on individual branches. Where previously ancestral states were implied in the model we now estimate them explicitly along with the rates and both are included in the calculation of the likelihood which follows the method of Elliot and Mooers, (2014):

$$L(x, \sigma; T) = \prod_{b} \phi(b_2 - b_1;\ t_n \sigma^2)$$

The likelihood is calculated given some data (*x*) for a continuously varying trait with a variance (σ^2) for a given tree (*T*). The probability of an ancestral state is calculated using the difference between the ancestral and descendant trait values at either end of the branch ($b_2 - b_1$) and the variance multiplied by that branch's length ($t_n\sigma^2$) where t_n denotes the time (branch length) of a given branch *'n'*. This probability is derived for every branch in the tree and then multiplied together and log-transformed to give the final log likelihood for a single iteration of the MCMC chain.

Lending credence to the realism of our model, 99.2% of our mean reconstructions are located within the bounds of the landmasses specific to the time period at which they occurred without having constrained the model with *a priori* information about the location of coastlines.

Converged chains

We ran five replicate MCMC chains (discarding at least the first 450 million iterations of each as burn-in). We sampled the chain every 50,000 iterations once all chains had reached convergence (as judged by visualizing the variation in the traces of each ancestral state and the likelihood). We concatenated the converged portions of these five chains and used a random 1,000 of these samples in all downstream analyses.

Branchwise and pathwise distances

Having included the ten dinosauromorphs in the phylogeny to aid in estimating an accurate location for the root ancestor of the dinosaurs, we subsequently removed them from all further analyses, being concerned with only the movement of the species within Dinosauria. To study the distances travelled through time by the dinosaurs, we calculated a pathwise distance for every dinosaur in the phylogeny (*n* = 595). We did this by taking one of the 1,000 samples of ancestral and tip locations at a time and calculating the distance between every ancestor and descendant in the tree. These branchwise distances were calculated using the 'distCosine' function of the 'geosphere' package in R (Hijmans, 2014; R Core Team, 2016). This method calculates the great circle distance (the shortest distance) between two points on a sphere measured in kilometres using the spherical law of cosines, which works for calculating these distances at both large and small scales. When all branchwise distances have been calculated, the result is a distribution of 1,000 distances for every branch in the tree.

Branchwise distances were then combined to make root-to-tip pathwise distances by summing all the distances along a tip's path. Again, this is done for every set of distances in the posterior which means we have 1,000 pathwise distances for every tip species in the tree. This means that our final measures of distance moved by the dinosaurs incorporates both the variation in fossil locations and the uncertainty in our ancestral location estimates. All pathwise distance measurements were log-transformed before use in further analyses.

We attribute the branchwise distances and thus also then the total distance associated with each species to biological or species' movement. However given the major continental conformation changes that occurred during the Mesozoic era, it is possible that some of the distance moved is attributable to continental movement, which we do not account for in our model. During each major time period of the Mesozoic era, we detect movement in every direction which would not be the case if the species were solely being carried by continental drift. This is particularly the case in times where we find directional movement as it is unlikely that all continents at this time were also exclusively moving in these directions, therefore meaning that it must have been biological movement. We believe that overall, given the global nature of these data that the effects of continental movement on the pattern of dinosaur spread we detect would be minimal. Given this pattern we also feel that the biological and ecological forces acting to determine where species could exist and how far they could move would outweigh the influence of continental movement (akin to previous results Dunhill *et al.,* 2016).

Phylogenetic regressions and model reduction

Pathwise distances allow us to quantify the convoluted paths that the ancestral dinosaurs traversed, which eventually resulted in the distributions of the dinosaur species that we have evidence of today. To explore whether there is a relationship between distances moved and time, and whether this differs amongst the major groups of dinosaurs, we ran phylogenetic generalized least-squares regressions in a Bayesian MCMC framework (Pagel *et al.*, 2004). We modelled log pathwise distance as the response variable with path length (PL, time elapsed from the root) as the predictor variable. In addition, we included several bias metrics as covariates in these regressions in order to account for the largely incomplete fossil record (Alroy, 2010). We included valid count, which quantifies the known under-representation of a sub-clade in a given phylogeny

(Sakamoto *et al.*, 2016). Formation count (the number of formations present at a particular geological time) is known to be associated with sampling bias (Barrett *et al.*, 2009; Upchurch *et al.*, 2011) and so we included stage-specific formation count, which describes the number of formations in each geological stage for every species in the tree, again using previously published data and protocol (Sakamoto *et al.*, 2016). To study the relationship between distance moved and speciation, we calculated the number of ancestral nodes in the phylogeny that preceded every species at the tips of the tree. These values were log-transformed, and log node count was used as a measure of speciation rate. Similarly to previous work (Sakamoto *et al.*, 2016), we used the sea level data of another study (Haq *et al.*, 1987) as a proxy for land area to see the impact of this on dinosaur movement. We also included data on diet (carnivore or not; Appendix 1, Table 1) and gait (quadruped, semi-biped or biped; Appendix 1, Table 1) to see whether these ecological factors had differential impacts on the dinosaurs' movements. Our sample size was reduced to 595 species owing to a lack of gait data for all of the species with geographical data.

We began with two regression models, one separating dinosaurs into Ornithischians, Sauropodomorphs, non-paravian Theropods and Paraves (henceforth to be referred to as the paravian model) and the other with dinosaurs split into Ornithischians, Sauropodomorphs, non-avian Theropods and Aves (henceforth the avian model). These groupings are well supported biologically and owing to prior knowledge regarding differences in the groups' overall biology it seemed logical to test whether these differences impacted their movement through time. The initial models estimated separate intercepts, slopes and quadratic terms for each of the four groups while also incorporating the above-mentioned covariates and group-gait interactions. We reduced these models using a strict protocol of removing the single most non-significant parameter and then rerunning the resulting models until we reached a single model where all of the parameters were significant. Parameter significance was judged by calculating a P_{MCMC} value for each posterior of regression coefficients, where <5% or >95% of the samples crossing zero indicates that the posterior of parameter estimates is significantly different from zero. Once this P_{MCMC} value had been calculated for all model parameters in all of the 1,000 regression posteriors, the percentage of the 1,000 regressions where a parameter was significant (P_{MCMC} <0.05 (5%) or P_{MCMC} > 0.95 (95%)) was calculated and is referred to as the $\%MCMC_{1,000}$ value. If the $\%MCMC_{1,000}$ value for a given parameter was > 95 (the parameter was significantly different from zero in >95% of the regressions) the parameter was considered as significant, otherwise it was considered for removal from the model.

The paravian and avian models reduced to the same model owing to the lack of significance of individual groups' quadratics, slopes and intercepts. This resulted in a model which estimated one intercept, slope and quadratic for all dinosaurs in one group, taking into account speciation (model: logDistance ~ PL + PL^2 + logNodeCount) and where all parameters were significant in all 1,000 regressions. On the basis that a previous study (Sakamoto *et al.*, 2016) found that speciation slowed through time, we tested our model with an additional quadratic term, $logNodeCount^2$, which we also found to be significant. Lastly, we modified our model to test whether there was an interaction between speciation and time, given that there is a statistical complication associated with estimating two quadratic terms without an interaction and likewise with estimating an interaction without two quadratics (Ganzach, 1997). We found that this product term significantly improved the model (logDistance ~ PL + PL^2 + logNodeCount + $logNodeCount^2$ + (PL x logNodeCount)). The percentage of the 1,000 regressions for which each parameter in the final model is significantly different from zero ($\%MCMC_{1,000}$; significant is >95): α (intercept) = 100, PL = 100, PL^2 = 100, logNodeCount = 100, $logNodeCount^2$ = 95.4 and PL x NodeCount = 99.3. These parameters explained almost half of the variation in distance moved (mean R^2 of the 1,000 regressions = 0.46).

Direction analyses

For every branch in the tree, given the ancestral and descendant locations, we calculated the bearing between the two points. We then categorized this bearing value into eight direction categories (north, northeast, east, southeast, south, southwest, west, northwest) with each describing a 45° portion of a circle. We did this for each branch (*n* = 1,084) for each set of ancestral locations (*n* = 1,000). To test whether branchwise speed of movement and branchwise distances were different in each direction in each of the geological time periods of the Mesozoic era (Triassic, Jurassic and Cretaceous) we ran standard least-squares regressions in JMP v.7 (JMP, 2007). We modelled branchwise distance (and speed in a second analysis) as the response variable with branchwise direction category as the explanatory variable with dataset (the 1,000 sets of branchwise data were concatenated but marked by a dataset number of 1 to 1,000) accounted for as a random effect. This allowed us to partition out the variance in branchwise distance or speed arising between the 1,000 samples of ancestral states. We carried out post hoc Tukey honestly significant difference tests on the three regressions (one for each time period of the Mesozoic) for the models with distance and speed in the eight directions.

The results of these indicated the magnitude of the mean distance or mean speed travelled in each direction and which of these were significantly different to each other.

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APPENDIX 1 | Dinosaur data

Table 1 | Diet and gait classifications for each dinosaur species (*n* = 595). Used in the phylogenetic regression analyses testing factors determining dinosaur movement

Species name	Diet	Gait
Pisanosaurus_mertii	Not carnivore	Bipedal
Echinodon_becklesii	Not carnivore	Bipedal
Fruitadens_haagarorum	Not carnivore	Bipedal
Tianyulong_confuciusi	Not carnivore	Bipedal
Lycorhinus_angustidens	Not carnivore	Semi-bipedal
Pegomastax_africanus	Not carnivore	Bipedal
Manidens_condorensis	Not carnivore	Bipedal
Abrictosaurus_consors	Not carnivore	Bipedal
Heterodontosaurus_tucki	Not carnivore	Bipedal
Lesothosaurus_diagnosticus	Not carnivore	Bipedal
Scutellosaurus_lawleri	Not carnivore	Semi-bipedal
Emausaurus_ernsti	Not carnivore	Quadrupedal
Scelidosaurus_harrisonii	Not carnivore	Quadrupedal
Chungkingosaurus_jiangbeiensis	Not carnivore	Quadrupedal
Huayangosaurus_taibaii	Not carnivore	Quadrupedal
Dacentrurus_armatus	Not carnivore	Quadrupedal
Kentrosaurus_aethiopicus	Not carnivore	Quadrupedal
Loricatosaurus_priscus	Not carnivore	Quadrupedal
Paranthodon_africanus	Not carnivore	Quadrupedal
Tuojiangosaurus_multispinus	Not carnivore	Quadrupedal
Stegosaurus_mjosi	Not carnivore	Quadrupedal
Stegosaurus_stenops	Not carnivore	Quadrupedal
Stegosaurus_ungulatus	Not carnivore	Quadrupedal
Minmi_paravertebra	Not carnivore	Quadrupedal
Cedarpelta_bilbeyhallorum	Not carnivore	Quadrupedal
Gobisaurus_domoculus	Not carnivore	Quadrupedal
Shamosaurus_scutatus	Not carnivore	Quadrupedal
Tsagantegia_longicranialis	Not carnivore	Quadrupedal
Zhongyuanosaurus_luoyangensis	Not carnivore	Quadrupedal
Crichtonsaurus_bohlini	Not carnivore	Quadrupedal
Crichtonsaurus_benxiensis	Not carnivore	Quadrupedal
Dyoplosaurus_acutesquamous	Not carnivore	Quadrupedal
Pinacosaurus_mephistocephalus	Not carnivore	Quadrupedal
Ankylosaurus_magniventris	Not carnivore	Quadrupedal
Euoplocephalus_tutus	Not carnivore	Quadrupedal
Pinacosaurus_grangeri	Not carnivore	Quadrupedal
Nodocephalosaurus_kirtlandensis	Not carnivore	Quadrupedal
Talarurus_plicatospineus	Not carnivore	Quadrupedal
Tianzhenosaurus_youngi	Not carnivore	Quadrupedal
Saichania_chulsanensis	Not carnivore	Quadrupedal
Tarchia_gigantea	Not carnivore	Quadrupedal
Antarctopelta_oliveroi	Not carnivore	Quadrupedal
Mymoorapelta_maysi	Not carnivore	Quadrupedal
Anoplosaurus_curtonotus	Not carnivore	Quadrupedal

Hylaeosaurus_armatus	Not carnivore	Quadrupedal
Tatankacephalus_cooneyorum	Not carnivore	Quadrupedal
Gargoyleosaurus_parkpinorum	Not carnivore	Quadrupedal
Hoplitosaurus_marshi	Not carnivore	Quadrupedal
Gastonia_burgei	Not carnivore	Quadrupedal
Peloroplites_cedrimontanus	Not carnivore	Quadrupedal
Polacanthus_foxii	Not carnivore	Quadrupedal
Struthiosaurus_transilvanicus	Not carnivore	Quadrupedal
Zhejiangosaurus_lishuiensis	Not carnivore	Quadrupedal
Hungarosaurus_tormai	Not carnivore	Quadrupedal
Animantarx_ramaljonesi	Not carnivore	Quadrupedal
Niobrarasaurus_coleii	Not carnivore	Quadrupedal
Nodosaurus_textilis	Not carnivore	Quadrupedal
Pawpawsaurus_campbelli	Not carnivore	Quadrupedal
Sauropelta_edwardsi	Not carnivore	Quadrupedal
Silvisaurus_condrayi	Not carnivore	Quadrupedal
Stegopelta_landerensis	Not carnivore	Quadrupedal
Texasetes_pleurohalio	Not carnivore	Quadrupedal
Panoplosaurus_mirus	Not carnivore	Quadrupedal
Edmontonia_longiceps	Not carnivore	Quadrupedal
Edmontonia_rugosidens	Not carnivore	Quadrupedal
Stormbergia_dangershoeki	Not carnivore	Bipedal
Agilisaurus_louderbacki	Not carnivore	Bipedal
Hexinlusaurus_multidens	Not carnivore	Bipedal
Goyocephale_lattimorei	Not carnivore	Bipedal
Homalocephale_calathocercos	Not carnivore	Bipedal
Colepiocephale_lambei	Not carnivore	Bipedal
Stegoceras_validum	Not carnivore	Bipedal
Stegoceras_novomexicanum	Not carnivore	Bipedal
Amtocephale_gobiensis	Not carnivore	Bipedal
Prenocephale_prenes	Not carnivore	Bipedal
Tylocephale_gilmorei	Not carnivore	Bipedal
Hanssuesia_sternbergi	Not carnivore	Bipedal
Pachycephalosaurus_wyomingensis	Not carnivore	Bipedal
Yinlong_downsi	Not carnivore	Semi-bipedal
Micropachycephalosaurus_hongtuyanensis	Not carnivore	Bipedal
Chaoyangsaurus_youngi	Not carnivore	Semi-bipedal
Xuanhuaceratops_niei	Not carnivore	Semi-bipedal
Psittacosaurus_mongoliensis	Not carnivore	Semi-bipedal
Psittacosaurus_neimongoliensis	Not carnivore	Semi-bipedal
Psittacosaurus_sinensis	Not carnivore	Semi-bipedal
Psittacosaurus_gobiensis	Not carnivore	Semi-bipedal
Liaoceratops_yanzigouensis	Not carnivore	Semi-bipedal
Yamaceratops_dorngobiensis	Not carnivore	Semi-bipedal
Archaeoceratops_oshimai	Not carnivore	Quadrupedal
Archaeoceratops_yujingziensis	Not carnivore	Semi-bipedal
Koreaceratops_hwaseongensis	Not carnivore	Quadrupedal
Asiaceratops_salsopaludalis	Not carnivore	Quadrupedal
Cerasinops_hodgskissi	Not carnivore	Quadrupedal
Montanoceratops_cerorynchus	Not carnivore	Quadrupedal
Prenoceratops_pieganensis	Not carnivore	Quadrupedal
Leptoceratops_gracilis	Not carnivore	Bipedal
Udanoceratops_tschizhovi	Not carnivore	Quadrupedal
Zhuchengceratops_inexpectus	Not carnivore	Semi-bipedal

Gryphoceratops_morrisoni	Not carnivore	Semi-bipedal
Unescoceratops_koppelhusae	Not carnivore	Bipedal
Graciliceratops_mongoliensis	Not carnivore	Quadrupedal
Bagaceratops_rozhdestvenskyi	Not carnivore	Quadrupedal
Protoceratops_andrewsi	Not carnivore	Quadrupedal
Turanoceratops_tardabilis	Not carnivore	Quadrupedal
Zuniceratops_christopheri	Not carnivore	Quadrupedal
Diabloceratops_eatoni	Not carnivore	Quadrupedal
Albertaceratops_nesmoi	Not carnivore	Quadrupedal
Centrosaurus_apertus	Not carnivore	Quadrupedal
Spinops_sternbergorum	Not carnivore	Quadrupedal
Styracosaurus_albertensis	Not carnivore	Quadrupedal
Centrosaurus_brinkmani	Not carnivore	Quadrupedal
Rubeosaurus_ovatus	Not carnivore	Quadrupedal
Einiosaurus_procurvicornis	Not carnivore	Quadrupedal
Achelousaurus_horneri	Not carnivore	Quadrupedal
Pachyrhinosaurus_lakustai	Not carnivore	Quadrupedal
Pachyrhinosaurus_canadensis	Not carnivore	Quadrupedal
Pachyrhinosaurus_perotorum	Not carnivore	Quadrupedal
Chasmosaurus_russelli	Not carnivore	Quadrupedal
Chasmosaurus_belli	Not carnivore	Quadrupedal
Agujaceratops_mariscalensis	Not carnivore	Quadrupedal
Pentaceratops_sternbergii	Not carnivore	Quadrupedal
Utahceratops_gettyi	Not carnivore	Quadrupedal
Coahuilaceratops_magnacuerna	Not carnivore	Quadrupedal
Kosmoceratops_richardsoni	Not carnivore	Quadrupedal
Vagaceratops_irvinensis	Not carnivore	Quadrupedal
Anchiceratops_ornatus	Not carnivore	Quadrupedal
Arrhinoceratops_brachyops	Not carnivore	Quadrupedal
Eotriceratops_xerinsularis	Not carnivore	Quadrupedal
Ojoceratops_fowleri	Not carnivore	Quadrupedal
Torosaurus_latus	Not carnivore	Quadrupedal
Triceratops_horridus	Not carnivore	Quadrupedal
Triceratops_prorsus	Not carnivore	Quadrupedal
Gideonmantellia_amosanjuanae	Not carnivore	Bipedal
Oryctodromeus_cubicularis	Not carnivore	Bipedal
Koreanosaurus_boseongensis	Not carnivore	Semi-bipedal
Orodromeus_makelai	Not carnivore	Bipedal
Zephyrosaurus_schaffi	Not carnivore	Bipedal
Parksosaurus_warreni	Not carnivore	Bipedal
Thescelosaurus_neglectus	Not carnivore	Bipedal
Thescelosaurus_assiniboiensis	Not carnivore	Bipedal
Jeholosaurus_shangyuanensis	Not carnivore	Bipedal
Changchunsaurus_parvus	Not carnivore	Bipedal
Haya_griva	Not carnivore	Bipedal
Hypsilophodon_foxi	Not carnivore	Bipedal
Gasparinisaura_cincosaltensis	Not carnivore	Bipedal
Anabisetia_saldiviai	Not carnivore	Bipedal
Macrogryphosaurus_gondwanicus	Not carnivore	Bipedal
Talenkauen_santacrucensis	Not carnivore	Semi-bipedal
Muttaburrasaurus_langdoni	Not carnivore	Semi-bipedal
Rhabdodon_priscum	Not carnivore	Semi-bipedal
Zalmoxes_robustus	Not carnivore	Semi-bipedal
Zalmoxes_shqiperorum	Not carnivore	Semi-bipedal

Mochlodon_suessi	Not carnivore	Semi-bipedal
Mochlodon_vorosi	Not carnivore	Semi-bipedal
Tenontosaurus_tilletti	Not carnivore	Semi-bipedal
Tenontosaurus_dossi	Not carnivore	Semi-bipedal
Callovosaurus_leedsi	Not carnivore	Semi-bipedal
Dryosaurus_altus	Not carnivore	Bipedal
Dysalotosaurus_lettowvorbecki	Not carnivore	Bipedal
Kangnasaurus_coetzeei	-	-
Valdosaurus_canaliculatus	Not carnivore	Bipedal
Camptosaurus_dispar	Not carnivore	Semi-bipedal
Cumnoria_prestwichii	Not carnivore	Semi-bipedal
Uteodon_aphanoecetes	Not carnivore	Semi-bipedal
Hippodraco_scutodens	Not carnivore	Semi-bipedal
Theiophytalia_kerri	Not carnivore	Semi-bipedal
Cedarorestes_crichtoni	Not carnivore	Semi-bipedal
Dakotadon_lakotaensis	Not carnivore	Semi-bipedal
Iguanacolossus_fortis	Not carnivore	Semi-bipedal
Lanzhousaurus_magnidens	Not carnivore	Semi-bipedal
Barilium_dawsoni	Not carnivore	Semi-bipedal
Iguanodon_bernissartensis	Not carnivore	Semi-bipedal
Ouranosaurus_nigeriensis	Not carnivore	Semi-bipedal
Mantellisaurus_atherfieldensis	Not carnivore	Semi-bipedal
Jinzhousaurus_yangi	Not carnivore	Semi-bipedal
Penelopognathus_weishampeli	Not carnivore	Semi-bipedal
Altirhinus_kurzanovi	Not carnivore	Semi-bipedal
Equijubus_normani	Not carnivore	Semi-bipedal
Probactrosaurus_mazongshanensis	Not carnivore	Semi-bipedal
Eolambia_caroljonesa	Not carnivore	Semi-bipedal
Probactrosaurus_gobiensis	Not carnivore	Semi-bipedal
Jeyawati_rugoculus	Not carnivore	Semi-bipedal
Protohadros_byrdi	Not carnivore	Semi-bipedal
Tethyshadros_insularis	Not carnivore	Semi-bipedal
Nanyangosaurus_zhugeii	Not carnivore	Semi-bipedal
Tanius_sinensis	Not carnivore	Semi-bipedal
Gilmoreosaurus_mongolensis	Not carnivore	Semi-bipedal
Bactrosaurus_johnsoni	Not carnivore	Semi-bipedal
Shuangmiaosaurus_gilmorei	Not carnivore	Semi-bipedal
Claosaurus_agilis	Not carnivore	Semi-bipedal
Telmatosaurus_transsylvanicus	Not carnivore	Semi-bipedal
Lophorhothon_atopus	Not carnivore	Semi-bipedal
Wulagasaurus_dongi	Not carnivore	Semi-bipedal
Acristavus_gagslarsoni	Not carnivore	Semi-bipedal
Brachylophosaurus_canadensis	Not carnivore	Semi-bipedal
Maiasaura_peeblesorum	Not carnivore	Semi-bipedal
Barsboldia_sicinskii	Not carnivore	Semi-bipedal
Kritosaurus_navajovius	Not carnivore	Semi-bipedal
Gryposaurus_notabilis	Not carnivore	Semi-bipedal
Gryposaurus_monumentensis	Not carnivore	Semi-bipedal
Gryposaurus_latidens	Not carnivore	Semi-bipedal
Secernosaurus_koerneri	Not carnivore	Semi-bipedal
Willinakaqe_salitralensis	Not carnivore	Semi-bipedal
Prosaurolophus_maximus	Not carnivore	Semi-bipedal
Saurolophus_osborni	Not carnivore	Semi-bipedal
Saurolophus_angustirostris	Not carnivore	Semi-bipedal

Kerberosaurus_manakini	Not carnivore	Semi-bipedal
Kundurosaurus_nagornyi	Not carnivore	Semi-bipedal
Shantungosaurus_giganteus	Not carnivore	Semi-bipedal
Edmontosaurus_annectens	Not carnivore	Semi-bipedal
Edmontosaurus_regalis	Not carnivore	Semi-bipedal
Aralosaurus_tuberiferus	Not carnivore	Semi-bipedal
Pararhabdodon_isonensis	Not carnivore	Semi-bipedal
Tsintaosaurus_spinorhinus	Not carnivore	Semi-bipedal
Jaxartosaurus_aralensis	Not carnivore	Semi-bipedal
Arenysaurus_ardevoli	Not carnivore	Semi-bipedal
Blasisaurus_canudoi	Not carnivore	Semi-bipedal
Charonosaurus_jiayinensis	Not carnivore	Semi-bipedal
Parasaurolophus_walkeri	Not carnivore	Semi-bipedal
Parasaurolophus_cyrtoctristatus	Not carnivore	Semi-bipedal
Amurosaurus_riabinini	Not carnivore	Semi-bipedal
Sahaliyania_elunchunorum	Not carnivore	Semi-bipedal
Magnapaulia_laticaudus	Not carnivore	Semi-bipedal
Lambeosaurus_lambei	Not carnivore	Semi-bipedal
Lambeosaurus_magnicristatus	Not carnivore	Semi-bipedal
Corythosaurus_casuarius	Not carnivore	Semi-bipedal
Olorotitan_arharensis	Not carnivore	Semi-bipedal
Hypacrosaurus_altispinus	Not carnivore	Semi-bipedal
Hypacrosaurus_stebingeri	Not carnivore	Semi-bipedal
Pampdromaeus	Not carnivore	Bipedal
Saturnalia	Not carnivore	Bipedal
Chromogisaurus	Not carnivore	Quadrupedal
Pantydraco	Not carnivore	Bipedal
Arcusaurus	Not carnivore	Semi-bipedal
Thecodontosaurus	Not carnivore	Bipedal
Efraasia	Not carnivore	Semi-bipedal
Plateosauravus	Not carnivore	Semi-bipedal
Ruehleia	Not carnivore	Semi-bipedal
Plateosaurus_engelhardti	Not carnivore	Semi-bipedal
Unaysaurus	Not carnivore	Semi-bipedal
Riojasaurus	Not carnivore	Semi-bipedal
Eucnemesaurus	Not carnivore	Semi-bipedal
Sarahsaurus	Not carnivore	Quadrupedal
Massospondylus	Not carnivore	Semi-bipedal
Leyesaurus	Not carnivore	Semi-bipedal
Adeopapposaurus	Not carnivore	Semi-bipedal
Coloradisaurus	Not carnivore	Semi-bipedal
Glacialisaurus	Not carnivore	Quadrupedal
Lufengosaurus	Not carnivore	Semi-bipedal
Jingshanosaurus	Not carnivore	Semi-bipedal
Yunnanosaurus_huangi	Not carnivore	Semi-bipedal
Chuxiongosaurus	Not carnivore	Semi-bipedal
Seitaad	Not carnivore	Quadrupedal
Anchisaurus	Not carnivore	Semi-bipedal
Aardonyx	Not carnivore	Semi-bipedal
Leonerasaurus	Not carnivore	Semi-bipedal
Melanorosaurus	Not carnivore	Quadrupedal
Antetonitrus	Not carnivore	Quadrupedal
Lessemsaurus	Not carnivore	Semi-bipedal
Lamplughsaura	Not carnivore	Quadrupedal

Camelotia	Not carnivore	Quadrupedal
Gongxianosaurus	Not carnivore	Quadrupedal
Isanosaurus	Not carnivore	Quadrupedal
Tazoudasaurus	Not carnivore	Quadrupedal
Vulcanodon	Not carnivore	Quadrupedal
Rhoetosaurus	Not carnivore	Quadrupedal
Kotasaurus	Not carnivore	Quadrupedal
Spinophorosaurus	Not carnivore	Quadrupedal
Shunosaurus	Not carnivore	Quadrupedal
Datousaurus	Not carnivore	Quadrupedal
Cetiosaurus	Not carnivore	Quadrupedal
Patagosaurus	Not carnivore	Quadrupedal
Barapasaurus	Not carnivore	Quadrupedal
Klamelisaurus	Not carnivore	Quadrupedal
Chuanjiesaurus	Not carnivore	Quadrupedal
Mamenchisaurus_youngi	Not carnivore	Quadrupedal
Mamenchisaurus_constructus	Not carnivore	Quadrupedal
Yuanmousaurus_jiangyiensis	Not carnivore	Quadrupedal
Cetiosauriscus	Not carnivore	Quadrupedal
Omeisaurus_junghsiensis	Not carnivore	Quadrupedal
Omeisaurus_jiaoi	Not carnivore	Quadrupedal
Omeisaurus_maoanus	Not carnivore	Quadrupedal
Omeisaurus_tianfuensis	Not carnivore	Quadrupedal
Ferganasaurus	Not carnivore	Quadrupedal
Turiasaurus	Not carnivore	Quadrupedal
Jobaria	Not carnivore	Quadrupedal
Atlasaurus	Not carnivore	Quadrupedal
Haplocanthosaurus_priscus	Not carnivore	Quadrupedal
Amphicoelias	Not carnivore	Quadrupedal
Nigersaurus	Not carnivore	Quadrupedal
Demandasaurus	Not carnivore	Quadrupedal
Cathartesaura	Not carnivore	Quadrupedal
Limaysaurus	Not carnivore	Quadrupedal
Zapalasaurus	Not carnivore	Quadrupedal
Rebbachisaurus	Not carnivore	Quadrupedal
Comahuesaurus	Not carnivore	Quadrupedal
Dicraeosaurus_sattleri	Not carnivore	Quadrupedal
Brachytrachelopan	Not carnivore	Quadrupedal
Amargasaurus	Not carnivore	Quadrupedal
Suuwassea	Not carnivore	Quadrupedal
Apatosaurus_ajax	Not carnivore	Quadrupedal
Apatosaurus_excelsus	Not carnivore	Quadrupedal
Apatosaurus_louisae	Not carnivore	Quadrupedal
Tornieria	Not carnivore	Quadrupedal
Barosaurus	Not carnivore	Quadrupedal
Diplodocus_carnegiei	Not carnivore	Quadrupedal
Diplodocus_hayi	Not carnivore	Quadrupedal
Diplodocus_hallorum	Not carnivore	Quadrupedal
Diplodocus_longus	Not carnivore	Quadrupedal
Lourinhasaurus	Not carnivore	Quadrupedal
Camarasaurus_lewisi	Not carnivore	Quadrupedal
Camarasaurus_supremus	Not carnivore	Quadrupedal
Camarasaurus_grandis	Not carnivore	Quadrupedal
Janenschia	Not carnivore	Quadrupedal

Tehuelchesaurus	Not carnivore	Quadrupedal
Aragosaurus	Not carnivore	Quadrupedal
Galveosaurus	Not carnivore	Quadrupedal
Europasaurus	Not carnivore	Quadrupedal
Brachiosaurus	Not carnivore	Quadrupedal
Lusotitan	Not carnivore	Quadrupedal
Giraffatitan	Not carnivore	Quadrupedal
Cedarosaurus	Not carnivore	Quadrupedal
Venenosaurus	Not carnivore	Quadrupedal
Dongbeititan	Not carnivore	Quadrupedal
Sauroposeidon	Not carnivore	Quadrupedal
Sonorasaurus	Not carnivore	Quadrupedal
Tastavinsaurus	Not carnivore	Quadrupedal
Pelorosaurus_becklesii	Not carnivore	Quadrupedal
Euhelopus	Not carnivore	Quadrupedal
Erketu	Not carnivore	Quadrupedal
Qiaowanlong	Not carnivore	Quadrupedal
Gobititan	Not carnivore	Quadrupedal
Tangvayosaurus	Not carnivore	Quadrupedal
Phuwiangosaurus	Not carnivore	Quadrupedal
Chubutisaurus	Not carnivore	Quadrupedal
Ruyangosaurus	Not carnivore	Quadrupedal
Wintonotitan	Not carnivore	Quadrupedal
Ligabuesaurus	Not carnivore	Quadrupedal
Andesaurus	Not carnivore	Quadrupedal
Futalognkosaurus	Not carnivore	Quadrupedal
Mendozasaurus	Not carnivore	Quadrupedal
Argentinosaurus	Not carnivore	Quadrupedal
Epachthosaurus	Not carnivore	Quadrupedal
Malawisaurus	Not carnivore	Quadrupedal
Nemegtosaurus	Not carnivore	Quadrupedal
Isisaurus	Not carnivore	Quadrupedal
Tapuiasaurus	Not carnivore	Quadrupedal
Gondwanatitan	Not carnivore	Quadrupedal
Aeolosaurus_maximus	Not carnivore	Quadrupedal
Aeolosaurus_sp.	Not carnivore	Quadrupedal
Aeolosaurus_rionegrinus	Not carnivore	Quadrupedal
Muyelensaurus	Not carnivore	Quadrupedal
Rinconsaurus	Not carnivore	Quadrupedal
Alamosaurus	Not carnivore	Quadrupedal
Opisthocoelicaudia	Not carnivore	Quadrupedal
Rocasaurus	Not carnivore	Quadrupedal
Neuquensaurus	Not carnivore	Quadrupedal
Saltasaurus	Not carnivore	Quadrupedal
Herrerasaurus	Carnivore	Bipedal
Staurikosaurus	Carnivore	Bipedal
Eoraptor	Carnivore	Bipedal
Daemonosaurus	Carnivore	Bipedal
Tawa	Carnivore	Bipedal
Skayentakatae	Carnivore	Bipedal
Coelophysis_bauri	Carnivore	Bipedal
Coelophysis_rhodesiensis	Carnivore	Bipedal
Liliensternus	Carnivore	Bipedal
Zupaysaurus	Carnivore	Bipedal

Dilophosaurus	Carnivore	Bipedal
Spinostropheus	Carnivore	Bipedal
Elaphrosaurus	Carnivore	Bipedal
Limusaurus	Carnivore	Bipedal
Ceratosaurus	Carnivore	Bipedal
Genyodectes	Carnivore	Bipedal
Masiakasaurus	Carnivore	Bipedal
Genusaurus	Carnivore	Bipedal
Noasaurus	Carnivore	Bipedal
Velocisaurus	Carnivore	Bipedal
Laevisuchus	Carnivore	Bipedal
Eoabelisaurus	Carnivore	Bipedal
Rugops	Carnivore	Bipedal
Abelisaurus	Carnivore	Bipedal
Indosaurus	Carnivore	Bipedal
Majungasaurus	Carnivore	Bipedal
Rajasaurus	Carnivore	Bipedal
Aucasaurus	Carnivore	Bipedal
Carnotaurus	Carnivore	Bipedal
Ekrixinatosaurus	Carnivore	Bipedal
Skorpiovenator	Carnivore	Bipedal
Ilokelesia	Carnivore	Bipedal
Cryolophosaurus	Carnivore	Bipedal
D_sinensis	Carnivore	Bipedal
Monolophosaurus	Carnivore	Bipedal
Marshosaurus	Carnivore	Bipedal
Condorraptor	Carnivore	Bipedal
Piatnizkysaurus	Carnivore	Bipedal
Spinosaurus	Carnivore	Bipedal
Angaturama	Carnivore	Bipedal
Irritator	Carnivore	Bipedal
Suchomimus	Carnivore	Bipedal
Baryonyx	Carnivore	Bipedal
Eustreptospondylus	Carnivore	Bipedal
Afrovenator	Carnivore	Bipedal
Magnosaurus	Carnivore	Bipedal
Dubreuillosaurus	Carnivore	Bipedal
Leshansaurus	Carnivore	Bipedal
Piveaeausaurus	Carnivore	Bipedal
Duriavenator	Carnivore	Bipedal
Megalosaurus	Carnivore	Bipedal
Torvosaurus	Carnivore	Bipedal
Shidaisaurus	Carnivore	Bipedal
Metriacanthosaurus	Carnivore	Bipedal
Sinraptor_hepingensis	Carnivore	Bipedal
Sinraptor_dongi	Carnivore	Bipedal
Siamotyrannus	Carnivore	Bipedal
Yangchuanosaurus_zigongensis	Carnivore	Bipedal
Yangchuanosaurus_magnus	Carnivore	Bipedal
Allosaurus	Carnivore	Bipedal
Saurophaganax	Carnivore	Bipedal
Neovenator	Carnivore	Bipedal
Chilantaisaurus	Carnivore	Bipedal
Aerosteon	Carnivore	Bipedal

Megaraptor	Carnivore	Bipedal
Australovenator	Carnivore	Bipedal
Fukuiraptor	Carnivore	Bipedal
Eocarcharia	Carnivore	Bipedal
Concavenator	Carnivore	Bipedal
Acrocanthosaurus	Carnivore	Bipedal
Shaochilong	Carnivore	Bipedal
Tyrannotitan	Carnivore	Bipedal
Carcharodontosaurus	Carnivore	Bipedal
Giganotosaurus	Carnivore	Bipedal
Mapusaurus	Carnivore	Bipedal
Zuolong	Carnivore	Bipedal
Tanycolagreus	Carnivore	Bipedal
Guanlong	Carnivore	Bipedal
Proceratosaurus	Carnivore	Bipedal
Sinotyrannus	Carnivore	Bipedal
Dilong	Carnivore	Bipedal
Stokesosaurus	Carnivore	Bipedal
Eotyrannus	Carnivore	Bipedal
Xiongguanlong	Carnivore	Bipedal
Dryptosaurus	Carnivore	Bipedal
Appalachiosaurus	Carnivore	Bipedal
Bistahieversor	Carnivore	Bipedal
Albertosaurus	Carnivore	Bipedal
Gorgosaurus	Carnivore	Bipedal
Alioramus	Carnivore	Bipedal
Teratophoneus	Carnivore	Bipedal
Daspletosaurus	Carnivore	Bipedal
Tarbosaurus	Carnivore	Bipedal
Tyrannosaurus	Carnivore	Bipedal
Nqwebasaurus	Not carnivore	Bipedal
Pelecanimimus	Not carnivore	Bipedal
Hexing	Not carnivore	Bipedal
Shenzhousaurus	Carnivore	Bipedal
Harpymimus	Not carnivore	Bipedal
Beishanlong	Not carnivore	Bipedal
Garudimimus	Not carnivore	Bipedal
Archaeornithomimus	Not carnivore	Bipedal
Sinornithomimus	Carnivore	Bipedal
Gallimimus	Not carnivore	Bipedal
Anserimimus	Not carnivore	Bipedal
Struthiomimus	Not carnivore	Bipedal
Ornithomimus	Not carnivore	Bipedal
Ornitholestes	Carnivore	Bipedal
Sinosauropteryx	Carnivore	Bipedal
Huixagnathus	Carnivore	Bipedal
Compsognathus	Carnivore	Bipedal
Haplocheirus	Not carnivore	Bipedal
Patagonykus	Not carnivore	Bipedal
Alvarezsaurus	Not carnivore	Bipedal
Parvicursor	Not carnivore	Bipedal
Mononykus	Not carnivore	Bipedal
Shuvuuia	Not carnivore	Bipedal
Incisivosaurus	Not carnivore	Bipedal

Caudipteryx	Not carnivore	Bipedal
Protarchaeopteryx	Not carnivore	Bipedal
Similicaudipteryx	Not carnivore	Bipedal
Avimimus	Not carnivore	Bipedal
Microvenator	Not carnivore	Bipedal
Gigantoraptor	Not carnivore	Bipedal
Caenagnathasia	Not carnivore	Bipedal
Elmisaurus	Not carnivore	Bipedal
Leptorhynchos	Not carnivore	Bipedal
Hagryphus	Not carnivore	Bipedal
Chirostenotes	Not carnivore	Bipedal
Caenagnathus	Not carnivore	Bipedal
Oviraptor	Not carnivore	Bipedal
Citipati	Not carnivore	Bipedal
Khaan	Not carnivore	Bipedal
Conchoraptor	Not carnivore	Bipedal
Machairasaurus	Not carnivore	Bipedal
Nemegtomaia	Not carnivore	Bipedal
Heyuannia	Not carnivore	Bipedal
Ingenia	Not carnivore	Bipedal
Falcarius	Not carnivore	Bipedal
Alxasaurus	Not carnivore	Bipedal
Erliansaurus	Not carnivore	Bipedal
Neimongosaurus	Not carnivore	Bipedal
Suzhousaurus	Not carnivore	Bipedal
Nanshiungosaurus	Not carnivore	Bipedal
Erlikosaurus	Not carnivore	Bipedal
Therizinosaurus	Not carnivore	Bipedal
Nothronychus_graffami	Not carnivore	Bipedal
Nothronychus_mckinleyi	Not carnivore	Bipedal
Epidexipteryx	Carnivore	Bipedal
Anchiornis	Carnivore	Bipedal
Xiaotingia	Carnivore	Bipedal
Jinfengopteryx	Carnivore	Bipedal
Mei	Carnivore	Bipedal
Sinovenator	Carnivore	Bipedal
Xixiasaurus	Carnivore	Bipedal
Byronosaurus	Carnivore	Bipedal
Sinornithoides	Carnivore	Bipedal
Troodon	Carnivore	Bipedal
Linhevenator	Carnivore	Bipedal
Saurornithoides	Carnivore	Bipedal
Zanzabazaar	Carnivore	Bipedal
Makhala	Carnivore	Bipedal
Rahonavis	Carnivore	Bipedal
Buitreraptor	Carnivore	Bipedal
Unenlagia	Carnivore	Bipedal
Austroraptor	Carnivore	Bipedal
Shanag	Carnivore	Bipedal
Microraptor_zhaoianus	Carnivore	Bipedal
Microraptor_gui	Carnivore	Bipedal
Hesperonychus	Carnivore	Bipedal
Graciliraptor	Carnivore	Bipedal
Sinornithosaurus	Carnivore	Bipedal

Tianyuraptor	Carnivore	Bipedal
Dromaeosaurus	Carnivore	Bipedal
Achillobator	Carnivore	Bipedal
Utahraptor	Carnivore	Bipedal
Atrociraptor	Carnivore	Bipedal
Bambiraptor	Carnivore	Bipedal
Tsaagan	Carnivore	Bipedal
Saurornitholestes	Carnivore	Bipedal
Balaur	Carnivore	Bipedal
Velociraptor	Carnivore	Bipedal
Deinonychus	Carnivore	Bipedal
Archaeopteryx	Carnivore	Bipedal
Sapeornis	Carnivore	Bipedal
Jeholornis	Carnivore	Bipedal
Jixianornis	Carnivore	Bipedal
Zhongornis	Carnivore	Bipedal
Eoconfuciusornis	Carnivore	Bipedal
Changchengornis	Carnivore	Bipedal
Confuciusornis_sanctus	Carnivore	Bipedal
Confuciusornis_dui	Carnivore	Bipedal
Jinzhouornis_zhangjiyingia	Carnivore	Bipedal
Protopteryx	Carnivore	Bipedal
Otogornis	Carnivore	Bipedal
Elsornis	Carnivore	Bipedal
Shenqiornis	Carnivore	Bipedal
Longipteryx	Carnivore	Bipedal
Boluochia	Carnivore	Bipedal
Rapaxavis	Carnivore	Bipedal
Iberomesornis	Carnivore	Bipedal
Shanweiniao	Carnivore	Bipedal
Longirostravis	Carnivore	Bipedal
Vescornis	Carnivore	Bipedal
Pengornis	Carnivore	Bipedal
Gobipteryx	Carnivore	Bipedal
Neuquenornis	Carnivore	Bipedal
Eoenantiornis	Carnivore	Bipedal
Concornis	Carnivore	Bipedal
Eocathayornis	Carnivore	Bipedal
Cathayornis	Carnivore	Bipedal
Liaoningornis	Not carnivore	Bipedal
Eoalulavis	Carnivore	Bipedal
Archaeorhynchus	Carnivore	Bipedal
Patagopteryx	Not carnivore	Bipedal
Jianchangornis	Carnivore	Bipedal
Schizooura	Carnivore	Bipedal
Vorona	Carnivore	Bipedal
Zhongjianornis	Carnivore	Bipedal
Chaoyangia	Carnivore	Bipedal
Hongshanornis	Carnivore	Bipedal
Longicrusavis	Carnivore	Bipedal
Yixianornis	Carnivore	Bipedal
Yanornis	Carnivore	Bipedal
Songlingornis	Carnivore	Bipedal
Gansus	Carnivore	Bipedal

Apsaravis	Carnivore	Bipedal
Ambiortus	Carnivore	Bipedal
Hollanda	Carnivore	Bipedal
Ichthyornis	Carnivore	Bipedal
Vegavis	Carnivore	Bipedal
Limenavis	Carnivore	Bipedal
Enaliornis	Carnivore	Bipedal
Baptornis_advenus	Carnivore	Bipedal
Baptornis_varneri	Carnivore	Bipedal
Parahesperornis	Carnivore	Bipedal
Hesperornis	Carnivore	Bipedal

Chapter 2 | The nature of morphological change

"*Nature gives to every time and season some beauties of its own; and from morning to night, as from the cradle to the grave, it is but a succession of changes so gentle and steady that we can scarcely mark their progress*".
Charles Dickens, (1839)[1]

ABSTRACT

Understanding the complexities of the evolutionary processes is central to revealing how diversity is generated. We use a model that detects varying rates of evolution to reconstruct ancestral body sizes in phylogenies spanning the tree of life. From these reconstructions we calculate changes in trait value along every phylogenetic branch and quantify two classes of evolutionary change: 'regular' and 'exceptional' on the basis of their magnitude. We test the relative frequencies of changes to increase and decrease body size and whether their magnitude differs depending on direction. We also test the dynamics of morphological change through time and whether regular and exceptional changes have evolved differently to each other. Given the influence of species ecologies and life histories on their evolution we investigate if the magnitude of changes is different in organisms occupying varying habitats, in different taxonomic groups and with different broad metabolic strategies. We reveal the mode of morphological evolution which is characterised predominantly by extremely small and Darwian-type changes, interspersed with those akin to Simpson's quantum leaps. Whilst body size reductions have occurred more frequently, changes to increase body size are larger in magnitude suggestive that the mode of evolution differs depending on the direction of change in trait being selected for. Habitat and taxonomic history were found to have a significant influence on the magnitude of changes meaning that traits such as body size are a product of the interplay between biological history and environmental forces. There is an increase in the magnitude of changes to body size through evolutionary time. We propose that this 'late burst' pattern may be indicative of large shifts in trait occurring within adaptive zones perhaps involving specialisation of species morphologies in sympatry.

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[1] Dickens, C. (1839). The life and adventures of Nicholas Nickleby. Hertfordshire, UK: Wordsworth Editions Limited

INTRODUCTION

Biological diversity has arisen from fundamental laws of physics and chemistry. From humble beginnings, the process of evolution has created a bewildering array of variation, seen in both extant organisms and those in the fossil record. It has fascinated biologists to characterise the processes of generating new, and honing existing species and morphologies such that doing so has been a major focus of research for over a century. Darwin, (1859) is attributed with suggesting that evolution has plodded for billions of years slowly and continually changing traits, differentially affecting which individuals, populations and lineages survive and which die out. That complexity must arise from a process which in itself must be complex, variable and dynamic has more explicitly played a part in subsequent ideas (Simpson, 1944; Simpson, 1953; Gould and Eldredge, 1977). Thus, in light of this, the concept of temporally and taxonomically varying tempos (speeds) of evolution combining to create a process (or mode) that is littered with pulses of fast rates (Simpson, 1944; Mahler *et al.*, 2010; Eastman *et al.*, 2011; Venditti *et al.*, 2011; Revell *et al.*, 2012; Landis *et al.*, 2013; Rabosky *et al.*, 2013; Hopkins and Smith, 2015; Cooney *et al.*, 2017; Landis and Schraiber, 2017) or large changes (O'Donovan *et al.*, 2018) has more recently defined modern, statistical manifestations of the evolutionary processes.

Modern phylogenetic comparative methods account for the fact that species show shared ancestry and thus their data are not statistically independent of each other (Felsenstein, 1985; Harvey and Pagel, 1991). In addition, they also provide powerful methods by which we can study evolutionary tempos and modes in clades of organisms from across the tree of life (Pagel, 1997; Pagel, 1999; Blomberg *et al.*, 2003; Eastman *et al.*, 2011; Venditti *et al.*, 2011; Revell *et al.*, 2012; Thomas and Freckleton, 2012; Landis *et al.*, 2013; Rabosky *et al.*, 2013; Elliot and Mooers, 2014; Duchen *et al.*, 2017). Many of these methods require *a priori* information regarding the frequency or locations of varying rates (or tempos) in a phylogeny (Eastman *et al.*, 2011; Rabosky *et al.*, 2013) or may confine conditions such as the magnitudes of rates or changes in traits to a fixed distribution (Landis *et al.*, 2013; Elliot and Mooers, 2014; Duchen *et al.*, 2017).

We use a relaxed model of evolution which estimates deviations in evolutionary rate away from the background rate on individual branches or in whole clades of a phylogenetic tree without the need for any *a priori* information regarding their temporal or taxonomic location (Venditti *et al.*, 2011). Our model, previously used in Chapter 1 (O'Donovan *et al.*, 2018) in the context of geographical movement is here applied to morphological data to estimate ancestral body sizes from organisms spanning the tree of life. Studying body size evolution on a branch by branch basis by estimating the size of each ancestor and descendant provides a different insight compared with studying pathwise rates as previously (e.g. Knouft and Page, 2003; Moen, 2006; Monroe and Bokma, 2010; Baker *et al.,* 2015). Using branchwise information reveals the magnitude and direction of the individual evolutionary steps that have culminated in the body sizes of extant and fossilised species and also importantly uncovers how rates of evolution translate into changes in trait size. We can answer questions regarding the relative frequencies of size increases and decreases and whether the magnitude of changes differs depending on the direction of change such that the mode of evolution is different in organisms getting smaller compared with those getting bigger. These tests enable us to shine a light on the presence of large scale trends in body size (Cope, 1887; Cope 1896, Stanley, 1973; Alroy, 1998) and characterise overarching patterns of evolution (Gould and Eldredge, 1977; Pagel, 1997; Pagel, 1999; Schluter, 2000; Harmon *et al.*, 2010; Venditti *et al.*, 2011; Brusatte *et al.*, 2014; Slater and Pennell, 2014; Cooney *et al.*, 2017; Landis and Schraiber, 2017). We also test whether the magnitude of morphological changes is different in species with different ecologies (Sibly and Brown, 2007; Evans *et al.*, 2012), classified into different Classes and Kingdoms (Hutchinson and MacArthur, 1959; Allen *et al.*, 2006) and with different metabolic strategies (Porter and Kearney, 2009).

METHODS

Data and phylogenetic trees

Body size evolution is a trait of major biological and ecological importance and interest (Schmidt-Nielsen, 1975; Calder, 1984; Peters, 1986; Brown *et al.*, 2004; Bonner, 2011) given the historical predictions about how evolution has shaped body size over time (Cope, 1887; Stanley, 1973; Alroy, 1998) and in different taxonomic groups. We collected continuous body size or body size proxy data spanning taxa from across the tree of life made available in published literature (Appendix 1, Table 1). We log transformed all data prior to analysis. To account for the statistical non-independence of species' data owing to shared ancestry (Felsenstein, 1985; Pagel, 1992) we also collected time calibrated phylogenetic trees with branch lengths measured in millions of years from the literature. Where possible the data and phylogeny were taken from the same source. In cases where this was not possible, we matched species data to taxa in a phylogeny from a different publication, using large, reliable databases to check for synonymy or spelling errors which prevented data matching to names in a tree automatically (AmphibiaWeb, 2005; BirdLife Taxonomic Working Group, 2015; IUCN, 2017).

Model of evolution and ancestral state reconstruction

We use ancestral state reconstruction to study the change in trait value along each branch of a phylogenetic tree. This means that we are able to calculate the magnitude and direction of every instance of change in body size that occurs at, or between speciation events on a tree. We reconstruct ancestral body size at every node in each of the 143 phylogenies in a Bayesian Markov chain Monte Carlo (MCMC) framework using the variable rates (VR) model of Venditti *et al.*, (2011) with explicit ancestral state estimation as in O'Donovan *et al.*, (2018). This model is implemented in Version 3 of the programme BayesTraits (Pagel *et al.*, 2004). Our model estimates a background rate of evolution (σ^2; the expected rate under a Brownian motion (BM) model) and also detects deviations away from this background rate in individual branches or whole clades of the phylogeny. Rate deviations are achieved by applying a rate scalar (r) to the branches of a tree which can be visualised by stretching or compressing their length according to the rate of evolution estimated to be acting on them. For example, if a branch was estimated to have undergone twice the amount of change possible under BM then its length would be doubled (r = 2), implying that the rate along this branch was double that of the background rate. Similarly if a branch was estimated to have undergone less change than expected by BM then a rate scalar of less than one would be applied and the length of the branch would be compressed. This stretching and compressing has the overall effect of changing the length of the tree to reflect the amount of time needed for the estimated change in trait to occur by pure BM. Where previously the ancestral states were implied in the model (Venditti *et al.,* 2011), they are now explicitly estimated and together with the rates, contribute to the calculation of the likelihood which follows the method of Elliot and Mooers, (2014):

$$\boldsymbol{L}\,(\boldsymbol{x}, \boldsymbol{\sigma}; \boldsymbol{T}) = \prod_{\boldsymbol{b}} \boldsymbol{\phi}(\boldsymbol{b}_2 - \boldsymbol{b}_1; \boldsymbol{t_n}\boldsymbol{\sigma}^2)$$

The likelihood is calculated given data for a continuously varying trait (x, here body size) with a standard deviation (σ) and belonging to the taxa in a phylogenetic tree (T). The probability of a proposed ancestral state is calculated from the difference in trait value between an ancestor (b_1) and the descendant (b_2) at either end of a given branch (n) and the product of the variance (σ^2) and the branch length (t_n). Once this probability is calculated for every branch in the tree for a given iteration of proposed ancestral states and rates in the MCMC chain, they are multiplied together and log transformed to give the final log likelihood for the iteration. We also reconstructed ancestral states in all trees using a BM model to have a simple, or null model to test against.

Run conditions and model selection

For datasets with more than 500 taxa we ran five replicates of both the variable rates and Brownian motion models for 1,010,000,000 iterations, discarding 10,000,000 as burnin and sampling every 100,000 iterations, yielding a posterior distribution of 10,000 rates and ancestral states. For datasets of less than 500 taxa we ran five replicates of both models with chains of 110,000,000 iterations, discarding 10,000,000 as burnin and sampling every 100,000 iterations yielding a posterior distribution of 1,000 rates and ancestral states.

We judged the convergence and mixing of the model on the basis of several criteria linked to the likelihood and variance of the replicates of each model. Firstly, for each model, we visually inspected the traces of the posterior distributions of likelihood values to check that they had all reached convergence. Secondly, to check that replicates of a model had converged in the same place we calculated the mean and standard deviation (SD) of the likelihood (Lh) values from the posterior distribution for each replicate. The standard deviation was then added to and subtracted from the average likelihood for each replicate. We chose the maximum of the Lh – 1SD and the minimum of the Lh + 1SD values to represent the smallest, acceptable range within which all of the average likelihoods from the replicates of one model should fall. We deemed that the replicates with an average likelihood outside of this range were inappropriate for use. We followed the same protocol for the variance of the replicates of each model. Conventionally, traces of the variance (σ^2) would also be used to judge convergence, however this model makes use of a Reversible Jump (RJ) MCMC algorithm (Green, 1995) which allows rate scalar parameters to 'jump' in and out of the model with each iteration as appropriate. In such cases, examination of the background rate alone can be misleading.

To test for the presence of rates outside of those expected by BM and thus to compare model fits we used a stepping stones sampler (Xie *et al.*, 2010) on all replicates of both models for every dataset, sampling 250 stones for 10,000 iterations each. This sampler estimates a marginal likelihood (mLh) value for each replicate for each dataset.

These were used to conduct Bayes Factor (BF) tests (Raftery, 1996) between every comparison of replicates of BM and VR models and also between the average mLh of the BM and VR replicates. We calculated the Bayes Factor as two times the difference between the marginal likelihoods of the VR model replicate and the BM model replicate (2 * (VR mLh – BM mLh)). A Bayes Factor of more than two was considered as positive support (Raftery, 1996) for the more complex, VR model, confirming if the heterogeneous model was a better fit to the data compared with a standard BM model (Appendix 2, Table 1). We randomly selected a single replicate for the supported model (excluding those that had not met our criteria for convergence and mixing). We then calculated the median rates (if the VR model was supported) and median ancestral states from the posterior distributions of the chosen replicate for further analyses.

Branchwise changes and Z values

For every branch in each dataset we calculated the change in trait value from ancestor to descendant (henceforth referred to as branchwise changes or dX) as:

$$dX = log_{10}(X_2) - \ log_{10}(X_1)$$

where X_2 and X_1 are the median estimated descendant and ancestral trait values respectively. These changes must be considered in the context of time, or rate of evolution and so we calculated a value we refer to as the branchwise change per unit time defined as:

$$change\ per\ unit\ time = \frac{dX}{\sqrt{t}}$$

where t here represents the branch length measured in millions of years. We square root t owing to the explicit assumption of Brownian motion that time is treated in this way. To study large scale evolutionary change we transformed these change per unit time values into z-scores (Z) such that they would be comparable between and across datasets. Within every dataset we calculated z-scores as follows:

$$Z = \frac{change\ per\ unit\ time}{SD\ change\ per\ unit\ time}$$

such that for each branch in a dataset we took the change per unit time and divided this by the standard deviation of all branchwise changes per unit time from the given dataset. These standardised values allow us to not only identify the direction of the change in body size along every branch, with positive Z values representing increases in body size and negative Z values representing decreases in body size (to be referred to as positive and negative changes respectively) but also the magnitude of these changes. Z values by definition take the form of a z distribution, or standard normal probability curve with a mean of zero and variance of one. This means we have an explicit expectation of the distribution of the standardised change per unit time values. As such, we define changes of less than -2 and more than 2 as 'exceptional changes' or those that fall in the tails of the distribution in the 2.5th and 97.5th percentiles of the data. This is the first time that exceptional changes, *sensu* Simpson, have been quantified, or defined in this way. We refer to the changes not classed as exceptional as 'regular changes'.

In addition to defining branches by their magnitude and direction of change, we also classified each branch by multiple ecologically important categories. We categorised the branches according to their Kingdom, Class, whether the organism was a vertebrate or not, metabolism (Endothermic, Ectothermic or Ecto-endothermic for the dinosaurs (Grady *et al.*, 2014)) and habitat (Terrestrial, Aquatic, Volant, Aquatic/Terrestrial for amphibians and Terrestrial/Volant for insects). Habitat categories were allocated based on where young are born however owing to the intense selection pressures placed on organisms that fly (Alexander, 1998; Hone and Benton, 2007) we added a 'volant' category for those terrestrial organisms that rely on this mode of locomotion. Some branches were labelled as 'unknown' owing to a lack of data, for example the branches in phylogenies of Serpentes for whom little is known about where species lay their eggs. For internal (or, non-terminal) branches we allocated a category based on the types of the terminal branches that arose from them. Where multiple types of each category arose from a single branch we allocated the type known to be ancestral to the group, for example the branch leading to cetaceans (aquatic) and artiodactyls (terrestrial) was allocated as 'terrestrial' because we know that the ancestor of Cetartiodactyla was terrestrial and that cetaceans transitioned to an aquatic lifestyle from a terrestrial one.

Statistical analyses

We combined all of the branchwise data (n = 66,355) from every phylogeny into a single dataset for analyses. All analyses were carried out on all branches combined, in addition to on regular (n = 63,422) and exceptional (n = 2,933) branches separately given that these changes may be underpinned by fundamentally different processes and thus might have evolved differently. In addition, we also ran all analyses on each dataset individually (n = 143), with the data from phylogenies of more than 500 taxa combined and with the data from phylogenies of less than 500 taxa combined. We present the results of the analyses run on the data from all 143 datasets combined given that this dataset gives a taxonomically holistic view of evolution and the analyses yield qualitatively the same results as the analyses with the subdivisions of the data. All of our statistical analyses were performed in JMP Version 7 (JMP, 2007).

To test whether there is a difference in the frequency of positive and negative changes in the data we ran binomial probability tests on the three datasets (all, regular and exceptional branches). Specifically we tested whether the observed outcome significantly deviates from the expectation that the two possible outcomes have an equal (50:50) chance of occurring. Secondly, to test whether there is a difference in the magnitude of changes to increase and decrease body size we carried out t-tests. Here we tested the difference in means of the positive and negative $\log_{10}$ transformed, absolute Z values accounting for dataset number (an arbitrary number used to identify all branches from the same phylogeny) and $\log_{10}$ transformed dataset size (n) as categorical and continuous random effects respectively. A p-value of less than 0.05 here means that there is a significant difference in the size of positive and negative changes.

To investigate whether the evolutionary process has altered temporally, specifically, whether the magnitude of the branchwise changes in body size have changed over time we ran regressions of $\log_{10}$ transformed, absolute Z values on mid-branch age (measured in millions of years and referring to the time from the present that the middle of each branch dates to). We treated $\log_{10}$ transformed dataset size and dataset number as random effects as previously. We use mid-branch age as a measure of time given that we do not know when along a branch change occurs and thus we use this date as a compromise between the ancestral and descendant ages. In addition, owing to the possibility that regular and exceptional changes are the products of fundamentally different evolutionary processes, or that they may not evolve in the same ways, we test whether these two types of changes behave differently to each other through time. To do this we regressed $\log_{10}$ transformed, absolute Z values on mid-branch age, however this time estimating separate intercepts and also separate slopes for the two types of change by the inclusion of an interaction term. We also treated $\log_{10}$ transformed dataset size and dataset number as random effects in this analysis.

To study the effects of the ecological variables we used to categorise each of the 66,355 branches we ran five ANOVAs (for Vertebrate or not, Habitat, Kingdom, Class and Metabolism) in a restricted maximum likelihood (REML) framework to estimate and compare group means, taking into account their variances. We then carried out post-hoc Tukey's honestly significant different tests to find out if the groups' means were significantly different to each other and if so, how the magnitude of change differed between groups. For each analysis, branches labelled as 'unknown' for the category in question were excluded. We again included $\log_{10}$ transformed dataset size and dataset number as random effects.

RESULTS

We find strong support for varying rates of evolution in 98 of our 143 datasets (Appendix 2, Table 1). Within these datasets, 25% of branches show a median rate that is accelerated with regards to the background rate of evolution ($r > 1$) and 9.6% of branches evolve slower than the background rate ($r < 1$). In total then, more than a quarter of morphological change across the tree of life can be characterised by significant shifts away from the background rate of evolution.

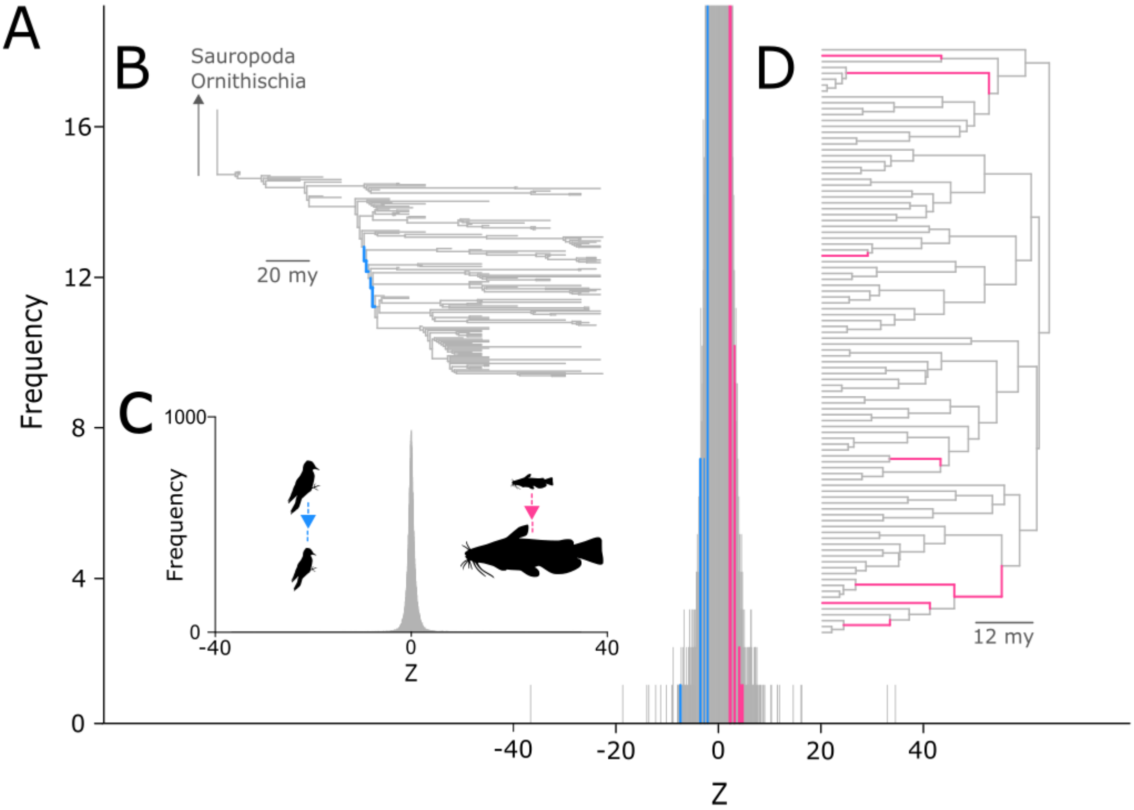

Figure 1 | Standardised branchwise changes per unit time (Z values). A – Base of the distribution of Z values for each branch (n = 66,355) in the 143 phylogenies studied. Blue bars correspond to the exceptional changes highlighted in the phylogeny inset as part **B**. Pink bars correspond to the exceptional changes highlighted in the phylogeny inset as part **D**. **B** – Theropod portion of the Benson *et al.,* (2014) dinosaur phylogeny. *(Figure caption continues on the next page)*

Figure 1 caption continued - The blue branches highlight the succession of exceptional changes to reduce femur length along the backbone of the tree leading to the avian subclade. These are also shown as the blue bars in the histogram in part **A**. (All other positive and negative exceptional changes in the phylogeny not shown). **C** – Complete view of the distribution of Z values for each branch (n = 66,355) in the 143 phylogenies studied. Silhouettes on the left hand side of the distribution are of *Picoides*†* and show the most extreme body size reduction in the distribution of -36 standard deviations from the mean in the woodpecker species *Picoides moluccensis*. Silhouettes on the right hand side of the distribution are of *Carias** and show the most extreme body size increase in the distribution of 34 standard deviations from the mean in the catfish species *Clarias buthupogaon.* Silhouettes are sized proportionally to real size and represent the relative body size changes. **D** – Phylogeny of *Anolis* lizards from Thomas and Freckleton, (2012). Pink branches highlight the instances where exceptional changes to increase body length have occurred. These are also shown as the pink bars in the histogram in part **A**. (Negative exceptional changes in the phylogeny not shown). * Silhouettes obtained from http://phylopic.org. † Credit given to Gareth Monger. https://creativecommons.org/licenses/by/3.0/

The pervasiveness of this variable tempo of evolution through time and in different lineages serves to create a distribution of morphological changes distinct from the expectation of a standard normal (Figure 1). Instead, we see a leptokurtic and thus fat-tailed distribution (kurtosis = 81) of changes with a mean and variance of 0.0167 and 0.998 respectively and a minimum value of -36.65 and a maximum of 34.55 (25th percentile = -0.43, median = -0.0073, 75th percentile = 0.44).

Table 1 | Summary of the frequency of and time spent on regular and exceptional changes in total across all phylogenies (n = 143)

Branch type	Direction of change	Time (my)	% Total time	Number of branches	% Total branches
Regular	Both	738,915	95.5	63,422	95.6
	Positive	360,408	46.6	31,210	47.0
	Negative	378,507	48.9	32,212	48.5
Exceptional	Both	34,801	4.50	2,933	4.42
	Positive	19,494	2.52	1,601	2.41
	Negative	15,307	1.98	1,332	2.01
All	**Total**	**773,716**	**-**	**66,355**	**-**

When considering all branches, regardless of their magnitude, we find that changes to reduce body size are more frequent in nature than those to increase body size (p = 0.0044; Table 1 and Figure 2). This pattern is however guided mostly by the high frequency of regular changes (Z < 2 and Z > -2) which make up 95.6% of all changes and which are biased towards more frequent negative changes (p = <0.0001; Table 1). Conversely, exceptional changes are more often positive, thus there are significantly more large changes to increase body size (p = <0.0001; Table 1). Taking all branches together, the magnitude of these abundant negative changes is significantly smaller on average than that of positive changes (t = -5.03, p = <0.0001; Figure 2). That is, changes to reduce body size are smaller than those to increase body size. This is also the case when studying regular changes in isolation (t = -3.19, p = 0.0014) but there is no significant difference in the magnitude of exceptional positive and exceptional negative changes (t = -1.07, p = 0.284).

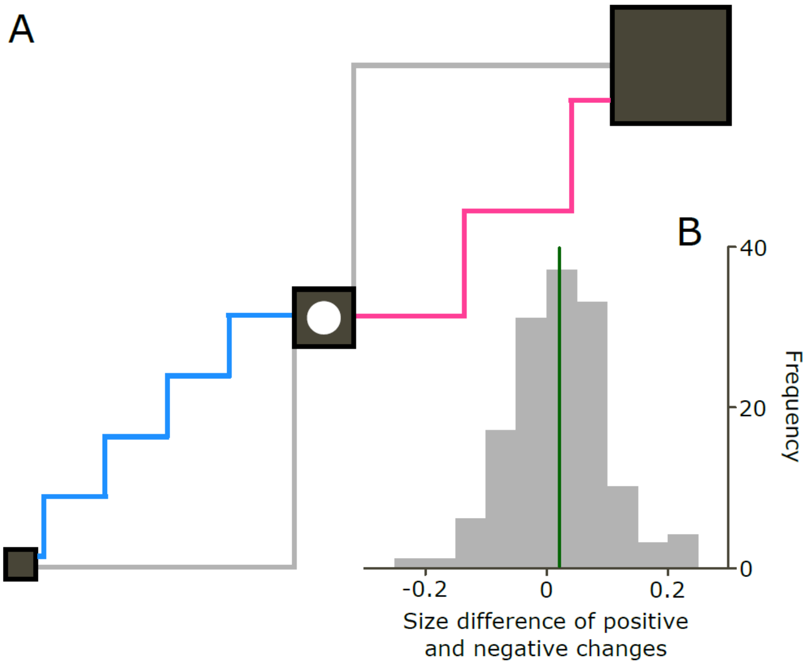

Figure 2 | The frequency and magnitude of positive and negative changes. **A** – A schematic illustrating the idea that negative changes (blue 'steps') are more frequent and occur in smaller 'steps' than positive changes (pink 'steps'). The heights and lengths of the steps are not to scale and thus only qualitatively represent the pattern found. These changes occur starting from the medium sized box in the middle of the diagram (the ancestor; grey square with white circle). The negative steps result in a 50% reduction in size (small grey square) and the positive steps result in a 50% increase in size (larger grey square). These changes in different directions occur in the same amount of time (horizontal, pale grey lines) and show the same amount of trait change (vertical pale grey lines). **B** – The difference between the mean size of positive and negative changes in each of the 143 datasets. The difference between the mean size of positive and negative changes from the analysis with all datasets combined is marked by the vertical green line.

Interested in whether the magnitude or direction of changes alters through time, we regressed $\log_{10}$ transformed, absolute Z (|Z|) values on mid-branch age to find that magnitude of change increases towards the present (β = -0.001987, p = <0.0001; Figure 3). This is also the case in regular (β = -0.001511, p = <0.0001) and exceptional changes (β = -0.000202, p = <0.0059) when tested independently. We find no evidence to suggest that regular and exceptional changes alter their magnitude differently through time (p = 0.5032) and thus no evidence that they are underpinned by different evolutionary processes.

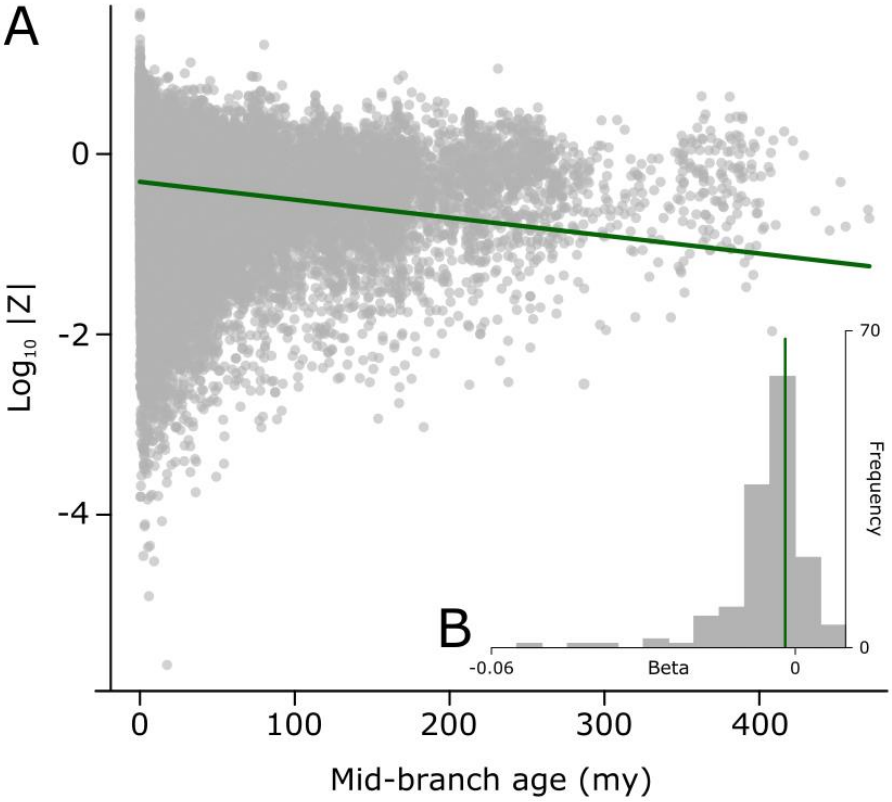

Figure 3 | The relationship between the magnitude of standardised, branchwise rates of change (Z) with time, measured as millions of years from the present. **A** - Z value for every branch (n = 66,355) plotted against the mid-branch age as grey circles with the predicted regression line from the regression of $\log_{10}$ |Z| on mid-branch age with all datasets combined plotted in dark green. **B** – Histogram of beta coefficients from the regression of $\log_{10}$ |Z| on mid-branch age for each of the 143 datasets individually. The beta from the regression with all datasets combined (seen in **A**) is marked by the vertical dark green line.

When comparing the average change in size in different ecological groups we find that there is no difference in the magnitude of changes in vertebrates and non-vertebrates (p = 0.7388). Similarly, there is no difference in the size of changes between endotherms, ectotherms and endo-ectotherms (p = 0.2733). However, whether an organism is terrestrial, volant or aquatic does influence the size of the steps evolution has taken to shape body size; terrestrial/ volant organisms (exclusively insects) undergo the largest changes with volant organisms changing the least between speciation events (p = 0.0117; Figure 4A). Animals and fungi evolve in similar step sizes, in contrast to plants which on average change less along each branch (p = <0.0001; Figure 4B). In addition, organisms of different classes also evolve by significantly different increment sizes (p = <0.0001; Figure 4C).

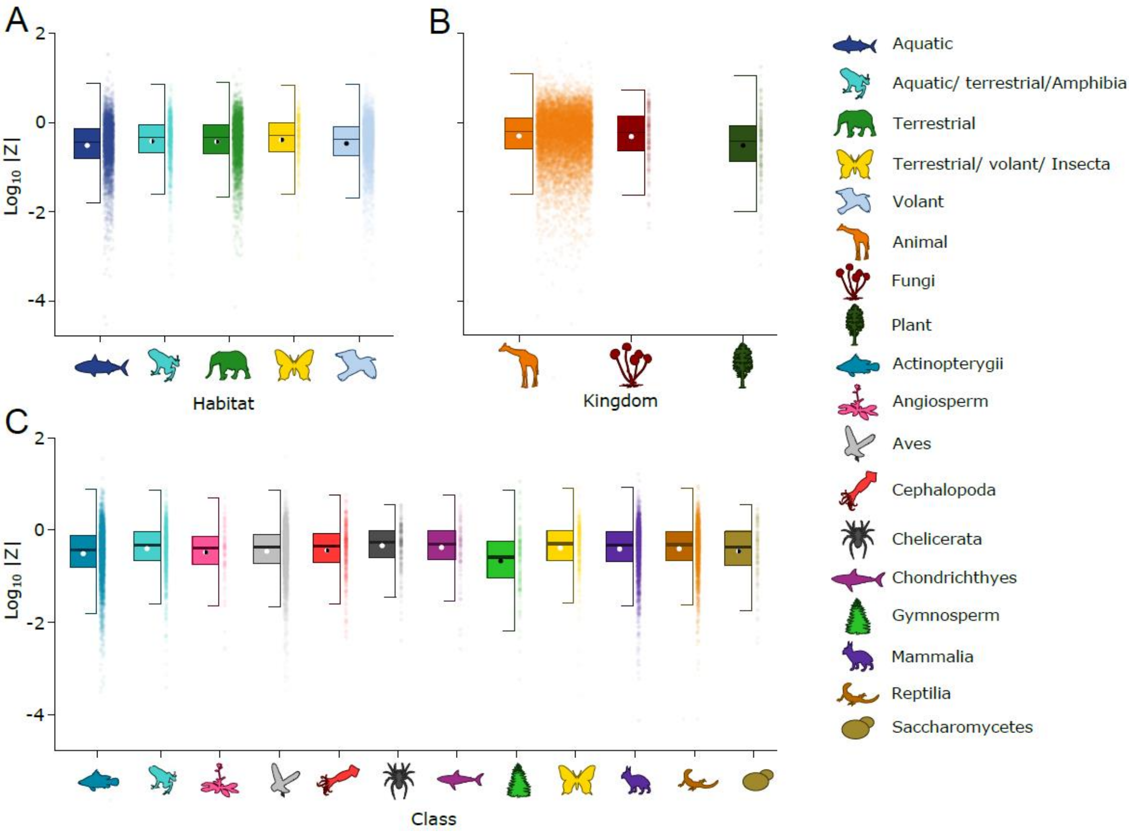

Figure 4 | The magnitude of standardised, branchwise rates of change (Z). The differences in magnitude of Z values between branches categorised by **A** – Habitat, **B** – Kingdom and **C** – Class. Coloured boxes represent the interquartile range of the data with the median marked as a solid, horizontal line across the box and mean marked as a coloured circle. The upper whisker of the boxes extends to the smallest of the maximum Z value or the sum of the upper quartile and 1.5 * interquartile range. The lower whisker of the boxes extends to the largest of the minimum Z value or the sum of the lower quartile and 1.5 * interquartile range. Where the mean Z value of ecological groups are significantly different they are marked with circles of differing colours. Where group means are not significantly different from others they are marked with a circle coloured to match those of the groups they are not significantly different from. Points to the right of each boxplot show a sample of 20% of the data with the jitter proportional to the original number of data points.

DISCUSSION

Previously, morphological data paired with a phylogenetic tree have been used in conjunction to detect the signatures of evolution, particularly deviations in rate away from the Brownian process (Eastman *et al.*, 2011; Venditti *et al.*, 2011; Revell *et al.*, 2012; Thomas and Freckleton, 2012; Rabosky *et al.*, 2013; Baker *et al.*, 2015). Here, we go one step further, to fill in the gaps and study the nuances of these evolutionary processes at a high resolution, branchwise level but unlike previously (e.g. Churchill et al., 2014; Huttenlocker, 2014, Moyers Arévalo *et al.,* 2018) these branchwise changes are estimated using a model which allows rates of evolution to vary. From studying actual amounts of change between ancestors and descendants, rather than expected change inferred from rates we can see how individual changes have built up over time and in different lineages to create the big, overarching processes previously detected (Schluter, 2000; Blomberg *et al.*, 2003; Harmon *et al.*, 2010; Mahler *et al.*, 2010), but not fully understood. In line with previous work (Venditti *et al.*, 2011; Landis *et al.*, 2013; Rabosky *et al.*, 2013; Baker *et al.*, 2015; Cooney *et al.*, 2017; Duchen *et al.*, 2017; Landis and Schraiber, 2017) we too find evidence of pervasive rate variation across the tree of life with 30% of branches scaled to reflect both accelerations and decelerations in rate of evolution away from the background rate. At the dataset level, 69% of datasets were better described by a variable rates model over a Brownian model. Where previously however only this rate variation could be studied, we can now see the effect that these variations in rate have on the reconstructed amount of change that occurs along each branch.

The shape of a distribution of phenotypic changes is the direct product of the evolutionary processes that created those changes. Thus, the expectation of shape comes from the model of evolution used. Many variable rates models define the distribution of expected changes *a priori* by characterising evolution with specific distributions such as Lévy (Landis *et al.*, 2013) or fat-tailed (Elliot and Mooers, 2014) distributions. In contrast, we use a relaxed method which automatically detects signal in the data without prior information about the phylogenetic or temporal location of this signal. Our expectation is that the branchwise changes should take the form of a normal distribution as the outcome of a Brownian random walk process (Felsenstein, 1985; Elliot and Mooers, 2014). However, we find that the standardised branchwise changes, Z values, take the form of a leptokurtic, or fat-tailed distribution (Figure 1). By definition this means that we detect many more small changes than would be expected by Brownian motion with only 4.42% of branches having undergone exceptional changes ($|Z| > 2$; Table 1). Reflected in both rates and in realised morphological changes, the mode of morphological evolution is characterised by mostly small changes occurring at the background rate punctuated with rare, large changes as a consequence of accelerated rates. Such a pattern has been found previously in ecological data (Uyeda *et al.*, 2011; Landis *et al.*, 2013; Cooney *et al.*, 2017; Duchen *et al.*, 2017; Landis and Schraiber, 2017), geographical data (O'Donovan *et al.*, 2018), in the fossil record (Hunt *et al.*, 2015) and in environmental and genetic data (Deline *et al.*, 2018). This characterisation fits with the historical tempos and modes of evolution proposed by Simpson (1944, 1953) whereby rates vary through time and across lineages and phenotypic changes range from exceptionally small (minimum |Z| = 2.16e-06) to exceptionally large (maximum |Z| = 36.648). We suggest that the small, or regular changes are those which occur within a single adaptive zone and the large, or exceptional changes are the ones which facilitate shifts to new adaptive zones, bridging fitness valleys between adaptive peaks in a fitness landscape (Landis and Schraiber, 2017). These exceptional changes also then potentially set the stage for adaptive, or evolutionary radiations (Venditti *et al.*, 2011). *Anolis* lizards are a frequently used example of a group that underwent an evolutionary radiation. In concordance with this we find many cases of exceptional changes having occurred across their phylogeny (Figure 1D). Another example of a case where exceptional changes link to radiations can be found within the dinosaur phylogeny (Benson *et al.*, 2014). In agreement with previous work (Benson *et al.*, 2014; Lee *et al.*, 2014; Baker *et al.*, 2016), we detect a succession of exceptional changes to reduce femur length (a close correlate of body size) along the backbone directly preceding the appearance of birds (Figure 1B). This is suggestive of the role that exceptional changes play in major evolutionary shifts or transitions.

Both the largest positive and negative changes across the 143 phylogenies however occur on terminal branches. The largest positive change (Z = 34.547) served to increase the body length of the ancestral populations resulting in the catfish species *Clarias buthupogon,* which is commonly harvested for human consumption. This change represents a three-fold increase in total body length over the course of just under 89,000 years (Figure 1C). The attribution of such a large amount of change to this terminal branch may be owing to the fact that fish are indeterminate growers and thus the maximum body length recorded for this species may have been unusually large. The largest negative change (Z = -36.648) occurred over the last 2,164 years along the branch leading to the Sunda pygmy woodpecker (*Picoides moluccensis*) and saw the body size of the ancestral species reduce by just under 4 grams (Figure 1C). This species and its closest relatives make up a small clade of pygmy woodpeckers whose geographical ranges all occur in the tropical or subtropical regions of Asia and South-east Asia. This is in contrast to its sister clade of larger woodpeckers which has an exclusively northern distribution spanning Canada, North America, Scandinavia and Russia, just south of the Arctic Circle. These geographical distributions may serve to explain the extreme size decrease in the pygmy woodpecker as its ancestors invaded regions of warmer climate (Bergmann, 1847).

By studying the changes that occur between an ancestor and descendant in a phylogeny it is possible to understand the amount of morphological change that accrues or distance moved (O'Donovan *et al.*, 2018) in order for an ancestral population to become a new species. This links to the historical idea of competitive exclusion, or Gause's principle, which suggests that competition between species that occupy the same ecological niche and coexist in the same habitat will result in extinction or displacement of all but one of those species (Gause, 1934). This idea was heavily criticised owing to a lack of clarity or quantification in terms of how similar these competing species should be for the theory to apply (Hardin, 1960). However, Gause's principle was followed up by Hutchinson, (1959) who discussed the idea in the context of limits on diversity and found that in birds and mammals at least, a quantifiable limit on how similar coexisting species can be does exist. Hutchinson, (1959) found that in co-occurring species the ratio of the larger to the smaller form of morphologies which are typically linked to trophic level is approximately 1.3. For example, if two ecologically similar primates were to co-occur in a rainforest, it would likely be the case that morphological features such as skull size would differ by a ratio of approximately 1.3 (one may have a skull length of 20cm and the other of 15.4cm). Given the high level of sampling in the large mammal, bird and fish phylogenies (79% (Burgin *et al.*, 2018), 55% (Barrowclough *et al.*, 2016) and 26% (Carrete Vega and Wiens, 2012) of all extant species respectively) and also given that they have all been used previously to study speciation or extinction rates (Fritz *et al.*, 2009; Jetz *et al.*, 2012; Rabosky *et al.*, 2013) we calculate the modal absolute change per unit time for each tree to see if we too detect a limit to how similar these taxa can be to one another. We find in fact that the distributions of absolute branchwise changes (|dX|) for the mammals, fish and birds do not have modes, or, that their modes are zero. Counter to the findings of Hutchinson, (1959) we find that there is no consistent degree to which species must differ from each other meaning that in these clades at least, there is no limit to similarity. This is consistent with having found an overabundance of small branchwise changes across all phylogenies which revealed that evolution has most commonly proceeded in small steps and that much of life's diversity has arisen from such small changes. This means that for the most part, descendants vary morphologically very little from their ancestors. We suggest this supports the idea that geographical isolation must play a major role in governing how new species arise; two populations need not be morphologically distinct from each other for them to not interbreed if there is geographical distance or barriers to separate them. In coexisting species too however, changes in features such as behaviour can mean that two morphologically similar, or even identical populations may coexist in the same habitat and yet be reproductively isolated, meaning that they are considered distinct species. Such changes in biology aside from those related to body size mean that two species do not directly compete and thus avoid competition, character displacement or extinction despite their morphological similarity. Rather than thinking of niches as compartmentalised shapes within which organisms may fit, with no two species filling the same niche in any one habitat, perhaps, if they exist at all, niches are more akin to shapes which themselves are faceted and overlapping, providing a much more complex and nuanced view of ecological opportunities and opportunities to generate diversity. Understanding this may relax our views on how similar species interact with each other in nature, which in reality is not as solidly defined as we have made it seem.

Increasing the resolution with which the natural world is viewed can reveal extraordinary features of the physical environment's fundamental structure and its implications for the organisms that inhabit it. It has been found that elements of the environment show self-similarity at ever decreasing scales and as such have been termed fractal (Mandelbrot, 1983) being subsequently linked to underpinning scaling laws of organismal biology (Brown *et al.*, 2002). 'Ecological organisation', itself a product of foundational laws of science, is likely to underpin ecological complexity and regulate diversity (Brown *et al.*, 2002), thus understanding this organisation can give us insight into the remits within which evolution can and has worked. We find that morphological changes differ in their magnitude and frequency depending on their direction and thus that the mode of evolution is fundamentally different for positive and negative changes (Figure 2). Where body size decreases, changes occur in smaller, more frequent steps. Conversely, when body size increases, it does so in fewer, larger steps. This result fits with the idea of nature being fractal, or fractal like (Brown *et al.*, 2002) in its structure; an organism can become only slightly smaller and yet myriad new niches are opened up to it. The smaller organisms become, the more nuanced and complex their environment becomes and the more dimensions they have available to them (Kenkel and Walker, 1993; West *et al.*, 1999) for foraging, hunting, evading predators, and other behaviours required for life. Organisms that get bigger however must do so in rare, large steps, given that habitats can support fewer large organisms than small ones (Hutchinson and

MacArthur, 1959), primarily owing to the loss of dimensions at larger scales (Morse *et al.*, 1985; Shorrocks *et al.*, 1991; Cotgreave, 1993; Haskell *et al.*, 2002).

An alternative explanation for why we find that organisms reduce their body size in small steps may be linked to the idea of there being a limit to how small a species can get. We see the bounds of this limit illustrated in the right skewed nature of the distribution of body sizes of most organisms (Stanley, 1973; Bokma, 2002; Clauset and Erwin, 2008). Such a 'small limit' could act as a catalyst for the processes underlying Cope's rule, whereby species' body sizes increase over time, having arisen as small bodied organisms (Cope, 1887; Cope, 1896), which then adapt to distance themselves from the lower size limit (Stanley, 1973; McShea, 1994). There has been frequent evidence in the past, that Cope's rule is supported in some fossil data (Alroy, 1998; Hone and Benton, 2007; Hone *et al.*, 2008), and contested in both other fossil (Stanley, 1973; Gingerich, 1974; Jablonski, 1997; Laurin, 2004) and extant data (Pianka, 1995; Knouft and Page, 2003; Finarelli and Flynn, 2006; Moen, 2006; Monroe and Bokma, 2010). However, necessary methodological advantages (Solow and Wang, 2008) have been made in order that such an evolutionary trend can be detected from extant data alone, and in mammals at least has been found to be present in the evolutionary history of the group (Baker *et al.*, 2015). Our results provide support for the hypothesis that organisms err away from a lower body size limit, if indeed such a lower limit exists (Baker *et al.*, 2015). Organisms increase their size in large increments and, if there is a selective advantage to being smaller as seems to frequently have been the case, species encroach on the lower limit to body size in ever smaller steps perhaps to avoid reaching the limit entirely.

Linking branchwise changes together along paths from the root of a phylogeny to each species at the tips gives us a picture of how individual branchwise changes sum together through time creating long term trends and culminate in a mode of evolution. The early burst or adaptive radiation pattern (Simpson, 1944; Schluter, 2000) has commonly been found (Grant, 1981; Seehausen, 2006; Mahler *et al.,* 2010; Sakamoto *et al.,* 2016; Landis and Schraiber, 2018; to list but a few examples). This feature of some groups' evolution is characterised by initially rapid rates of either morphological evolution or speciation (or both), followed by a gradual slow-down in rates through time. Osborn, (1900) suggested that such a pattern was likely to arise in response to some ecological opportunity driving mechanical changes in organisms which results in the generation of new species. As empty or underexploited niches are filled and opportunities become more limited, the rates of phenotypic changes and of generating new species subsequently decline with time (Sakamoto *et al.*, 2016; O'Donovan *et al.*, 2018). Contrary to this, we find that the magnitude of branchwise changes increases through time (Figure 3). This pattern goes against that of an adaptive radiation or early burst pattern and rather can be classed as a late burst of evolution. There has been increasing evidence in fact that early bursts are perhaps not the norm (Harmon *et al.*, 2010; Slater, 2015; Puttick, 2018). There is a growing appreciation for the idea that the presence of idiosyncratic rate heterogeneity in individual lineages early in a clade's history can result in an early burst model of evolution being erroneously detected and favoured over other models (Harmon *et al.*, 2010). Given that we do not set out to define an evolutionary mode such as an early or late burst *a priori* (Blomberg *et al.,* 2003) we have been able to detect such a large scale feature of evolutionary mode through studying temporally and taxonomically idiosyncratic rates alone, meaning that our model is unlikely to have been tricked in this way. In line with our results, it has previously been found that late bursts of morphological evolution are a feature in nature and have been detected in comparative data (Hopkins and Smith, 2015). It seems unlikely that a clade should exclusively encounter ecological novelty and thus opportunity at the time at which it arises, meaning that large changes associated with shifts in adaptive zones should be able to occur at any time in a clade's history (Schluter, 2000; Slater, 2015). This potentially links again to Cope's ideas; as species become larger through time they also increase in complexity having started as a relatively small, generalist ancestor (the 'Law of the Unspecialised'; Cope, 1896). This may imply that the large changes we see later in clades' evolutionary history are broadly responsible for specialisation. Exceptional changes are rare, making up less than 5% of branches however they may represent a combination of changes that enable species to leap between adaptive peaks (Simpson, 1944; Simpson, 1953; Landis and Schraiber, 2017; Chira *et al.*, 2018) and also those that facilitate specialisation within an adaptive zone. The latter, in addition may then in turn lay the foundation for a radiation, if specialisation opens up opportunities that had been previously inaccessible.

It is clear that the main driver of the traits that evolve and the speed at which this happens is the environment that an organism evolves in (Gillis and Blob, 2001); this is particularly the case in the context of body size. We find that habitats and the mode of locomotion required to successfully inhabit them has a significant effect on how organisms evolve (Figure 4A). The body size of aquatic organisms changes differently from volant organisms, in a way that terrestrial-aquatic (amphibians), terrestrial and terrestrial-volant (insects) organisms do not differ from any other groups. This may be owing to the fundamental physical and chemical differences in the media within which volant and aquatic organisms exist; water is 800 times as dense and 60 times as viscous as air and the diffusion constants of oxygen and other molecules differ by 10,000 times in the two (Strathmann, 1990). Volant organisms evolve on average by smaller changes or in smaller steps compared to aquatic organisms. Biomechanical, physical and metabolic constraints may explain this limited size of changes in volant organisms. We see evidence for such constraints in the similar distributions of body sizes in distantly related flying organisms (Maurer *et al.,* 2004) given their common 'environment' and thus also common selective pressures (Alexander, 2002). Conversely, aquatic organisms may evolve in larger steps owing to the lack of constraint on their body size (Schmidt-Nielsen, 1984) relating to the physical support provided by water (Humphries, 2007). For example, the minimum body size for a marine mammal is several orders of magnitude larger than that of terrestrial mammals (Smith and Lyons, 2011). In addition, the maximum body size of volant organisms is lower than that of both aquatic and terrestrial groups (Alexander, 1998).

In conjunction with the effects of environment, as perhaps would be expected, taxonomy, or, evolutionary history and ancestry also impacts the ways in which groups of organisms evolve (Figure 4B and C). Potentially reflecting their deep phylogenetic relationship the tempo of evolution in fungi and animals differs from that of plants which diverged first from other metazoans (Baldauf and Palmer, 1993; Wainright *et al.*, 1993) and which on average evolve in steps that are 0.73 and 0.64 times smaller, or slower than in fungi and animals respectively. This lower average change size in plants may be driven by the average change size of gymnosperms which is smaller than that of angiosperms (although not significantly so; Figure 4C). Gymnosperms, particularly the ginkgo tree (*Ginkgo biloba*) which has been referred to as a 'living fossil' (Royer *et al.*, 2016), in many cases show little change from their fossilised ancestors (Crisp and Cook, 2011) thus indicating their small, stepwise mode of evolution. It has been proposed that competition with the speciose, morphologically and ecologically diverse angiosperms (Bond, 1989) may have limited the opportunities available to the gymnosperms thus somewhat limiting their ability to shift between adaptive zones, and enforcing minor, slow changes in morphology. Potentially owing to intense and ancient competition, this limitation may be a special feature of the evolution of non-flowering plants which evolve differently to the majority of other taxonomic classes. On a broader scale, differences in how classes of organisms evolve have been noted in terms of the pervasive rate variation that has been found between lineages in the tree of life and in each of those lineages through time (Venditti *et al.*, 2011). We find that whilst differences in trait change magnitude exist between different classes of organisms, that mostly, evolution has shaped their body sizes in much the same way. Given the rarity of exceptional changes across the natural world and conversely then the evidence to suggest that evolution has worked mostly in a regular and unexceptional fashion, it seems reasonable that organisms as distantly related as yeasts, mammals, flowering plants and fish share one signature of evolution. Whilst organisms within each of these classes, whether considered at the species, population or individual level, occupy both different niches within an adaptive zone and different adaptive zones altogether, they are all working within the realms of Earth's (adaptive) landscape. Thus, the nuanced evolutionary processes acting on lineages can be viewed together in a macroevolutionary sense to understand the sweeping process that shapes life on Earth.

The work presented here is based on our ability to accurately and realistically reconstruct how evolution has worked and how it has shaped the morphologies of ancestral organisms. It is widely known that phylogenies are not taxonomically complete and this may have implications for estimates of ancestral states and evolutionary rates (Pybus and Harvey, 2000; Heath *et al.*, 2008a; Heath *et al.*, 2008b; Folk *et al.*, 2018). Ultrametric trees particularly, suffer from missing extant diversity and also by definition do not sample, and thus consider the data of extinct, fossil lineages. There is a need for both rigorous, systematic simulation and real examples where phylogenetic analyses are run with and without fossils to test their precise effects. So far, work has revealed mixed conclusions with some evidence to suggest that fossils improve inferences (Finarelli and Flynn, 2006; Slater *et al.*, 2012; Pant *et al.*, 2014; Mitchell, 2015) but also evidence to the contrary that fossils have limited or no influence on reconstructed rates and ancestral states (Puttick and Thomas, 2015). It seems that more important than the inclusion of fossils is the model of evolution (Puttick and Thomas, 2015) and that when realistic, enables analyses using only extant data to yield estimates of ancestral traits exactly in line with the fossil record (Baker *et al.*, 2015). In the case that missing taxa are extremely numerous and spread across a phylogeny or make up a single, missing clade with extreme trait variation, their addition into a tree may alter the estimate of the background variance. However, we believe these to be unlikely scenarios in reality and the probability that our data and inferences have been biased in this way is limited. Potentially more realistic is that single lineages or clades that represent very different trait values from those already represented in the phylogenies used are discovered and sampled in future tree topologies. However, our variable rates model would account for these exceptional additions, limiting their influence on the background rate or the ancestral states estimated across the whole tree. This mitigates any impact of missing data as much as is possible and means that at least qualitatively our results, interpretations and conclusions presented here would remain unaltered. As more data regarding extant and extinct diversity become available and tree inference methods improve the outputs of evolutionary models too are likely to improve in accuracy (Heath *et al.*, 2008a).

The study of evolution has itself evolved over the centuries that biologists have questioned the nature of the processes generating and regulating the abundance and diversity of organisms we see present today and in the fossil record. From considering individual lineages, to higher levels of taxonomy, to the entire tree of life, studying 'the bigger picture' of macro-evolutionary processes has become a major focus. Evolutionary biology has also in that time become a field not just for observations of natural history but one that can be analysed in an ever improving, quantitative framework. With this analytical transition, we have gained the power to reveal signatures of the past evolutionary processes in data from modern and fossil species. Having identified these processes we have gone on to reveal an ever increasing level of detail regarding their vast diversity and the nuances therein. Here, continuing this theme we study the ways that evolution has acted across the tree of life to generate the body sizes of organisms from the smallest bacteria to the largest whale. We quantify evolution at a higher resolution than has previously been possible by revealing its individual increments. We then piece these together to show how localised tempos scale up and orchestrate through time to generate the evolutionary modes considered by Darwin, Simpson, Eldredge and Gould and many more besides. We show that evolution has created and honed morphologies mostly in small steps, which have been interspersed with very rare, large jumps. The selection pressures acting on organisms to constantly improve how they interact with their environment result in fundamentally different processes depending on the direction of change being selected for. We show that evolution is a product of the interaction of organisms with the myriad facets of their environment (including both conspecifics and other species); ultimately, a product of the fundamental laws of physics and chemistry. We are far from the days where evolution was considered a homogeneous, universal process. Rather, it is a vast, continual process which is dynamic and nuanced and becomes more so at every scale at which it is studied.

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APPENDIX 1 | Morphological datasets

Table 1 | Datasets and phylogenies used to study morphological change. 'Analysis' is an arbitrary number used for dataset identification purposes and matches that in Appendix 2, Table 1. 'Data n' and 'Tree n' are the original numbers of taxa included from the sources. 'Data source' and 'Tree source' are the references for the published literature from which the data and trees were used. 'Matched n' is the number of taxa from a dataset that could be matched to the corresponding phylogenetic tree

Analysis	Kingdom	Class	Group	Trait	Unit	Data n	Data source	Tree n	Tree source	Matched n
001	Animalia	Insecta	-	Body length	mm	775	[1]	774	[1]	774
002	Animalia	Mammalia	-	Brain size	g	676	[2]	50,632	[3]	676
003	Animalia	Reptilia	Dinosaurs	Femur length	cm	507	[4]	624	[4]	380
004	Animalia	Chondrichthyes	Sharks	Body length	cm	254	[5]	265	[6]	254
005	Animalia	Amphibia	Salamanders	Snout eye distance	mm	190	[7]	189	[7]	189
006	Animalia	Reptilia	Anolis	Femur length	mm	100	[8]	100	[8]	100
007	Fungi	Saccharomycetes	Yeast	Cell size	µm	77	[9]	75	[9]	75
008	Plantae	Angiosperms	Angiosperm trees	Wood density	g/cm^3	55	[10]	55	[10]	55
009	Animalia	Reptilia	Ceratopsids	Body mass	kg	34	[11]	37	[11]	34
010	Animalia	Amphibia	Salamanders	Body width	mm	190	[7]	189	[7]	189
011	Animalia	Amphibia	Salamanders	Femur length	mm	190	[7]	189	[7]	189
012	Animalia	Amphibia	Salamanders	Humerus length	mm	190	[7]	189	[7]	189
013	Animalia	Amphibia	Salamanders	Hindlimb length	mm	190	[7]	189	[7]	189
014	Animalia	Amphibia	Salamanders	Snout-vent length (SVL)	mm	190	[7]	189	[7]	189
015	Animalia	Amphibia	Salamanders	Tail length	mm	190	[7]	189	[7]	189
016	Animalia	Amphibia	Frogs	SVL	mm	233	[12]	233	[12]	233
017	Animalia	Amphibia	Frogs	Maximum SVL	mm	41	[13]	2,871	[14]	36
018	Animalia	Insecta	Ants	Body length	mm	115	[15]	115	[15]	115
019	Animalia	Aves	-	Bill length	mm	208	[16]	50,632	[3]	177
020	Animalia	Aves	-	Tarsus length	mm	158	[16]	50,632	[3]	126

021	Animalia	Aves	-	Telencephalon mass	g	135	[17]	135	[17]	135
022	Animalia	Actinopterygii	-	Egg diameter	mm	434	[5]	7,822	[18]	434
023	Animalia	Actinopterygii	-	Gut length	mm	35	[19]	7,822	[18]	35
024	Animalia	Reptilia	Archosaurumorphs	Femur length	mm	149	[20]	150	[20]	145
025	Animalia	Reptilia	Dinosaurs	Humerus length	cm	430	[4]	624	[4]	316
026	Animalia	Reptilia	Synapsids	Maximum basal skull length	mm	71	[21]	71	[21]	71
027	Animalia	Cephalopoda	Ammonites	Mean shell diameter	cm	241	[11]	241	[11]	241
028	Animalia	Arachnida	Spiders	Female body length	mm	47	[22]	47	[22]	47
029	Animalia	Arachnida	Spiders	Male body length	mm	47	[22]	47	[22]	48
030	Animalia	Mammalia	-	Semicircular canal radius	mm	243	[23, 24]	234	[23, 24]	208
031	Animalia	Reptilia	Turtles	Carapace length	cm	226	[25]	233	[25]	194
032	Animalia	Amphibia	Frogs	Egg size	mm	77	[26]	2,871	[14]	31
033	Animalia	Amphibia	Frogs	Testes mass	g	102	[26]	2,871	[14]	36
034	Animalia	Mammalia	Euarchontan primates	Cranial area	mm^2	75	[27]	74	[27]	65
035	Animalia	Mammalia	Euarchontan primates	Endocranial volume	cm^3	75	[27]	74	[27]	67
036	Animalia	Mammalia	Euarchontan primates	Promonotrial canal area	mm^2	75	[27]	74	[27]	65
037	Animalia	Amphibia	Frogs	Body mass	g	100	[28]	2,871	[14]	36
038	Animalia	Amphibia	Frogs	Sperm head length	µm	100	[28]	2,871	[14]	36
039	Animalia	Amphibia	Frogs	Sperm tail length	µm	100	[28]	2,871	[14]	36
040	Animalia	Amphibia	Frogs	SVL	mm	100	[28]	2,871	[14]	36
041	Animalia	Amphibia	Frogs	Maximum male SVL	mm	248	[29]	2,871	[14]	92
042	Animalia	Actinopterygii	Surgeonfish	Eye diameter	mm	30	[30]	65	[30]	30
043	Animalia	Actinopterygii	Surgeonfish	Eye to fin distance	mm	30	[30]	65	[30]	30
044	Animalia	Actinopterygii	Surgeonfish	Fin to jaw distance	mm	30	[30]	65	[30]	30
045	Animalia	Actinopterygii	Surgeonfish	Gill raker length	mm	30	[30]	65	[30]	30
046	Animalia	Actinopterygii	Surgeonfish	Jaw length	mm	30	[30]	65	[30]	30
047	Animalia	Actinopterygii	Surgeonfish	Jaw to eye distance	mm	30	[30]	65	[30]	30
048	Animalia	Actinopterygii	Surgeonfish	Jaw to eye angle	°	30	[30]	65	[30]	30

049	Animalia	Actinopterygii	Surgeonfish	Jaw width	mm	30	[30]	65	[30]	30
050	Animalia	Actinopterygii	Surgeonfish	Maximum body depth	mm	30	[30]	65	[30]	30
051	Animalia	Actinopterygii	Surgeonfish	Maximum body width	mm	30	[30]	65	[30]	30
052	Animalia	Actinopterygii	Surgeonfish	Pectoral fin length	mm	30	[30]	65	[30]	30
053	Animalia	Actinopterygii	Surgeonfish	Premaxilla length	mm	30	[30]	65	[30]	30
054	Animalia	Reptilia	Pterosaurs	Humerus length	mm	74	[31]	104	[31]	68
055	Animalia	Reptilia	Pterosaurs	Mandible length	mm	63	[31]	104	[31]	59
056	Animalia	Reptilia	Pterosaurs	Radius length	mm	59	[31]	104	[31]	57
057	Animalia	Reptilia	Pterosaurs	Rostrum length	mm	65	[31]	104	[31]	62
058	Animalia	Reptilia	Pterosaurs	Skull length	mm	64	[31]	104	[31]	62
059	Animalia	Reptilia	Pterosaurs	Ulna length	mm	66	[31]	104	[31]	62
060	Animalia	Mammalia	-	Axial eye diameter	mm	266	[32]	4,510	[33]	242
061	Animalia	Mammalia	-	Corneal diameter	mm	266	[32]	4,510	[33]	242
062	Animalia	Mammalia	-	Transverse eye diameter	mm	266	[32]	4,510	[33]	242
063	Animalia	Mammalia	Pinnipeds	Total body length	cm	73	[34],[35]	73	[34]	73
064	Animalia	Reptilia	Anolis	Fourth finger length	mm	100	[8]	100	[8]	100
065	Animalia	Reptilia	Anolis	Humerus length	mm	100	[8]	100	[8]	100
066	Animalia	Reptilia	Anolis	Radius length	mm	100	[8]	100	[8]	100
067	Animalia	Reptilia	Anolis	SVL	mm	100	[8]	100	[8]	100
068	Animalia	Reptilia	Anolis	Tibia length	mm	100	[8]	100	[8]	100
069	Animalia	Reptilia	Anolis	Fourth toe length	mm	100	[8]	100	[8]	100
070	Plantae	Gymnosperm	-	Wood density	mg/cm^3	83	[36]	31,389	[37]	82
071	Plantae	Gymnosperm	-	Bark thickness	cm	83	[36]	31,389	[37]	83
072	Plantae	Gymnosperm	-	Plant height	m	83	[36]	31,389	[37]	83
073	Plantae	Gymnosperm	-	Leaf length	cm	83	[36]	31,389	[37]	83
074	Plantae	Gymnosperm	-	Seed size	mg	83	[36]	31,389	[37]	83
075	Animalia	Amphibia	Salamanders	Body length	mm	194	[38]	194	[38]	194
076	Animalia	Amphibia	Frogs	Body length	mm	107	[38]	107	[38]	107
077	Animalia	Amphibia	Hylidae	Body length	mm	244	[38]	244	[38]	244

078	Animalia	Amphibia	Ranoidea	Body length	mm	185	[38]	185	[38]	185
079	Animalia	Aves	Accipitridae	Body mass	g	138	[38]	138	[38]	138
080	Animalia	Aves	Anatidae	Body mass	g	101	[38]	101	[38]	99
081	Animalia	Aves	Columbidae	Body mass	g	113	[38]	113	[38]	113
082	Animalia	Aves	Cucuildae	Body mass	g	106	[38]	106	[38]	106
083	Animalia	Aves	Furnaridae	Body mass	g	174	[38]	174	[38]	174
084	Animalia	Aves	Lari	Body mass	g	91	[38]	91	[38]	91
085	Animalia	Aves	Phasianidae	Body mass	g	104	[38]	104	[38]	104
086	Animalia	Aves	Picidae	Body mass	g	112	[38]	112	[38]	109
087	Animalia	Aves	Procellariidae	Body mass	g	80	[38]	80	[38]	80
088	Animalia	Aves	Psittacidae1	Body mass	g	79	[38]	79	[38]	79
089	Animalia	Aves	Psittacidae2	Body mass	g	92	[38]	92	[38]	92
090	Animalia	Aves	Ramphastidae	Body mass	g	59	[38]	59	[38]	59
091	Animalia	Aves	Scolopaci	Body mass	g	70	[38]	70	[38]	70
092	Animalia	Aves	Strigidae	Body mass	g	73	[38]	73	[38]	73
093	Animalia	Aves	Thamnophilidae	Body mass	g	140	[38]	140	[38]	140
094	Animalia	Aves	Tityranrest	Body mass	g	264	[38]	264	[38]	264
095	Animalia	Aves	Trochilidae	Body mass	g	189	[38]	189	[38]	189
096	Animalia	Actinopterygii	Acanthuridae	Body length	cm	58	[38]	58	[38]	58
097	Animalia	Actinopterygii	Atheriniformes	Body length	cm	46	[38]	46	[38]	46
098	Animalia	Actinopterygii	Balistidae	Body length	cm	81	[38]	81	[38]	81
099	Animalia	Actinopterygii	Chaetodontidae	Body length	cm	93	[38]	93	[38]	93
100	Animalia	Actinopterygii	Clupeiformes	Body length	cm	117	[38]	117	[38]	117
101	Animalia	Actinopterygii	Cyprinidae	Body length	cm	218	[38]	218	[38]	218
102	Animalia	Actinopterygii	Etheostoma	Body length	cm	122	[38]	122	[38]	122
103	Animalia	Actinopterygii	Holocentridae	Body length	cm	41	[38]	41	[38]	41
104	Animalia	Actinopterygii	Labridae	Body length	cm	263	[38]	263	[38]	263
105	Animalia	Actinopterygii	Loricariinae	Body length	cm	68	[38]	68	[38]	68
106	Animalia	Actinopterygii	Percomorphaceae	Body length	cm	87	[38]	87	[38]	87
107	Animalia	Actinopterygii	Pomacentridae	Body length	cm	184	[38]	184	[38]	184

108	Animalia	Mammalia	Bovidae	Body mass	g	97	[38]	97	[38]	97
109	Animalia	Mammalia	Carnivora	Body mass	g	233	[38]	233	[38]	233
110	Animalia	Mammalia	Cetacea	Body mass	g	75	[38]	75	[38]	75
111	Animalia	Mammalia	Marsupalia	Body mass	g	167	[38]	167	[38]	167
112	Animalia	Mammalia	Muroidea	Body mass	g	223	[38]	223	[38]	223
113	Animalia	Mammalia	Noctiolionoidea	Body mass	g	163	[38]	163	[38]	163
114	Animalia	Mammalia	Primates	Body mass	g	126	[38]	126	[38]	126
115	Animalia	Mammalia	Rhinolophoidea	Body mass	g	173	[38]	173	[38]	173
116	Animalia	Mammalia	Vespertolionidae	Body mass	g	197	[38]	197	[38]	197
117	Animalia	Reptilia	Agamidae	Body length	mm	204	[38]	204	[38]	204
118	Animalia	Reptilia	Anguimorpha	Body length	mm	99	[38]	99	[38]	99
119	Animalia	Reptilia	Chamaelionidae	Body length	mm	106	[38]	106	[38]	106
120	Animalia	Reptilia	Chelonia	Body length	mm	226	[38]	226	[38]	226
121	Animalia	Reptilia	Dactyloidae	Body length	mm	202	[38]	202	[38]	202
122	Animalia	Reptilia	Diplodactylidae	Body length	mm	78	[38]	78	[38]	78
123	Animalia	Reptilia	Gekkonidae1	Body length	mm	182	[38]	182	[38]	182
124	Animalia	Reptilia	Gekkonidae2	Body length	mm	150	[38]	150	[38]	150
125	Animalia	Reptilia	Gerrhosauridae-Cordylidae	Body length	mm	76	[38]	76	[38]	76
126	Animalia	Reptilia	Gymnophthalmoidea	Body length	mm	123	[38]	123	[38]	123
127	Animalia	Reptilia	Lacertidae	Body length	mm	175	[38]	175	[38]	175
128	Animalia	Reptilia	Liolaemidae	Body length	mm	100	[38]	100	[38]	100
129	Animalia	Reptilia	Lygosominae-Eugongylus-Egernia	Body length	mm	153	[38]	153	[38]	153
130	Animalia	Reptilia	Lygosominae-Sphenomorphus	Body length	mm	180	[38]	180	[38]	180
131	Animalia	Reptilia	Phrynosomatidae	Body length	mm	103	[38]	103	[38]	103
132	Animalia	Reptilia	Serpentes-Boa-Python-Shieldtail	Body length	mm	60	[38]	60	[38]	60
133	Animalia	Reptilia	Serpentes-Colubridae-Colubrinae	Body length	mm	219	[38]	219	[38]	219

134	Animalia	Reptilia	Serpentes-Colubridae-Natricinae	Body length	mm	67	[38]	67	[38]	67
135	Animalia	Reptilia	Serpentes-Colubridae-Xenodontinae	Body length	mm	114	[38]	114	[38]	114
136	Animalia	Reptilia	Serpentes_Elapidae	Body length	mm	126	[38]	126	[38]	126
137	Animalia	Reptilia	Serpentes-Lamprophiidae	Body length	mm	109	[38]	109	[38]	109
138	Animalia	Reptilia	Serpentes-Viperidae	Body length	mm	161	[38]	161	[38]	161
139	Animalia	Reptilia	Sphaerodactylidae	Body length	mm	91	[38]	91	[38]	91
140	Animalia	Reptilia	Tropiduridae	Body length	mm	78	[38]	78	[38]	78
141	Animalia	Mammalia	-	Body mass	g	3,321	[35], [39]	5,020	[40]	3,321
142	Animalia	Actinopterygii	-	Body length	cm	6,760	[18]	7,822	[18]	6,760
143	Animalia	Aves	-	Body mass	g	6,160	[41]	9,993	[42]	6,160

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APPENDIX 2 | Model selection

Table 1 | Bayes factor support for either a Brownian motion (BM) or variable rates (VR) model of evolution. 'Analysis' is an arbitrary number used for dataset identification and matches that in Appendix 1, Table 1. The Bayes factors are calculated using the mean marginal likelihood (mLh) from multiple replicates.

Analysis	Mean BM mLh	Mean VR mLh	Bayes factor	Model Supported	No. of comparisons supporting VR (BF > 2) (/25)
001	197.545	224.639	54.188	VR	25
002	273.819	307.207	66.776	VR	25
003	443.650	506.942	126.584	VR	25
004	212.431	226.403	27.944	VR	25
005	419.247	428.326	18.159	VR	25
006	201.605	203.374	3.537	VR	17
007	134.259	143.948	19.377	VR	25
008	111.790	123.926	24.271	VR	25
009	26.914	29.657	5.486	VR	25
010	351.347	375.634	48.575	VR	25
011	327.851	354.938	54.175	VR	25
012	411.036	421.587	21.104	VR	25
013	321.936	353.613	63.355	VR	25
014	418.081	422.633	9.103	VR	25
015	330.962	350.332	38.740	VR	25
016	436.060	435.883	-0.354	BM	6
017	57.921	57.671	-0.499	BM	0
018	281.354	319.744	76.781	VR	25
019	315.744	346.095	60.702	VR	25
020	330.184	360.973	61.580	VR	25
021	6.693	6.158	-1.069	BM	0
022	404.770	585.048	360.555	VR	25
023	9.756	9.589	-0.335	BM	0
024	38.128	42.248	8.241	VR	25
025	331.965	352.507	41.085	VR	25
026	54.385	52.092	-4.586	BM	0
027	-26.615	10.260	73.750	VR	25
028	70.792	71.890	2.198	VR	15
029	97.554	96.706	-1.696	BM	0
030	508.652	517.353	17.402	VR	25
031	119.389	216.971	195.163	VR	25
032	50.398	49.707	-1.383	BM	0
033	-46.833	-40.228	13.211	VR	25
034	119.219	117.342	-3.753	BM	0

035	14.067	3.586	-20.963	BM	0
036	4.661	-1.992	-13.306	BM	0
037	-30.384	-22.760	15.247	VR	25
038	73.606	74.105	0.997	BM	5
039	49.018	47.799	-2.438	BM	0
040	44.178	52.530	16.705	VR	25
041	134.441	183.909	98.935	VR	25
042	37.828	47.764	19.871	VR	25
043	59.440	58.849	-1.183	BM	0
044	51.128	50.973	-0.310	BM	0
045	25.373	25.068	-0.610	BM	0
046	30.218	30.558	0.679	BM	1
047	52.495	51.976	-1.039	BM	0
048	94.520	93.330	-2.378	BM	0
049	37.346	36.859	-0.973	BM	0
050	55.675	54.679	-1.991	BM	0
051	47.520	47.189	-0.662	BM	0
052	56.942	56.609	-0.665	BM	0
053	44.786	43.867	-1.839	BM	0
054	29.951	30.783	1.665	BM	7
055	22.381	22.852	0.942	BM	5
056	19.772	24.408	9.271	VR	25
057	-7.821	4.098	23.838	VR	25
058	18.924	22.654	7.461	VR	25
059	23.433	27.727	8.589	VR	25
060	443.733	459.473	31.481	VR	25
061	452.561	465.148	25.175	VR	25
062	438.085	460.662	45.153	VR	25
063	165.685	165.523	-0.323	BM	6
064	192.694	192.262	-0.865	BM	10
065	203.042	204.335	2.586	VR	16
066	201.109	199.948	-2.323	BM	3
067	213.547	226.186	25.279	VR	25
068	206.970	207.649	1.360	BM	10
069	193.052	193.793	1.482	BM	13
070	222.998	295.208	144.421	VR	25
071	-89.224	-37.805	102.838	VR	25
072	-9.124	40.006	98.260	VR	25
073	-146.924	2.916	299.681	VR	25
074	-118.151	-78.706	78.891	VR	25
075	-30.147	27.483	115.261	VR	25
076	33.348	50.975	35.255	VR	25
077	48.289	57.741	18.903	VR	25
078	31.193	28.217	-5.953	BM	0
079	106.995	122.141	30.292	VR	25
080	149.750	172.845	46.191	VR	25

081	159.534	167.732	16.397	VR	25
082	112.000	118.941	13.881	VR	25
083	354.901	375.179	40.556	VR	25
084	41.302	113.808	145.011	VR	25
085	58.825	132.531	147.413	VR	25
086	168.597	168.784	0.374	BM	18
087	86.638	88.031	2.785	VR	25
088	56.120	84.398	56.555	VR	25
089	143.720	144.843	2.246	VR	25
090	77.007	131.658	109.303	VR	25
091	8.337	52.610	88.546	VR	25
092	77.865	78.809	1.887	BM	19
093	348.890	356.322	14.864	VR	25
094	525.004	599.949	149.889	VR	25
095	384.413	475.136	181.446	VR	25
096	-29.896	-9.053	41.685	VR	25
097	-51.880	-42.896	17.969	VR	25
098	-79.922	-53.831	52.181	VR	25
099	52.617	64.109	22.983	VR	25
100	-128.645	-111.223	34.843	VR	25
101	-115.563	7.338	245.801	VR	25
102	81.064	105.630	49.132	VR	25
103	-4.098	-4.439	-0.682	BM	8
104	-166.008	-135.649	60.719	VR	25
105	6.743	8.436	3.386	VR	25
106	-118.067	-101.453	33.227	VR	25
107	76.301	88.218	23.835	VR	25
108	47.678	45.064	-5.227	BM	0
109	125.199	127.272	4.145	VR	25
110	156.848	157.316	0.937	BM	19
111	-0.962	10.760	23.443	VR	25
112	113.819	134.196	40.754	VR	25
113	181.468	200.673	38.410	VR	25
114	153.764	152.895	-1.738	BM	5
115	-31.407	140.379	343.571	VR	25
116	281.965	286.050	8.169	VR	25
117	17.543	46.800	58.515	VR	25
118	-29.851	-24.292	11.119	VR	25
119	-14.391	-14.240	0.303	BM	15
120	-193.443	-84.922	217.041	VR	25
121	103.104	106.920	7.632	VR	25
122	23.939	45.508	43.139	VR	25
123	65.951	75.710	19.518	VR	25
124	5.383	39.449	68.132	VR	25
125	2.345	5.801	6.911	VR	25
126	-57.386	2.219	119.210	VR	25

127	75.705	112.526	73.642	VR	25
128	116.421	113.863	-5.116	BM	4
129	18.597	18.084	-1.026	BM	11
130	95.164	102.071	13.814	VR	25
131	73.726	72.162	-3.128	BM	1
132	-63.659	-64.474	-1.631	BM	4
133	-60.326	-61.498	-2.345	BM	4
134	-48.706	-37.882	21.647	VR	25
135	-35.329	-35.506	-0.354	BM	10
136	-101.879	-84.990	33.779	VR	25
137	-23.532	-26.615	-6.165	BM	0
138	-37.256	-26.374	21.763	VR	25
139	-17.018	8.294	50.624	VR	25
140	46.976	67.781	41.611	VR	25
141	462.251	870.422	816.341	VR	20
142	-8233.286	-4345.051	7776.471	VR	20
143	5390.336	8435.947	6091.223	VR	25

Chapter 3 | The evolutionary and ecological consequences of exceptional changes

"In all things of nature there is something of the marvellous"
Aristotle, (350 BC)[1]

ABSTRACT

Exceptional changes in body size have been littered throughout the evolutionary histories of the major vertebrate radiations. We test to see whether such changes occur in clusters on the branches of the mammal, bird and fish phylogenies or conversely, whether they are randomly distributed. As rare, but special features of evolution that define the extremities of evolutionary mode, we sought to understand why such changes occur in nature at all. To do this, we investigated the influence of environment on the frequency of exceptional changes that occur in birds and mammals. The consequences of undergoing large jumps in body size are potentially far reaching; we test the impact of these jumps on the body sizes and propensity to speciate in all three taxonomic groups. There is taxonomic variation in the number of exceptional changes experienced across vertebrate history with mammals undergoing the largest number. In mammals too, we find that exceptional changes show phylogenetic signal. In birds and fish we find some evidence of exceptional changes being clustered however relative to the mammals, these quantum leaps in body size are more sporadically distributed both temporally and taxonomically. We find that exceptional changes contribute to whole clades of species undergoing major evolutionary transitions in both birds and mammals, explaining the difference in the frequencies of these changes in organisms occupying different environments. Further, in all three groups exceptional changes are associated with larger body size and more frequent speciation events with the relationships therein influenced by an organism's environment.

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[1] Aristotle. (350 BC). Parts of animals. Movement of animals. Progression of animals. (Translated by Peck, A. L. and Forster, E.S.). Cambridge, Massachusetts: Harvard University Press

INTRODUCTION

The biological diversity we see today and in the fossil record is vast but how does such variation arise? Darwin is attributed to having taken a 'gradualistic' viewpoint suggesting that diversity is achieved through small, continual steps. We show previously (Chapter 2) that across the tree of life, evolution has worked by relatively small changes making up the vast majority of species evolution. However, there has been growing evidence of exceptional periods of evolution where large leaps occur and that such jumps may make a considerable contribution to generating species and their divergent morphologies (Simpson, 1944; Venditti *et al.,* 2011; Cooney *et al.,* 2017; Landis and Schraiber, 2017; Chapter 2).

With the development of phylogenetic inference and sophisticated phylogenetic comparative methods (PCMs), evolutionary tempos and modes can be studied across thousands of species using a variety of biological data. Biologists can study how traits (Harmon *et al.*, 2010; Clarke *et al.*, 2017; Cooney *et al.*, 2017; Gill *et al.*, 2017; Schnitzler *et al.*, 2017) and rates (Nee *et al.*, 1994; Pybus and Harvey, 2000; Nee, 2001; Rabosky and Lovette, 2008; Venditti *et al.*, 2011; Rabosky *et al.*, 2013; Rabosky, 2017; Revell, 2018) evolve, in a quantitative framework accounting for species shared evolutionary history (Felsenstein, 1985; Harvey and Pagel, 1991) and reveal key characteristics of the processes underpinning them (Felsenstein, 1985; Hansen, 1997; Pagel, 1997; Pagel, 1999; Blomberg *et al.*, 2003; Harmon *et al.*, 2010; Uyeda *et al.*, 2011; Venditti *et al.*, 2011; Bartoszek, 2017; Duchen *et al.*, 2017; Landis and Schraiber, 2017; Chira *et al.*, 2018). It is also possible to uncover large scale trends of directional change in traits (Pagel, 1999; Monroe and Bokma, 2010; Baker *et al.*, 2015), associations between rates such as that of speciation with directional change in morphological traits (Freckleton *et al.*, 2008; Avaria-Llautureo *et al.*, 2012) and how species' ecology relates to their morphological trait evolution (Hansen, 1997; Slabbekoorn and Smith, 2002; Streelman and Danley, 2003; Goodman *et al.*, 2008; Ezard *et al.*, 2011; Chira *et al.*, 2018).

The modes of trait and rate evolution on a phylogeny can be tested using a measure of phylogenetic signal, or heritability (Fisher, 1918; Wright, 1920; Lush, 1936; Lynch, 1991; Pagel, 1999). Historically, the contexts in which these metrics have been used has varied (Blomberg and Garland Jr, 2002). Phylogenetic signal has often been used in comparative studies to test whether a dataset need be subjected to phylogenetic analyses or not (Ashton, 2002; Hansen, 2014) and heritability used almost exclusively in quantitative genetic studies on pedigrees (Leventhal and Bonhoeffer, 2016). However, both can be used as powerful tools to reveal biological, rather than statistical properties of both trait data and the organisms the data come from. Phylogenetic signal and heritability both measure the extent to which a trait evolves according to the branching pattern of a phylogeny or, how similar a given trait is in related individuals (Lynch, 1991; Pagel, 1999). There have been many methods developed with which to quantify phylogenetic signal (Moran, 1950; Gittleman and Kot, 1990; Lynch, 1991; Pagel, 1999; Blomberg *et al.*, 2003; Fritz and Purvis, 2010). These have typically been used to study the signal in data concerning morphological traits such as body size (Blomberg *et al.*, 2003; Naisbit *et al.*, 2011; Kamilar and Cooper, 2013) and in rates such as extinction rates (Purvis, 2008; Roy *et al.*, 2009; Fritz and Purvis, 2010; Hardy *et al.*, 2012; Puttick *et al.*, 2017). Most recently, Sakamoto and Venditti, (2018) found that there is phylogenetic signal in rates of morphological trait evolution in mammalian body size, avian beak morphology (akin to Cooney *et al.,* 2017) and amniote bite force.

Where previously (Chapter 2) we were interested in how each individual evolutionary change has combined to characterise the evolutionary process, we now consider only the 'exceptional' changes; those changes in trait value which fall two or more standard deviations away from the mean. These represent instances where evolution has made remarkably large jumps and provides a novel definition and quantification of exceptional, or quantum evolution *sensu* Simpson. This is also the first time that the frequency of exceptional changes in trait value has been used as a biological trait itself. These exceptional changes represent large and rare modifications in body size (to become both bigger and smaller) in three major radiations of vertebrates. To investigate the mode of body size evolution in mammals, bony fish and birds, we first test how exceptional changes are distributed across the respective phylogenies; whether they occur in clusters, implying that there is phylogenetic signal in the propensity to undergo such changes or whether they are randomly distributed across the branches of the trees. Given that an organism's environment is deemed the major driving force for how it evolves (Darwin, 1859; Carroll, 2001; Schoener, 2011), we test whether organisms which differ in their ecology undergo a greater or lesser number of exceptional changes, to shine a light on perhaps why they occur. We also seek to understand whether and how the occurrence of these exceptional changes relates to body size, enabling us to uncover the existence of directional trends in body size evolution and also how exceptional changes associate with the frequency of speciation events. These analyses allow us to reveal the consequences of exceptional changes for the evolution and ecology of three large clades comprised of over 16,000 species contributing to extant diversity.

METHODS

Phylogenetic trees and exceptional change data

In Chapter 2 we used phylogenetic trees matched with body size data to reconstruct ancestral body sizes using a model of evolution which detects variations in rates of change on individual branches or in whole clades of a phylogeny. Using these ancestral states we calculated the change per unit time along each branch of every phylogeny as:

$$change\ per\ unit\ time = \frac{log_{10}(X_2) - log_{10}(X_1)}{\sqrt{t}}$$

where X_1 and X_2 are the ancestor and descendant at either end of a single branch, the length of which is measured in millions of years (t). To make these change per unit time values comparable between phylogenetic trees we transformed them into Z scores:

$$Z = \frac{change\ per\ unit\ time}{SD\ change\ per\ unit\ time}$$

To calculate Z for each branch we took the change per unit time and divided this by the standard deviation of the change per unit time values across all branches of a single tree. We classified Z values of more than 2 and less than -2 as 'exceptional' given that these changes occur two or more standard deviations away from the mean and thus make up a conservative fraction of the 2.5th and 97.5th percentiles of the data.

We used the exceptional change data associated with three of the 143 phylogenies used in Chapter 2 – the largest trees of mammals, fish and birds. We used the mammal phylogeny of Fritz *et al.,* (2009) matched with the body mass of 3,321 mammalian species (Ernest, 2003; Jones *et al.*, 2009). For actinopterygian fish we used the tree from Rabosky *et al.*, (2013) matched with the maximal body length of 6,760 actinopterygians from the same source as the phylogeny. We used the maximum clade credibility tree of 1,000 trees from Jetz *et al.*, (2012) containing 9,993 species of birds which uses the backbone structure of Hackett *et al.*, (2008). This was matched with the body mass of 6,160 bird species (Dunning, 2007). These trees were selected on the basis that they have previously been used to study speciation and extinction rates (Fritz *et al.*, 2009; Jetz *et al.*, 2012; Rabosky *et al.*, 2013) and owing to their comprehensive sampling: the mammal phylogeny contains 79% of all wild living, extant mammals (Burgin *et al.*, 2018), the bird tree 55% of extant avian species (Barrowclough *et al.*, 2016) and the fish tree 26% of extant, actinopterygian species (Carrete Vega and Wiens, 2012).

Phylogenetic clustering (H^2) of exceptional changes

We summed the number of exceptional changes ($Z < -2$ and $Z > 2$) along a path from the root of the phylogeny to every species at the tips. We refer to these as the pathwise exceptional changes (PECs). We used these PEC values to run Poisson regressions for each tree using the R package (R Core Team, 2016) MCMCglmm (Hadfield, 2010) to estimate the phylogenetic signal of exceptional changes. We modelled PEC as the response variable with node count (the number of nodes between the root and each tip) as the independent variable such that when estimating phylogenetic signal we account for the fact that the opportunity for exceptional changes to occur increases on paths with more branches. We ran the three Poisson regression models in MCMC with a parameter expanded prior ($V = 1$, $\nu = 1$, $\alpha\mu = 0$, and $\alpha V = 25^2$) for the phylogenetic random effect and the default priors of an inverse Wishart distribution for the residual variance ($\nu = 0.002$, $V = 1$) and a wide normal distribution for the fixed effects ($\mu = 0$, $V = 10^8$) (Sakamoto *et al.*, 2016). The mammal dataset was run for 1,252,000 iterations, 2,000 of which were discarded as burnin, with the remainder sampled every 1,250 iterations. The fish dataset was run for 2,004,000 iterations, 4,000 of which was discarded as burnin after which we sampled every 2000 iterations. The bird dataset was run for 1,502,000 iterations with the first 2,000 discarded as burnin after which we sampled every 1,500 iterations. These conditions were used in order to achieve effective sample sizes for all parameters of more than 100 in the final converged chains.

We use heritability (H^2) as a measure of phylogenetic signal, or, the percentage of the variation in PECs that is attributable to the structure of the phylogeny (the random effect) aside from that attributable to fixed effects (here, node count). We calculate H^2 using the variance associated with both the random and the fixed effects:

$$H^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$$

where σ_a^2 is equal to the variance in trait value associated with the phylogeny and σ_e^2 is that associated with the fixed effect (Hadfield and Nakagawa, 2010). This is mathematically equivalent to estimating Pagel's lambda (λ; Pagel, 1999) which estimates the extent to which a continuously varying trait has evolved according to a Brownian motion model, with trait variance increasing proportionally with time and where trait values for related individuals can be predicted given the structure of the phylogeny. When phylogenetic signal is high, there is an inherited propensity for traits to be similar in ancestors and descendants - descent with modification (Darwin, 1859). Conversely, in cases where phylogenetic signal is low, or perhaps absent, traits have evolved in species at or towards their terminal branches on a tree and thus have evolved independently of each other, equivalent to having evolved over the branches of a star phylogeny. In these cases, when visualised on a tree, a trait would be randomly distributed having not been inherited along lineages.

The two metrics (λ and H^2) whilst on a mathematical and philosophical basis are equivalent, differ however in their direct, or quantitative interpretation. Where H^2 is a ratio of the variance attributed to the random and fixed effects, lambda describes the extent to which the terminal branches of a tree must be transformed in order to make the data best fit a Brownian motion model of evolution (Pagel, 1997; Pagel, 1999; Freckleton *et al.*, 2002). The term heritability is often used in the context of understanding heritability within populations – in its traditional context of pedigrees. We however calculate heritability at the species level and thus cannot deduce levels of direct trait inheritance along the branches of a phylogenetic tree in the same way as in pedigrees. To say that exceptional changes are, or are not heritable implies that there may be some direct genetic mechanism by which the ability to change trait value by large amounts can be passed between ancestral and descendant species. Whilst this may be the case, it may also be that what is genetically heritable is an underlying trait which promotes exceptional changes – for example, tendency to disperse. To avoid semantic confusion, we therefore refer to estimates of both lambda and H^2 as measures of phylogenetic signal or phylogenetic clustering rather than using the term heritability.

Phylogenetic clustering of randomised exceptional changes

Lambda and H^2 are often used to test for phylogenetic signal in continuous data, but less so in binary or count data. Thus, to test whether our values of H^2 were significant, or, whether the clustering patterns detected in the PEC values is significantly different from random, we needed to estimate phylogenetic signal in datasets with PECs generated by random. To create these randomised datasets we took the original number of branchwise exceptional changes in each tree (257 in the mammal tree, 511 in the fish tree and 405 in the bird tree) and allocated this number of exceptional changes to a random selection of the branches in each tree. The number of exceptional changes was then summed along the paths to generate PEC values for each tip, as with the observed data. This process was done 1,000 times, generating 1,000 randomised datasets for each tree.

These datasets were each treated in the same way as the three observed datasets with phylogenetic signal in PECs being estimated in Poisson regressions in MCMCglmm (Hadfield, 2010; R Core Team, 2016) using both the same priors and run conditions. We found that the H^2 values associated with the randomised datasets were as high, (if not higher, in the case of the fish and birds) than those for the observed data. As a consequence, we determine significant clustering of PECs by comparing the difference in the Deviance Information Criterion (DIC) value when the Poisson regression is run with and without the random effect of the phylogeny. The bigger the difference in DIC value, the higher the percentage of variation in PEC is explained by the phylogeny. We calculate this DIC difference for the observed data and all of the 1,000 randomisations for each tree. If the difference in DIC is bigger in the observed data run with and without phylogeny than in 95% or more of the randomisations, then we can say that the PECs are significantly more clustered than would be expected by random. Conversely, if the DIC difference between the models for the observed data is less than that for 95% (or more) of the randomised datasets then we can say that they are less clustered than would be expected by random. Equally, there may be overlap in the differences of the randomisations and the observed data such that we can say the PECs in the given tree are distributed randomly.

Phylogenetic signal (λ) in PECs

To support the Poisson regressions run in MCMCglmm (Hadfield, 2010; R Core Team, 2016) we ran the same data in a maximum likelihood, phylogenetic, Gaussian regression model in BayesTraits (Pagel *et al.*, 2004) first fixing lambda to one, and then fixing lambda to zero. We then calculated the difference in the log likelihood values between the lambda = 1 and the lambda = 0 models (equivalent to running the model with and without phylogeny respectively). Whilst we violate the assumptions of this type of regression model by using count, rather than continuous data as the dependent variable, we expect that the relative differences between the likelihoods of the observed and the random data should corroborate what we find when using the Poisson regression models. In the same way as before, we expect that if there is phylogenetic signal in the PECs then the difference in likelihood in the observed data between the two models should be greater than that for at least 95% of the randomisations. If there is no phylogenetic signal then the likelihood difference between the two models for the observed data should be less than for 95% or more of the randomisations.

Exceptional changes, ecology, speciation and body size

In Chapter 2 we studied the effect of habitat on the magnitude and direction of branchwise changes in body size. Here we use this ecological data again to test whether mammals and birds in different environments show different relationships regarding speciation, body size and exceptional changes. The fish could not be used here given their lack of habitat variation (in the way that we classify habitat). Where before we generated ecological data for every branch in the tree, here we use pathwise data and as such we use the habitat category associated with just the terminal branches of the phylogeny as the data for each tip species. The habitats represent the environment in which a species reproduces – either terrestrial or aquatic. For those species that reproduce on land, but that also have the ability to fly we have added the category of 'volant' given the major differences in selective pressures acting on ground based terrestrial organisms in comparison to flying species. All three categories of environment are present in the mammal tree with cetaceans and sirenians classed as aquatic, bats as volant and the remainder as terrestrial. The bird tree contains terrestrial species which consist of the ratites, kakapo, kiwis and penguins and volant species which describes the remainder of neognath birds.

We ran three regression models on each of the three trees in order to investigate the relationships between environment, PECs, speciation and body size. All regressions were run using the R package (R Core Team, 2016) MCMCglmm (Hadfield, 2010). Firstly we regressed PEC on habitat, body size and node count in a multiple Poisson regression, adding interaction terms between habitat and node count and habitat and body size (henceforth the 'PEC regression'). These interaction terms allow us to identify whether the relationships between the dependent and independent variables exist in different groups of species and if present whether they differ to each other, by estimating separate intercepts and slopes for the different ecological groups. No interaction terms were estimated in the regressions on the fish data owing to the lack of habitat variation. Secondly we modelled node count as the dependent variable on habitat, body size and PEC count, again adding in interaction terms between habitat and body size and habitat and PEC (henceforth the 'node count regression'). Finally, we ran a Gaussian regression of body size on habitat, node count and PEC with interactions between habitat and node count and habitat and PEC (henceforth the 'body size regression').

All regression models for the mammals were run for 1,754,000 iterations, with 4,000 discarded as burnin and sampling every 1,750 iterations to generate a posterior distribution of 1,000 samples. All models for the fish were run for 31,000,000 iterations, discarding 1,000,000 as burnin and sampling every 30,000 iterations to produce a posterior distribution of 1,000 samples. The bird models were run for 2,005,000 iterations, with 5,000 discarded as burnin and sampled every 2,000 to produce a posterior distribution of 1,000 samples. We use a parameter expanded prior ($V = 1$, $\nu = 1$, $\alpha\mu = 0$, and $\alpha V = 25^2$) for the phylogenetic random effect and the default priors of an inverse Wishart distribution for the residual variance ($\nu = 0.002$, $V = 1$) and a wide normal distribution for the fixed effects ($\mu = 0$, $V = 10^8$) (Sakamoto *et al.*, 2016).

We established whether a significant relationship between the independent and dependent variables existed by calculating whether the coefficients associated with the regression slopes for each group were significantly different from zero. To do this, we summed the number of samples in the posterior distributions of these coefficients that were less than zero and then converted this to a percentage to generate a %MCMC value. If less than 5 or more than 95, this %MCMC value indicates that a significant percentage of the posterior of coefficients is different to zero. To then understand whether relationships differed in organisms inhabiting different habitats we calculated the difference in their slopes and similarly, calculated the percentage of the posterior of these differences that were different from zero.

RESULTS

Phylogenetic clustering in exceptional changes as indicated by H^2 and lambda (λ)

In all cases, we find that the Poisson regression models run using the observed datasets show increases in DIC value upon removing the random effect of phylogeny from the model. This indicates that a model which includes phylogeny better fits the mammal, bird and fish PEC data by explaining a significant portion of the variance in PEC count across the trees. However, this is also the case for all 1,000 of the randomisations for each group meaning that all datasets show some level of phylogenetic signal in exceptional changes (Figure 1). In mammals, the difference in the DICs of the regression models run with and without the phylogeny is greater in the observed data than in 99.6% of the randomised datasets (Figure 1A). This means that exceptional changes are not randomly distributed in mammals, rather, we suggest that they occur in phylogenetically structured clusters (Figure 2).

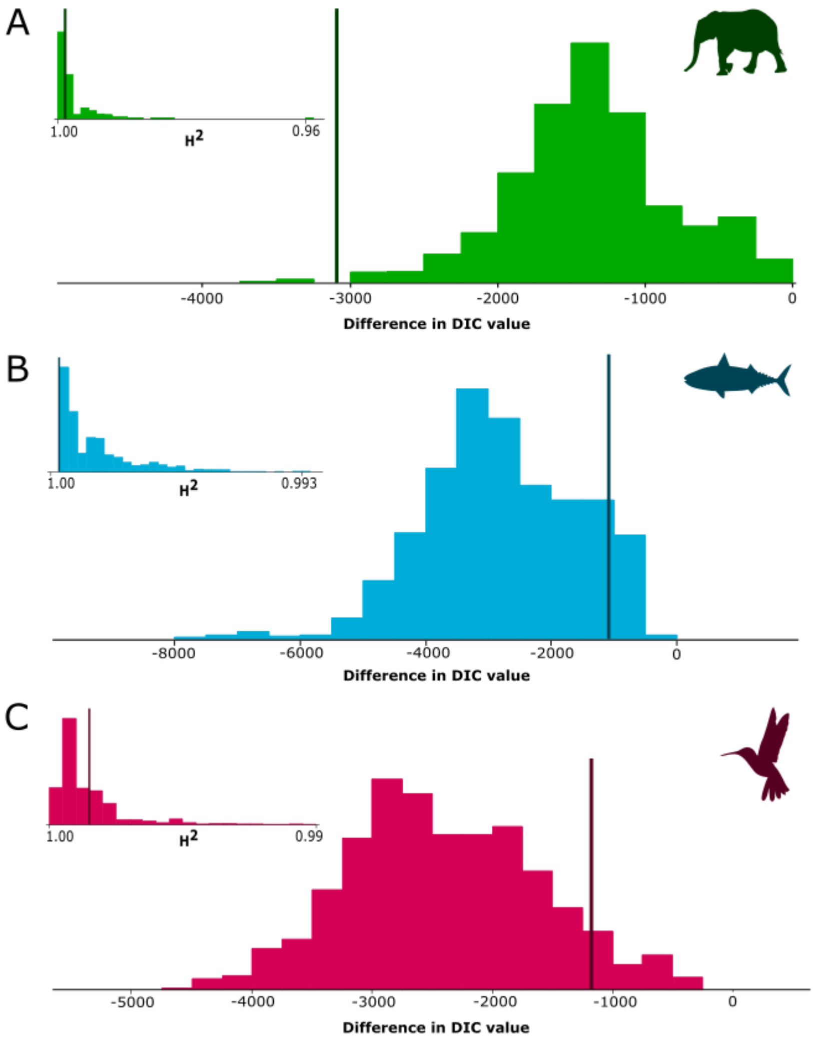

Figure 1 | Distribution of differences in DIC value of Poisson regressions of PEC on node count with and without the phylogeny as a random effect. For **A** – mammals, **B** – fish and **C** – birds. Histograms show the distribution of differences in the DIC of models run with and without phylogeny for the 1,000 randomised datasets. The DIC difference of the models for the observed data is shown by the dark, vertical lines. Inset in each are the distributions of median heritability (H^2) values estimated from the Poisson regressions of PEC on node count including phylogeny as a random effect for the 1,000 randomised datasets. The median H^2s for the observed data are shown by the inset dark, vertical lines. Note: inset histograms' scales go from high to low values where the main histograms' scales are conventionally arranged from low to high values.

In both fish and birds however, the differences in DICs of the models with and without phylogeny are smaller in the observed data than in 90.7% and 80.6% of the randomisations in fish and birds respectively (Figure 1B and C). This means that exceptional changes in these two groups show little phylogenetic signal in the occurrence of exceptional changes, or at least less than is seen in the mammals.

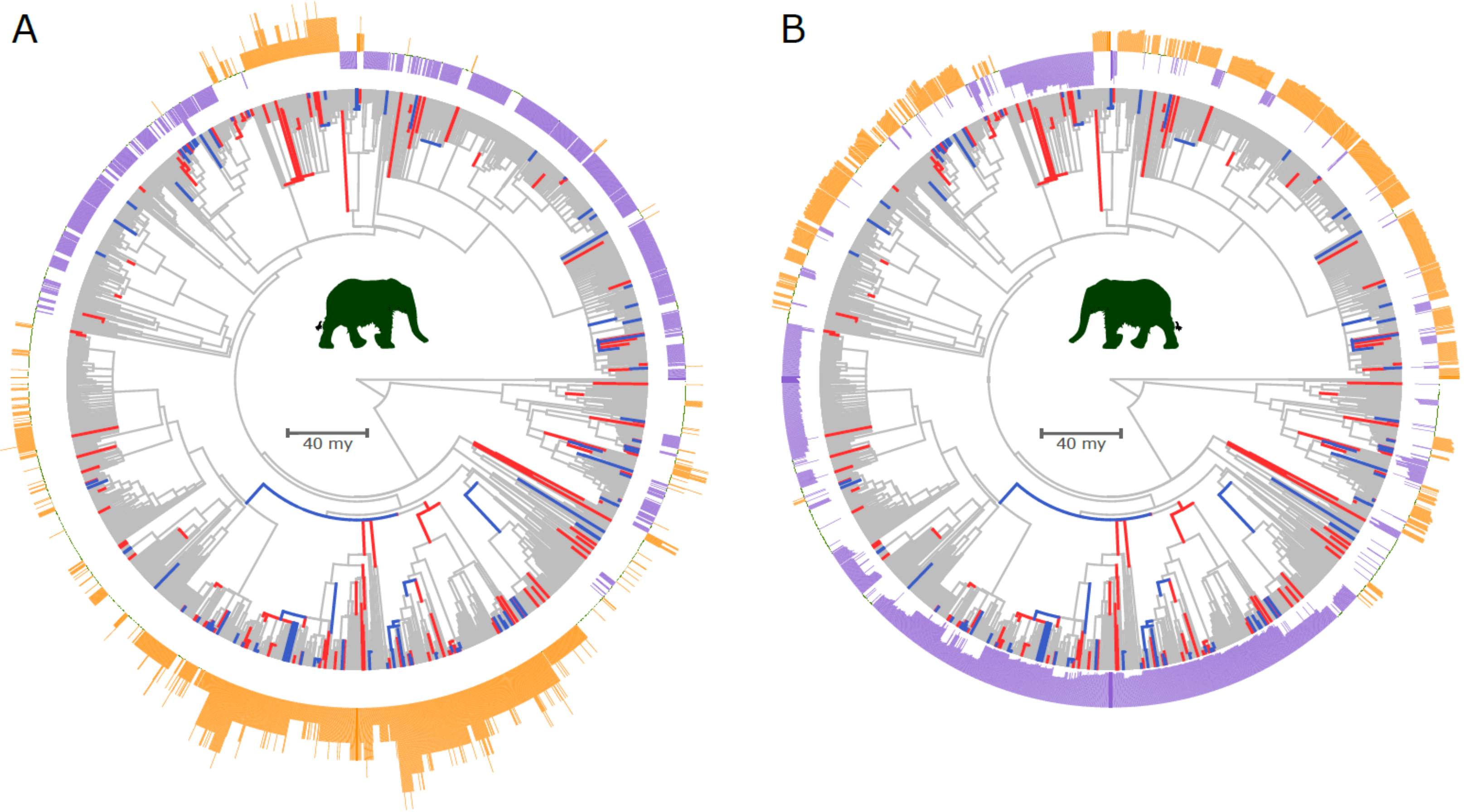

Figure 2 | Phylogenetic clustering of exceptional changes in observed data compared with 1,000 randomised exceptional change datasets in mammals. A - Bars at the tips represent the difference between the observed PEC count and the median of the 1,000 randomised PECS. The length of these bars shows the magnitude of the difference between the observed and median *(Caption continues on next page)*

Figure 2 caption continued - randomised PECs. Bars are orange where the observed PEC is greater than the median of the randomised PECS and purple where the observed PEC is less than the median randomised PEC. Where a green dot is present (and no bar is present), the observed PEC is the same as the median randomised PEC. **B** - Bars at the tips show the percentage of the 1,000 randomised PECs that are greater than, less than or equal to the observed number of PECs. The length of the bars is equal to this percentage. Orange bars indicate that the largest portion of the randomised PECs are greater than the observed value. Purple bars indicate that the largest portion of the randomised PECs is less than the observed value. Where the largest portion of the randomised PECs is equal to the observed PEC there is a green dot and no bar is present.

Nevertheless, despite both showing low levels of clustering, the distribution of exceptional changes across the fish and bird trees are very different. The fish undergo exceptional changes mostly on terminal branches with none deep in the phylogeny (Figure 3) and the birds' exceptional changes have a distribution more intermediate between that of the mammals and fish (Figure 4). These results are qualitatively supported by the differences seen in the likelihood of regression models run in BayesTraits estimating lambda (Appendix 1).

The relationships between exceptional changes, ecology, speciation and body size

We found evidence for environmental variation in the number of exceptional changes that occur in both birds and mammals (Appendix 2, Table 1). Aquatic mammals experience the greatest number of PECs, followed by volant species, with terrestrial mammals undergoing the smallest number of exceptional changes (Figure 5A). In birds however, this is reversed, with terrestrial species associated with more exceptional changes than volant species (Figure 7A).

The results of the node count regressions reveal that there is a significant and positive relationship between exceptional changes and speciation in all animal groups (Figures 5B, 6A and 7B). However, in mammals this relationship only exists in terrestrial and volant species and in birds only in volant species (Appendix 2, Table 2). Similarly, in all three groups there is a significant, positive relationship between the number of PECs and body size (Appendix 2, Table 3; Figures 5C, 6B and 7C) meaning that the species that have experienced more exceptional changes along their path are the species with larger body sizes. In addition, in mammals we find that this positive relationship differs for organisms in different habitats, with aquatic mammals increasing in body size the most

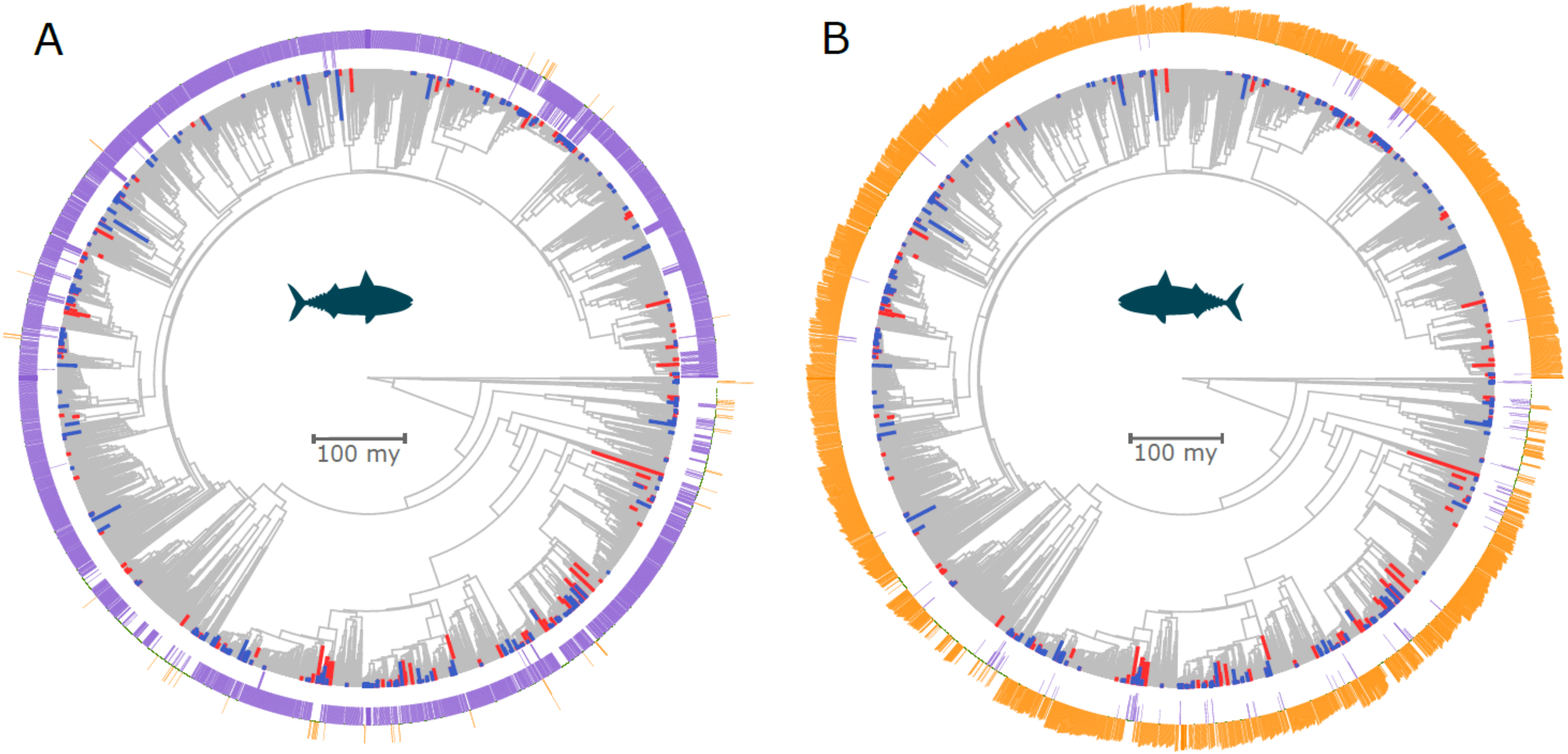

Figure 3 | Phylogenetic clustering of exceptional changes in observed data compared with 1,000 randomised exceptional change datasets in fish. A - Bars at the tips represent the difference between the observed PEC count and the median of the 1,000 randomised PECS. The length of these bars shows the magnitude of the difference between the observed and median randomised PECs. Bars are orange where the observed PEC is greater than the median of the randomised PECS and purple where the observed PEC is less than the median randomised PEC. Where a green dot is present (and no bar is present), the observed PEC is the same as the median *(Caption continues on next page)*

Figure 3 caption continued - randomised PEC. **B** - Bars at the tips show the percentage of the 1,000 randomised PECs that are greater than, less than or equal to the observed number of PECs. The length of the bars is equal to this percentage. Orange bars indicate that the largest portion of the randomised PECs are greater than the observed value. Purple bars indicate that the largest portion of the randomised PECs is less than the observed value. Where the largest portion of the randomised PECs is equal to the observed PEC there is a green dot and no bar is present.

per exceptional change that occurs, followed by volant mammals and lastly, terrestrial species which undergo the smallest change in body size for every exceptional change.

Finally, also using the coefficients of the body size regression, we found no relationship between body size and speciation in birds (Appendix 2, Table 3; Figure 7D). In fish there is a significant and negative relationship such that organisms with more speciation events along their path are typically smaller bodied (Figure 6C). In aquatic mammals, similarly to fish, there is a significant negative relationship between speciation and body size unlike in volant and terrestrial mammalian species, where there is a significant, positive relationship between these variables (Figure 5D). In addition, phylogenetic signal in exceptional changes remains high in ecological regressions in all three taxonomic groups.

DISCUSSION

Changes in body size of an exceptional magnitude have occurred thousands of times in mammals, fish and birds but as well as interest in their frequency (Chapter 2), we are also concerned with when and where they have occurred across these three major vertebrate radiations. We find that exceptional changes are distributed very differently in the mammal, fish and bird phylogenies implying that body size evolution in these groups has been far from uniform (Venditti *et al.*, 2011).

In mammals, as one might expect, we see exceptional changes occurring to increase body size in clades such as the proboscideans, perissodactyls, and cetartiodactyls and those to decrease body size in the branches leading to the root of chiropterans and in the clade eulipotyphla, to name but a few examples (Figure 2). Overall, we find evidence to suggest that there is phylogenetic signal in the number of exceptional changes along the lineages of the mammal tree; exceptional changes occur in clusters (Figures 1A and 2).

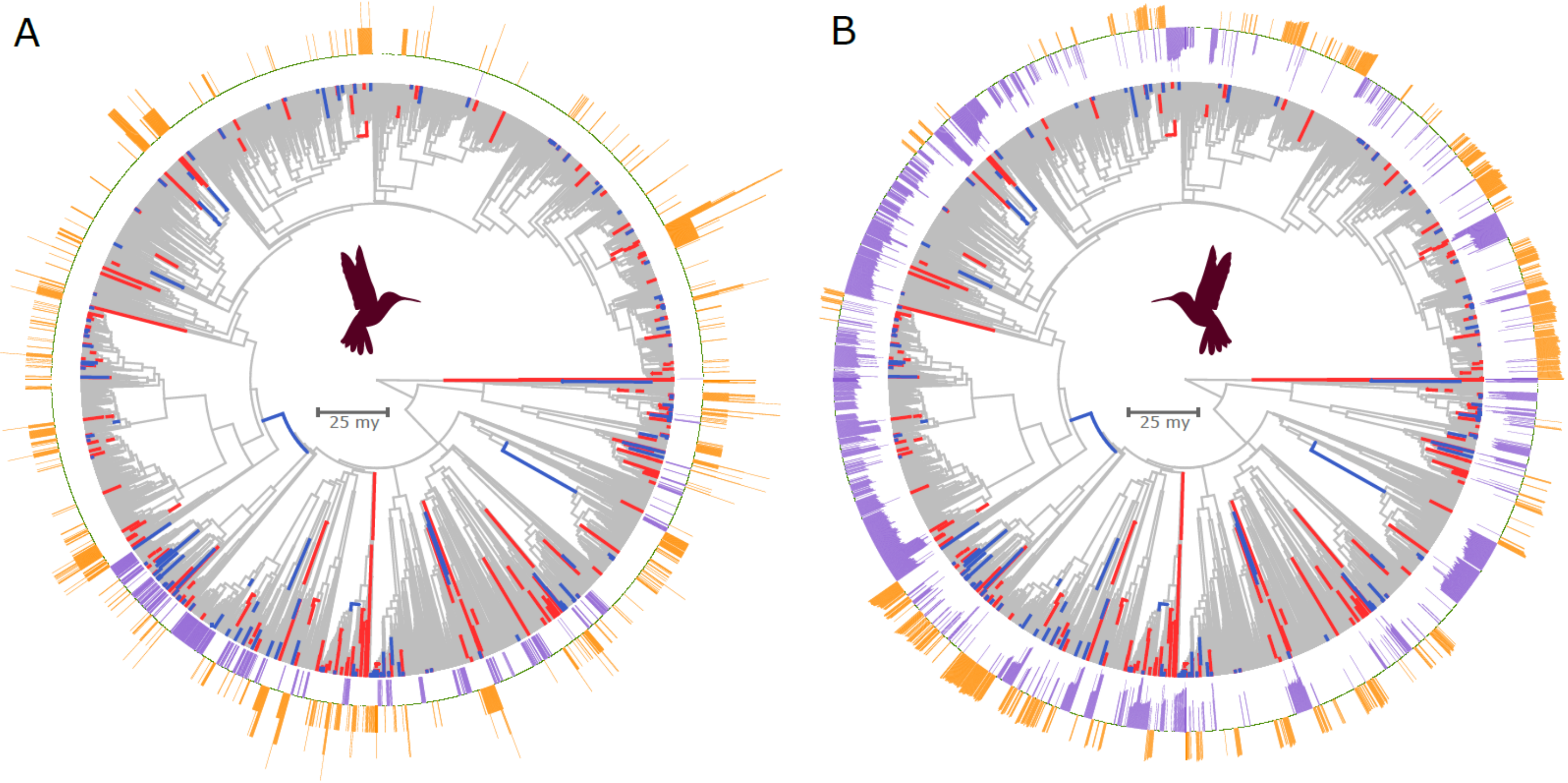

Figure 4 | Phylogenetic clustering of exceptional changes in observed data compared with 1,000 randomised exceptional change datasets in birds. A - Bars at the tips represent the difference between the observed PEC count and the median of the 1,000 randomised PECS. The length of these bars shows the magnitude of the difference between the observed and median randomised PECs. Bars are orange where the observed PEC is greater than the median of the randomised PECS and purple where the observed *(Caption continues on next page)*

Figure 4 caption continued - PEC is less than the median randomised PEC. Where a green dot is present (and no bar is present), the observed PEC is the same as the median randomised PEC. **B** - Bars at the tips show the percentage of the 1,000 randomised PECs that are greater than, less than or equal to the observed number of PECs. The length of the bars is equal to this percentage. Orange bars indicate that the largest portion of the randomised PECs are greater than the observed value. Purple bars indicate that the largest portion of the randomised PECs is less than the observed value. Where the largest portion of the randomised PECs is equal to the observed PEC there is a green dot and no bar is present.

The presence of these clusters may show distinctive periods when particular lineages were under intense selection pressure (Baker *et al.,* 2016) to drastically alter their body size perhaps owing to factors such as competition (Schluter and McPhail, 1992; Bothwell *et al.*, 2015), climate change (Hunt and Roy, 2006; Hoffmann and Sgrò, 2011; Clavel and Morlon, 2017; Martin *et al.*, 2018), or new ecological opportunities (Osborn, 1900; Revell *et al.*, 2012; Eastman *et al.*, 2013; Chira *et al.*, 2018). The clusters of exceptional changes are not evenly distributed throughout the tree (Figure 2). We see a large section of the phylogeny, which encompasses primates, lagomorphs and all clades of rodents (Euarchontoglires; with the exception of the porcupine-like rodents) with fewer exceptional changes than would be expected by chance, given the number of speciation events that have occurred. Conversely, the majority of the remainder of the tree has seen more instances of exceptional changes than would be expected by chance. This implies that the signal of clustering in exceptional changes is primarily driven by the changes distributed across this remainder of the placental mammals and parts of the marsupials and monotremes. In support of this, given we find that lineages with more exceptional changes along them are associated with species with large body sizes (Figure 5C) and that previously (Chapter 2) we found increases in body size to occur by infrequent, large steps it fits that exceptional changes are more clustered in the portion of the tree with the largest mammals. On the other hand, rodents, new world primates and lagomorphs are mostly small bodied and given that decreases in body size along the paths to extant species are most often achieved by frequent, small reductions, this potentially explains why these groups have experienced fewer exceptional changes than expected.

Unlike in mammals, understanding whether the exceptional changes in birds and fish have occurred randomly across lineages is more challenging. We find that values of both H^2 and lambda are high in both datasets, particularly so in birds (Figures 1B, 1C, A.1B and A.1C) and also that the fish and bird data are both better explained by models that include phylogeny as a random effect.

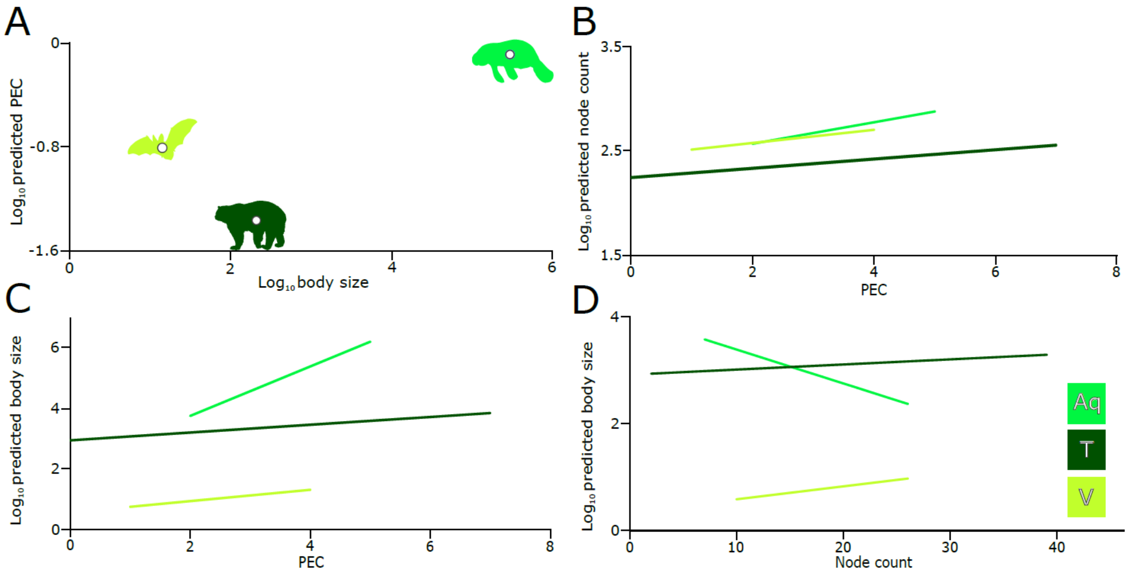

Figure 5 | Phylogenetic regression predictions for mammals. A - The number of $\log_{10}$ transformed pathwise exceptional changes (PECs) predicted for aquatic, terrestrial and volant mammals holding both node count and body size at the median values of each habitat group. **B** - The $\log_{10}$ transformed predicted number of speciation events (node count) along the paths of aquatic, terrestrial and volant mammals given the number of PECs and holding body size at its median value. **C** - Log_{10} transformed body size of aquatic, terrestrial and volant mammals predicted from the number of PECs, holding node count to its median value. **D** - Log_{10} transformed body size of aquatic, terrestrial and volant mammals predicted from the number of speciation events along their paths, holding the number of PECs to its median value.

These results point to the same conclusion which can be drawn without caution in the mammals, that there is phylogenetic signal in exceptional changes in fish and birds. However, this inference comes to be questioned by our lack of ability to significantly differentiate the observed datasets' signal from that of the randomised datasets. We however come to note that the benchmark set by our randomisations for judging phylogenetic signal is perhaps unreasonably high. Having randomised the positions of the branchwise changes in the trees, we counted these along paths, and thus their accumulation through time exactly follows the branching pattern of the trees. This means that by definition, we have introduced some phylogenetic signal into the exceptional changes in these randomised datasets. We therefore judge whether the signal detected in the observed datasets is 'true' against datasets which are somewhat phylogenetic. Thus, our conclusions about clustering of exceptional changes will err on the side of conservative. This means that in mammals, where the signal in the observed data far exceeds that of the randomisations, we have unequivocal evidence that exceptional changes occur in clusters across the phylogeny. However, given that this phylogenetic artefact has been introduced into the randomisations equally in all three datasets, we can compare the level of clustering between mammals, birds and fish. In fish and birds then, we can say that there is evidence of some phylogenetic signal in exceptional changes but less so than in mammals and slightly more in birds than in fish. It will be an important area of future research to further explore how best to test for significant phylogenetic signal in count data, whether this is through the use of randomisations or by some other means.

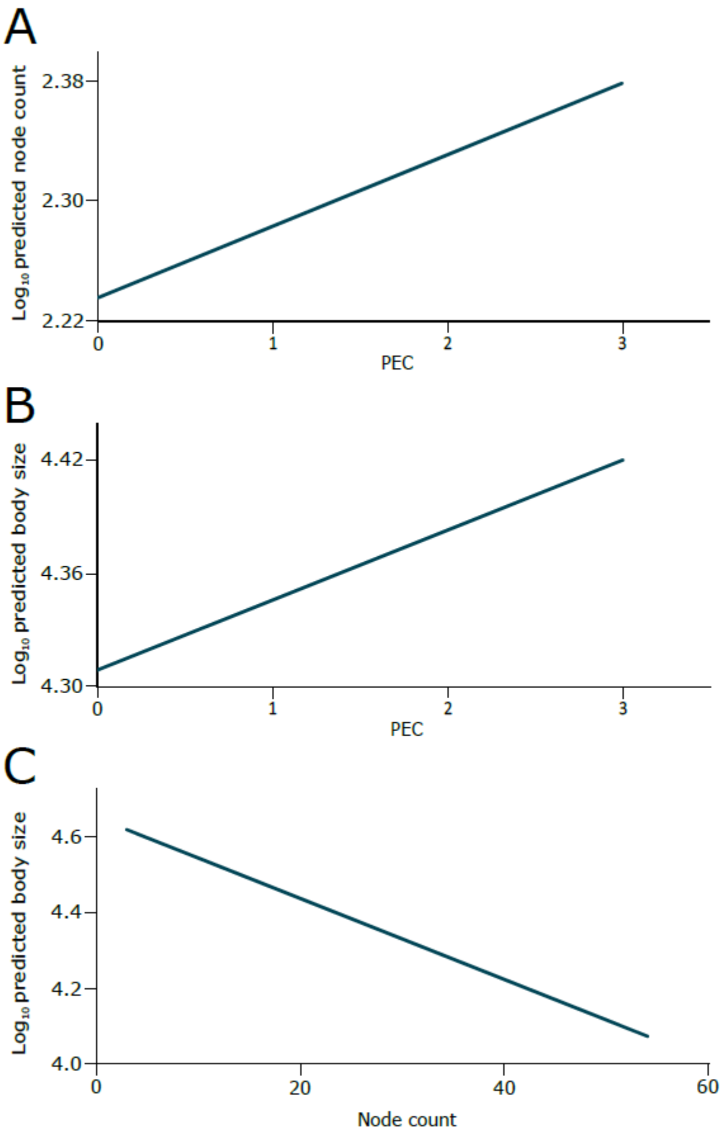

Figure 6 | Phylogenetic regression predictions for fish. A - The predicted $\log_{10}$ transformed number of speciation events along the paths leading to extant bony fish given the number of PECs and holding body size at its median value. **B** - The predicted $\log_{10}$ transformed body size given the number of PECs and holding node count to its median value. **C** - The predicted $\log_{10}$ transformed body size given the number of pathwise speciation events (node count) and holding the number of PECs to its median value.

Whilst the birds and fish may share their relatively lower level of phylogenetic signal in comparison to the mammals, their exceptional changes are by no means distributed in the same way across the trees. This implies that similar levels or values of phylogenetic signal can be detected from data which varies hugely in its phylogenetic nature (for example, the temporal distribution of traits and differences in trait variances). In all but a few lineages of the fish tree, the observed number of PECs is less than the median number of PECs from the 1,000 randomisations and the majority of the posteriors of randomised PECs (Figure 3A and B). This likely arises because 88% of the exceptional changes in body size in fish are distributed on the terminal branches meaning that rather than accumulating along the paths to extant species, they occur independently, concentrated close to the present. In comparison, the birds and mammals have 73% and 67% of their exceptional changes occurring on terminal branches respectively. The propensity of these changes to occur close to the present in the fish and the lack of exceptional changes deep in the tree is corroborated by the mean of the poisson model which indicates the waiting time or frequency with which an exceptional change occurs. Relative to the birds (mean poisson intercept = -1.58) and mammals (mean poisson intercept = -1.73) the fish's poisson mean is over four times smaller (mean poisson intercept = -7.01). With the smallest estimate of the poisson mean, the fish have undergone relatively fewer exceptional changes (the variance in PECs is smaller) than the birds and mammals and in addition, waited longer for them to occur. These statistical parameterisations of the evolutionary process reveal to us that mammals and birds have both experienced 'hot-streaks' - where exceptional changes have occurred sequentially over periods of millions of years (Figures 2 and 4). There are thousands of lineages in the mammal and bird trees that have undergone more exceptional changes than expected by chance (Figures 2 and 4) owing to the occurrence of these changes deep in the trees – for example the exceptional reduction in body size of the ancestor of passerines. Conversely, fish show a lack of exceptional changes deep in the tree and thus large changes in their body size have been rarer and more randomly occurring both taxonomically and through time. Fish are indeterminate growers and therefore the intraspecific variance of fish body size may be higher than for determinate growers such as mammals and birds. This may introduce 'noise' into the species level data which may be why much of fish body size evolution is attributed to terminal branches rather than to phylogenetic history. Given the evidence discussed we therefore find the high H^2 (median H^2 = 0.9998; Figure 1B) and lambda (maximum likelihood lambda = 0.7036; Figure A.1B) values we detect in the fish surprising, given that by definition, evolution that happens on terminal branches should equate to a complete lack of phylogenetic signal (Pagel, 1999) implying the data fits a phylogeny with a non-informative star structure (Pagel, 1997; Freckleton *et al.*, 2002; Blomberg *et al.*, 2003). It has recently been shown that phylogenetic comparative methods can sometimes be sensitive to tree shape (e.g. Rabosky and Goldberg, 2015; Cooper *et al.,* 2016). Understanding exactly how and why tree shape influences the way comparative methods work represents an interesting area for future research.

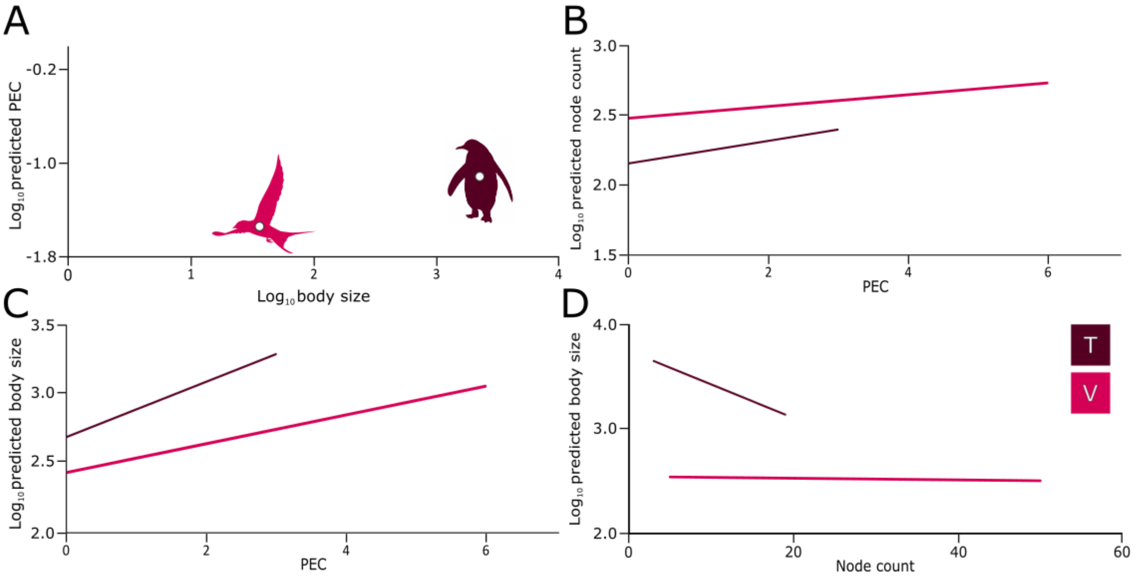

Figure 7 | Phylogenetic regression predictions for birds. A - The number of $\log_{10}$ transformed pathwise exceptional changes (PECs) predicted for terrestrial and volant birds holding both node count and body size at the median values for each habitat group. **B** - The $\log_{10}$ transformed predicted number of speciation events (node count) along the paths of terrestrial and volant birds given the number of PECs and holding body size at its median value. **C** - Log_{10} transformed body size of terrestrial and volant birds predicted from the number of PECs, with node count held at its median value. **D** - Log_{10} transformed body size of terrestrial and volant birds predicted from the number of speciation events along their paths (node count), holding the number of PECs to its median value.

Understanding the distributions of exceptionally large evolutionary leaps occurring in major vertebrate radiations only paints part of the picture of the mode of body size evolution. The environment, including both biotic (e.g. intra and interspecific competition) and abiotic characteristics (e.g. temperature and rainfall) is what generates the myriad, dynamic selection pressures exerted on its inhabitants at an individual, population and species level. It is therefore interesting to see whether different environments foster lineages of animals which undergo exceptional changes at different frequencies. One might suppose for example that aquatic animals have undergone more exceptional changes (of a positive nature) to their body size owing to the buoyancy of their environment enabling them to get bigger (Schmidt-Nielsen, 1984; Humphries, 2007; Evans *et al.*, 2012). We find evidence in birds and mammals that where an organism exists influences its morphological evolution (Figures 5A and 7A). Somewhat in line with expectations, in mammals, aquatic organisms undergo five times more exceptional changes (at the median body size and node count) than volant mammals. However, terrestrial species have undergone the fewest exceptional changes - twenty times less than their aquatic relatives and just under four times less than volant mammals (at the median body size and node count). This result is however reversed in the birds with terrestrial species undergoing large changes in body size at over double the rate of volant birds (at the median body size and node count). Potentially explaining some of this environmental variation we find that in both mammals and birds there is a positive relationship between body size and the number of exceptional changes along a path (Figures 5C and 7C). The largest mammalian organisms are those which live and breed in aquatic habitats - cetaceans and sirenians - and one of the largest radiations within mammals is bats (698 taxa), of which approximately 20% are large bodied fruit bats. Equally, some of the largest birds are the terrestrial ratites. This positive relationship between body size and PECs therefore goes some way to simply explaining why we see volant and aquatic mammals and terrestrial birds showing elevated numbers of exceptional changes along their lineages.

A perhaps more complex view of these seemingly opposing results is that the species in both mammals and birds that occupy the ancestral habitats (terrestrial in mammals and volant in birds) are the ones with the lowest occurrence of exceptional changes. The groups with the most exceptional changes then are those that have gone through major evolutionary transitions: terrestrial to aquatic and terrestrial to volant in mammals and the secondary loss of flight in birds. It has been suggested that rapid changes in morphologies such as body size can form the basis for evolutionary radiations (Venditti *et al.*, 2011) as exceptional changes create or allow access to new ecological opportunities (Osborn, 1900). Simpson (1944; 1953) proposed 'quantum evolution' as a means of explaining how evolutionary mode could facilitate these leaps between adaptive peaks preceding radiations. Identifying episodes of quantum evolution, manifesting as extreme pulses of morphological change (not exclusively occurring at speciation events as in Gould and Eldredge, 1977) has been a feature of recent works (Landis *et al.*, 2013; Cooney *et al.*, 2017; Duchen *et al.*, 2017; Landis and Schraiber, 2017) and these pulses have been found to characterise the evolution of vertebrate body sizes

(Venditti *et al.*, 2011; Landis and Schraiber, 2017). 'Quantum evolution' (Simpson, 1944) was described by Simpson as both an important and controversial feature of evolution (Wright, 1945). We here suggest that in fact, exceptional or quantum changes in body size at least, are not controversial. Rather, they are a real feature of the evolutionary mode which has acted over the tree of life to facilitate major transitions between adaptive peaks and the radiations that follow them.

In birds, fish and mammals, the species with more exceptional changes along their path are the species with the largest body size (Figures 5C, 6B and 7C). This association suggests that in all of these vertebrate groups exceptional changes may drive or contribute to driving evolution towards larger body size (Cope, 1896; Baker *et al.*, 2015). This is concordant with the ideas proposed previously (Chapter 2) regarding the differences in the mode of evolution acting to increase and decrease body size. Reductions in body size are characterised by frequent, small changes and conversely, increases in body size occur in fewer, larger steps. We suggest that this pattern may be owing to the fractal nature of environments (Mandelbrot, 1983). Organisms need only get slightly smaller to increase the dimensions of physical space they have available to exploit, but must get bigger in large steps given the loss of exposure to small-scale environmental nuances for species at the larger end of the body size distribution (Morse *et al.*, 1985; Shorrocks *et al.*, 1991; Haskell *et al.*, 2002). The relationship between exceptional changes and body size differs in nature between organisms living in different habitats. In aquatic mammals, the occurrence of one exceptional change results in a 6.5 gram increase in body size which is 4.8 times bigger than the increase seen in terrestrial mammals and 4.2 times bigger that that seen in volant mammals (Figure 5C). Organisms that live in water have a body size distribution that is shifted to the right and with a larger variance (Noren and Williams, 2000; Venditti *et al.*, 2011; Clauset, 2013) owing to their lack of need to support their own weight. The nature of aquatic exceptional changes illustrates how in this environment, whilst limits on body size might still exist (e.g. Potvin *et al.,* 2012) there is a greater portion of the body size landscape that can be explored (Pyenson and Sponberg, 2011).

The mechanisms involved in the generation of new species are varied and complex (Venditti *et al.*, 2010). Traditional theories include speciation by geographical separation, whereby populations of a species that are physically isolated from one another accrue enough differences that they can no longer interbreed (Mayr, 1996). A more controversial idea is speciation in sympatry whereby specialisation occurs within a single environment, generating new species *in situ* (Poulton, 1904; Fitzpatrick *et al.*, 2008). This may occur owing to pressure from factors such as intra- or inter-specific competition (Schluter, 1994; Rainey and Travisano, 1998) that can either force character displacement or local extinction (Brown and Wilson, 1956; Schluter, 2000) or owing to pressures such as sexual selection (Higashi *et al.*, 1999; Servedio and Boughman, 2017) or lack of un-colonised physical space (O'Donovan *et al.*, 2018). Where selection pressure on an organism is extreme enough, traits can change rapidly (Baker *et al.*, 2016) possibly also in large steps. On a larger scale both taxonomically and temporally, we have found evidence to suggest that exceptional changes facilitate wholly or even partially to ancestral organisms 'jumping' between adaptive peaks and opening up new ecological opportunities which has often resulted in large scale radiations (e.g. bats). This links directly to the original concept of an 'adaptive radiation' whereby Osborn, (1900) believed that speciation occurs in response to 'mechanical changes' associated with the novel, underused or 'open' niches in the environment. Is it possible then, that the exceptional changes that enable species to access ecological opportunities are also contributing to the formation of new species, triggering evolutionary radiations? Whether exceptional changes occur in geographically isolated populations or contiguous populations coexisting in the same environment, we find that lineages of volant and terrestrial mammals, fish and volant birds with more exceptional changes are also those lineages that have undergone more speciation events (Figures 5B, 6A and 7B). This is not the case for terrestrial birds or aquatic mammals where we find no association between the frequency of large changes in body size and the number of speciation events. Other factors, rather than the occurrence of exceptional changes must have triggered and perpetuated the radiation of these groups.

Given that speciation and body size are both associated with exceptional changes we also tested to see whether they were associated with each other. We find no relationship between the number of speciation events in a clade and the body size of its extant species in birds (Figure 7D). The positive association that we find in terrestrial and volant mammals demonstrates that clades where there has been more speciation are those containing large bodied species (Figure 5D). This makes sense in the light of the relationships between body size and exceptional changes and speciation and exceptional changes; if PECs are associated with larger body size and also with increased instances of speciation then it follows that those lineages with more speciation will lead to larger species, for example, the radiation of fruit bats. Conversely, in aquatic mammals, the paths with most speciation events are those that lead to the species with smaller body sizes, a relationship probably determined by the small bodied, but speciose dolphins. This relationship is the same in the case of the fish too (Figure 6C) implying that perhaps a characteristic of their common aquatic environment means that both fish and aquatic mammals show more speciose groups of small animals.

As was the case for Chapter 2, the work presented here is ultimately reliant on the accuracy of the methods used to reconstruct ancestral traits. These methods can be misled by uneven or incomplete taxon sampling however we believe our variable rates model to mitigate the potential biases introduced by sampling issues (see Chapter 2, page 77 for in-depth discussion on the implications of incomplete taxon sampling). Data availability is a problem that plagues both inference of phylogenetic trees and subsequent phylogenetic comparative methods. The availability of precise ecological data which could be applied to the branches of phylogenetic trees may have limited the current work. We here study the effects of 'habitat' on the frequency with which exceptional changes occur and the differential effect that habitat has on the relationships between speciation, body size and exceptional changes in morphological traits. We consider habitat in three categories which reflect where species' young are born ('terrestrial' and 'aquatic'), with the additional category of 'volant' given extensive evidence that volant organisms experience vastly different selection pressures in comparison to other terrestrial organisms. These three categories could be considered broad and coarsely defined and perhaps limiting to our ability to make ecological inferences and tease apart realistic relationships to truly understand environmental influences on the evolutionary process. For example, future work could define 'aquatic' species into freshwater and marine species or go further to split freshwater into riverine and lacustrine. The collection and allocation of data at a finer ecological resolution would serve to provide a more nuanced view of evolution in different environments than is currently available. This being said, despite using these coarse categories, we find significant differences in the way that evolution has worked in the different habitats and therefore have collected data at a level that distinguishes different evolutionary regimes. A finer view would be informative and interesting, and would serve to enhance rather than discredit the current findings.

"*Natura non facit saltum*" (Nature does not make jumps; Linnaeus, 1751) is a phrase often discussed in biological literature, including in the Origin of Species (Darwin, 1859). It is a phrase that we now know to be incorrect (Simpson, 1944; Gould and Eldredge, 1977; Venditti *et al.*, 2011; Baker *et al.*, 2016; Cooney *et al.*, 2017; Landis and Schraiber, 2017; O'Donovan *et al.*, 2018). Our results provide evidence that not only do 'jumps' happen in nature, but that they have happened thousands of times over hundreds of millions of years of vertebrate evolution. As well as understanding more about the mode of body size evolution in mammals, fish and birds, we have gained insight into the mechanisms by which determining features of evolutionary mode may be perpetuated along vertebrate lineages. Whether the propensity for exceptional changes to occur is inherited or idiosyncratic, our results show that they are a major contributor to macroevolutionary trends in body size, to shaping the distributions of body sizes that we see in extant taxa and have implications for the process of generating new species both at the scale of individual lineages and also in evolutionary radiations. The environment that organisms evolve in fundamentally controls the way that evolutionary processes act, differentially effecting the frequency with which exceptional changes occur and the evolutionary and ecological consequences of them when they do happen. Ultimately, we bring Simpson's quantum leaps between adaptive peaks to life; they are not a theoretical character but are a real feature of nature and its evolution. Exceptional changes are rare and special and can be seen as defining moments in the evolutionary history of biological diversity.

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APPENDIX 1 | Phylogenetic signal (λ) in exceptional changes

As an additional test of whether there is phylogenetic signal in exceptional changes in the mammal, fish and bird phylogenies we ran regression models of PEC on node count in BayesTraits (Pagel *et al.*, 2004) in maximum likelihood (ML). Given that our phylogenies each contain thousands of taxa (mammals = 3,321 taxa; fish = 6,760 taxa; birds = 6,160 taxa), the regression models were run using independent contrasts (Felsenstein, 1973; Felsenstein, 2012) which uses a more computationally efficient restricted likelihood method than generalised least squares regression. For each regression, we first fixed lambda to zero ($\lambda = 0.000001$) and then fixed lambda to one. Fixing lambda in these models has the equivalent effect of including and removing the phylogeny from the model (see Main text) allowing us to understand how important the tree is for explaining the variance in the PEC data and more importantly enabling us to quantify how much the tree contributes to model fit. To this end, we calculated the difference in the likelihoods of the two models (lambda = 1 and lambda = 0) for the observed data and for all of the 1,000 randomisations (Figures A.1 and A.2).

RESULTS

Mammals

In the observed data (Figure A.2A) and in all of the 1,000 randomisations (Figure A.1A), the likelihood is higher for the model with lambda fixed to one. This means that in all cases, there is phylogenetic signal in exceptional changes. However, the difference in likelihood between the two models is greater for the observed data than for 99.1% of the randomised datasets (Figure A.1A). Thus, the observed exceptional changes in the mammal tree show more phylogenetic signal than the randomisations.

Fish

In fish the likelihood is lower for the model where lambda is fixed to one such that the model better fits the data without attributing any variance in the trait to the structure of the phylogeny (Figure A.1B). The relationship between lambda and the model likelihood is illustrated by the likelihood landscape (Figure A.2B) which has a relatively flat form with the likelihood drastically declining as lambda approaches one. Whilst exceptional changes in fish have not evolved precisely phylogenetically, the maximum likelihood estimate of lambda is 0.7, implying that there is some phylogenetic signal, albeit less than in all of the randomisations which show stronger phylogenetic signal (Figure A.1B). There is no overlap in the likelihood differences of the observed and randomised datasets given that the former is negative and the latter all positive in value; the difference for the observed data is more than 2.5 times smaller than the minimum difference seen in the randomised datasets (Figure A.1B), again suggesting that relatively there is less signal in the observed exceptional change data than in the randomisations and also less than in the mammals' data.

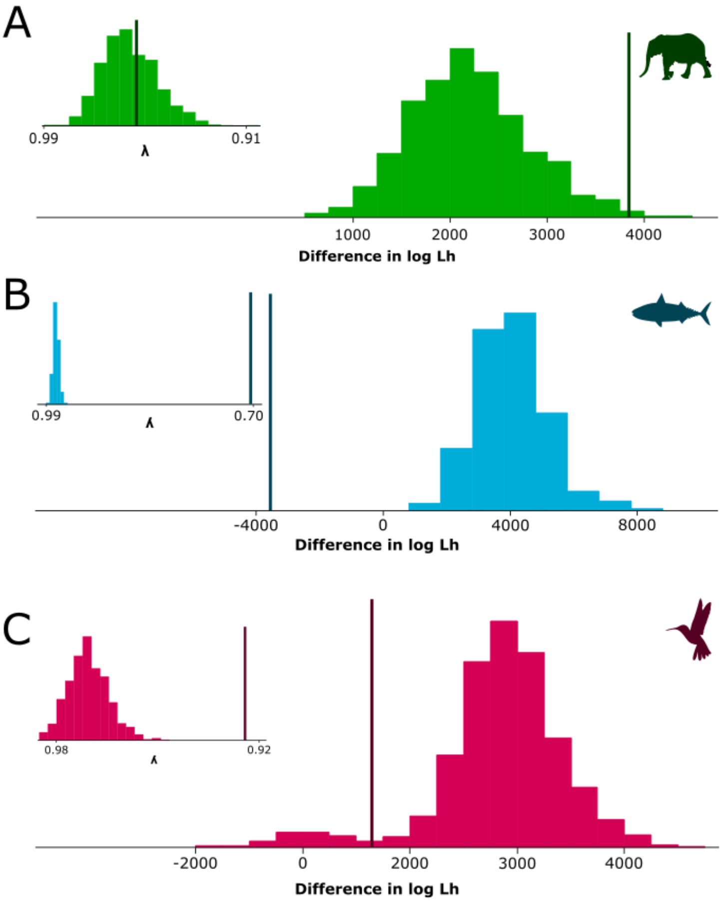

Figure A.1 | Phylogenetic signal in exceptional changes. Distributions of the differences in likelihood (Lh) between phylogenetic regression models of PEC on node count with lambda fixed to zero and with lambda fixed to one for **A** – mammals, **B** – fish and **C** - birds. Differences were calculated by subtracting the Lh of the model with lambda fixed to zero from the likelihood of the model with lambda fixed to one. Histograms show the differences from models run with the 1,000 randomised datasets with the thick, vertical line showing the difference between the models run with the observed datasets. Inset in each are the distributions of the maximum likelihood values of lambda for each of the 1,000 randomised datasets with the maximum likelihood value of lambda for the observed datasets marked by the thick, vertical lines. Note: inset histograms' scales go from high to low values where the main histograms' scales are conventionally arranged from low to high values.

Birds

The birds provide an intermediate case between the mammals and fish. There is some clustering of exceptional changes in the bird phylogeny given that the model with lambda fixed to one has a higher likelihood than the model with lambda fixed to zero (Figure A.1C). However, the likelihood landscape shows a decline as values of lambda near one more than in mammals but less than in fish (Figure A.2C). The maximum likelihood value of lambda is high (ML λ = 0.92) albeit not higher than those of the randomised datasets. Given the overlap in the differences of model likelihood between the observed and randomised data (94.3% of the randomisations show a bigger likelihood difference between the two models than the observed data does (Figure A.1C)), any clustering of exceptional changes in birds is not distinguishable from that which arises by random chance.

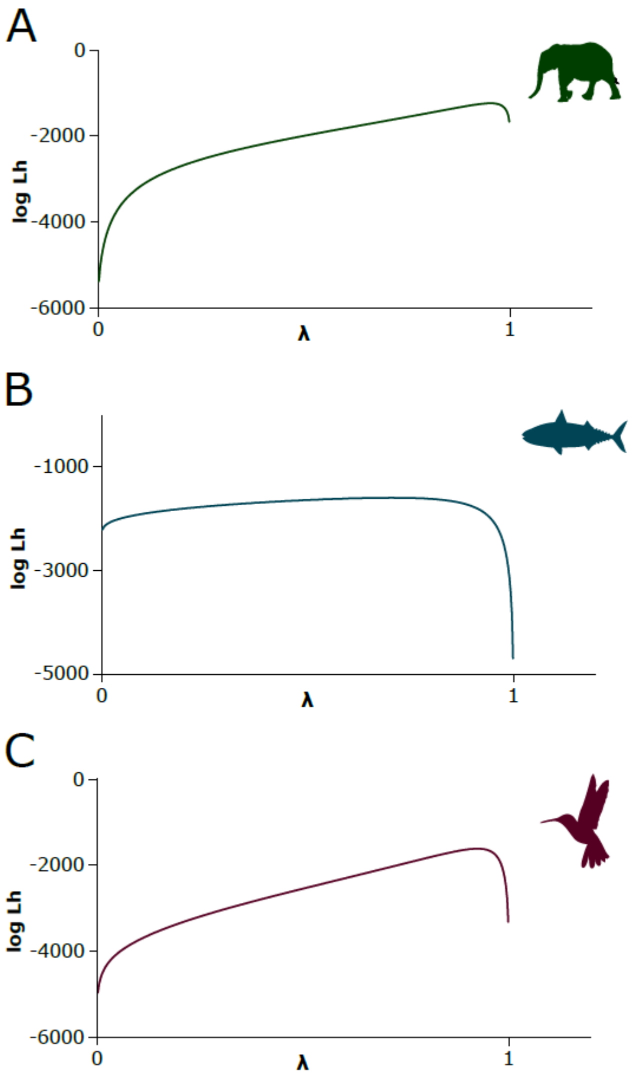

Figure A.2 | The log likelihood (log Lh) landscape of lambda. The log likelihood of the model PEC ~ node count, fixing lambda to 1,000 equally spaced values between zero and one for **A** – mammals, **B** – fish and **C** – birds.

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APPENDIX 2 | The relationships between exceptional changes, ecology, speciation and body size

Table 1 | Mean coefficient values, confidence intervals and %MCMC values for the PEC (pathwise exceptional change) regression. Where variables are listed with a colon in between them this denotes an interaction term. Habitat categories are abbreviated as T – terrestrial, V – volant with the implied group as aquatic for mammals and terrestrial for birds.

Dataset	Coefficient	Mean coefficient	Lower 95th CI	Upper 95th CI	%MCMC	
Mammals	Intercept	-0.28445	-2.9887	1.87162	58.5	
	Habitat T	-2.45912	-4.70318	-0.15167	100	*
	Habitat V	-1.31478	-3.75849	1.1359	99.2	*
	Node count	-0.01656	-0.0904	0.06901	63.9	
	Body size	0.09564	-0.14916	0.34732	21.5	
	Habitat T : Node count	0.05249	-0.03031	0.13383	0	*
	Habitat V : Node count	0.0435	-0.04361	0.13743	11.9	
	Habitat T : Body size	0.23436	-0.03929	0.48035	0	*
	Habitat V : Body size	0.21473	-0.13898	0.56446	0.6	*
Fish	Intercept	-8.2108	-12.0646	-4.5306	100	*
	Node count	0.1589	0.1288	0.1909	0	*
	Body size	0.2996	0.1773	0.4348	0	*
Birds	Intercept	-5.585849	-8.843066	-2.317361	100	*
	Habitat V	2.789686	-0.757667	6.038303	100	*
	Node count	0.127438	-0.001962	0.255369	2.8	*
	Body size	1.067991	0.391265	1.782816	0.1	*
	Habitat V : Node count	-0.103973	-0.231765	0.025954	0	*
	Habitat V : Body size	-0.668166	-1.392628	-0.003642	0	*

Table 2 | Mean coefficient values, confidence intervals and %MCMC values for the NC (node count) regression. Where variables are listed with a colon in between them this denotes an interaction term. Habitat categories are abbreviated as T – terrestrial, V – volant with the implied group as aquatic for mammals and terrestrial for birds.

Dataset	Coefficient	Mean coefficient	Lower 95th CI	Upper 95th CI	%MCMC	
Mammals	Intercept	2.639722	2.094878	3.20325	0	*
	Habitat T	-0.387508	-0.910383	0.151164	0	*
	Habitat V	-0.323237	-0.927325	0.208452	0	*
	Number of PECs	0.102637	-0.059067	0.295583	13.4	
	Body size	-0.084653	-0.189823	0.035975	93.3	
	Habitat T : Number of PECs	-0.058476	-0.249562	0.110857	0.1	*
	Habitat V : Number of PECs	-0.039751	-0.230934	0.143853	2.8	*
	Habitat T : Body size	0.082672	-0.025462	0.199857	57.8	
	Habitat V : Body size	0.125419	0.009873	0.275471	13.5	
Fish	Intercept	2.2738	2.06072	2.52563	0	*
	Node count	0.04766	0.03287	0.06234	0	*
	Body size	-0.01266	-0.02051	-0.00475	100	*
Birds	Intercept	2.24775	1.46532	2.95964	0	*
	Habitat V	0.26021	-0.40599	1.11789	0	*
	Number of PECs	0.08064	-0.08825	0.26753	19.7	
	Body size	-0.05887	-0.27866	0.18715	68.9	
	Habitat V : Number of PECs	-0.03866	-0.22093	0.14012	0	*
	Habitat V : Body size	0.03995	-0.20084	0.26594	96.9	*

Table 3 | Mean coefficient values, confidence intervals and %MCMC values for the BS (body size) regression. Where variables are listed with a colon in between them this denotes an interaction term. Habitat categories are abbreviated as T – terrestrial, V – volant with the implied group as aquatic for mammals and terrestrial for birds.

Dataset	Coefficient	Mean coefficient	Lower 95th CI	Upper 95th CI	%MCMC	
Mammals	Intercept	3.198514	1.463568	4.834997	0	*
	Habitat T	-0.415072	-1.786124	1.208356	0	*
	Habitat V	-3.042831	-4.8478	-1.435309	38.9	
	Number of PECs	0.81517	0.527993	1.09724	0	*
	Node count	-0.063357	-0.128349	0.013784	95.9	*
	Habitat T : Number of PECs	-0.68666	-0.963031	-0.392454	0	*
	Habitat V : Number of PECs	-0.62834	-0.917714	-0.337079	0	*
	Habitat T : Node count	0.072885	0.006929	0.148851	1.5	*
	Habitat V : Node count	0.087506	0.008537	0.15969	2.3	*
Fish	Intercept	4.652512	3.270126	5.942754	0	*
	Number of PECs	0.03712	-0.002359	0.070391	2.7	*
	Node count	-0.010733	-0.017333	-0.005238	100	*
Birds	Intercept	3.54237	2.813	4.15327	0	*
	Habitat V	-1.10069	-1.87944	-0.38752	0	*
	Number of PECs	0.20167	0.04577	0.35895	0.8	*
	Node count	-0.03195	-0.09391	0.02139	86	
	Habitat V : Number of PECs	-0.09663	-0.25238	0.05894	0	*
	Habitat V : Node count	0.03116	-0.02204	0.0941	71.1	

Discussion

"Nothing in evolution or ecology makes sense except in the light of each other"
Pelletier *et al.,* (2009)[1]

This thesis began with the sentence that concludes Darwin's famous view of an 'entangled bank' and also concludes 'On the Origin of Species' as a whole. Having spent hundreds of pages noting and theorizing on a singular mechanism by which every feature of life could arise, Darwin summarises the last four billion years of natural history in a single, profound sentence. Ironically, the end of this thesis now turns to the beginning of Darwin's description of the 'entangled bank':

> *"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us.......Thus from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one......"*

Darwin's observation of the bank is a simple one that any ordinary person with the consideration to look could see. However, his subsequent reflection synthesises the totality of the concepts that have motivated and continue to motivate biologists and ecologists alike both before and after Darwin's work was published. He considers life from the individual organisms, to interspecific interactions, to the physical environment that sets the scene for it all. Darwin emphasises the varying scales with which nature and natural processes can be described and studied, glorifying the minute details of an individual organism whilst similarly putting these in the context of a 'grand' view with every detail being a product of universal, fundamental laws. In a similar vein, the aim of this thesis was to consider, and importantly test ideas about 'the evolutionary paths to diversity' at these varying scales. At the smallest scale, to determine how much a

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[1] Pelletier, F., Garant, D. and Hendry, A. (2009). Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society: Biological Sciences.* **364**, 1438 - 1489

population must move or change from its ancestor to become a new species by identifying the tempos of evolution acting across individual branches of phylogenetic trees (Chapter 1 and Chapter 2). Then, how these tempos scale up to characterise the evolutionary mode; whether of a large scale geographical distribution (Chapter 1) or of morphological evolution (Chapters 2 and 3). In all three chapters the characterisations of evolutionary mode are studied in the context of ecology and thus are subsequently discussed in the light of fundamental natural laws from gravity to the chemical qualities of water and air and how these vast concepts or their effects scale down to minute dimensions perhaps owing to the fractal like nature of the physical environment (Burrough, 1981; Mandelbrot, 1983; Tarboton *et al.*, 1988; Voss, 1988; Brown *et al.*, 2002). An interesting future direction would be to use ideas about self-similarity to test whether the evolutionary mode acts in the same way at different orders of magnitude; if magnitude here were to be scales of time or levels of taxonomy.

The idea of studying evolution at differing scales is not a new one. For example, the debate regarding whether macro and micro evolutionary processes are the same, or even whether they are reconcilable has been raging for over a century (reviewed in Carroll, 2001; Simons, 2002; Reznick and Ricklefs, 2009). In addition, 'The Modern Synthesis' and its subsequent extensions (reviewed in Mayr and Provine, 1980; Mayr, 1993; Pigliucci, 2007) serve to draw in areas of biological research at different scales such as Mendel's genetic theory, Darwin's natural selection, Mayr's ideas on what constitutes a species and many works on the fossil record. Such efforts bring ideas and even vocabulary together creating a congruent research environment - a paradigm within which nature as a whole, at all levels can be studied. Thus, it is important to consider that processes identified in this thesis such as the regular and exceptional changes identified and studied in Chapters 2 and 3 which are viewed from a macroevolutionary stance, must have underlying genetic mechanisms - they cannot be studied in isolation as if changes to morphology that occurred along a branch of a phylogenetic tree happened only at a species morphological level. The methods used to identify changes at the species' morphology level have been developed from those used to study change at the genetic level (Cavalli-Sforza and Edwards, 1967) thus highlighting how one underpins the other even methodologically. Whilst genetic rates of change are known to vary (Vawter and Brown, 1986; Thorne *et al.*, 1998; Bromham and Penny, 2003; Drummond *et al.*, 2006; Yang and Rannala, 2006; Bromham, 2009; Lartillot and Poujol, 2011), changes in genetic code are traditionally viewed as occurring in small, incremental steps (Kimura, 1983). This is because mutations of any variety if too large, are highly likely to be deleterious and may reduce the fitness of the individual organism. This mode of genetic evolution fits with the findings presented here (Chapter 2) about evolution mostly altering species' morphologies by extremely small amounts. However, what does this mean for the enormous, 'exceptional' changes that are found along branches of a phylogenetic tree? Are exceptional morphological changes the products of millions of years of many, tiny alterations to individuals' genetic material? Or are they too produced by small changes to genes, some of which have large morphological implications (McGregor *et al.*, 2007), such as Hox gene mutations (Small and Potter, 1993)? Or, are they the signature of an evolutionary mode at a molecular scale which is also littered with exceptional changes – examples of which may be genome duplications, large regulatory changes or large scale structural changes (Eichler and Sankoff, 2003; Hoekstra and Coyne, 2007; Deline *et al.*, 2018)? It has been found that genetic evolution is punctuated with periods of large amounts of change (Webster *et al.*, 2003; Pagel *et al.*, 2006; Deline *et al.*, 2018) and it is also known that large genetic changes such as genome duplications and structural rearrangements have occurred numerous times in the history of life (Zhang, 2003). Research that links rates of genotypic and phenotypic evolution is currently gaining pace (Nadeau *et al.*, 2007; Lartillot and Poujol, 2011; Montgomery *et al.*, 2011; Montgomery and Mundy, 2012) despite difficulties such as identifying candidate genes which directly contribute to a measurable morphology. The evolutionary mode identified in this thesis and elsewhere (Uyeda *et al.*, 2011; Elliot and Mooers, 2014; Cooney *et al.*, 2017; Landis and Schraiber, 2017) is of steps ranging in size from the overabundant and extremely small to the very rare, exceptionally large. Understanding whether this mode is a ubiquitous feature of natural evolution will be an important element of future research. Given that such a pattern exists in traits as different in character as movement and morphology (although these are linked) it would be interesting to see whether this pattern holds at corresponding micro evolutionary scales too.

An organism's spatial distribution is a function of its biological features, evolutionary history and how these interact with the physical characteristics of the environments that it encounters. Ultimately, geographical distribution is then also determined by the genetic mode of change. However, as species' morphological changes are underpinned directly by genetic changes, movement seen here at the species' level along the branches of a phylogenetic tree must have some underlying mechanism that arises from the movements of populations and also individuals within their ranges. These movements combine together to generate the signature seen in Chapter 1 of populations moving across available space and dividing into new species owing to physical separation, morphological changes associated with invading new habitats, or a combination of the two. How individual organisms move within their range is tightly linked to conservation science particularly in endangered organisms such as elephants (Dai *et al.*, 2007) and also to landscape management research which aims to gain an understanding of how organisms such as butterflies (Loos *et al.*, 2015) sample their environment and how best to facilitate this given these animals' ecological importance. However regardless of the reason, these bodies of research attempt to characterise and explain movement patterns below the species level. There is some evidence to suggest that just as at the species level, individual organisms explore their physical environments for example to defend their territory, search for food and attract mates with movements which are mostly small but interspersed with rarely occurring, relatively large movements. These data have frequently been characterised by a Lévy distribution (e.g. Atkinson *et al.,* 2002; Reynolds *et al.,* 2007; Focardi *et al.,* 2009 although see Smouse *et al.,* 2010). This suggests that the mechanism by which organisms spatially radiate may be very similar at varying scales, even those as different as the individual and whole species levels.

A huge amount of emphasis is placed on identifying and understanding rates of evolution which act at many times the speed of the background rate, and changes in a trait that are exceptionally large. However, there are genetic and ecological events presented in this thesis and elsewhere which can go at least some way towards explaining how and why these large changes and fast rates occur. Perhaps more puzzling though, is the overabundance of very small changes in location and morphology that are found. The majority of changes to morphological traits are smaller than would be expected by the single underlying normal distribution associated with a phylogenetic Brownian motion model of evolution and suggest that species can be delimited by extremely fine details. Future research will be needed to explain these tiny changes and slow relative rates in the same way that most current research looks at fast rates and their large changes. Ecologically, the abundance of small changes implies the vastness of the potential in niche space and the opportunities which can arise and be created; a highly faceted environment, with each facet itself faceted and thus representing an ever increasing number of niches or dimensions which organisms can occupy.

Much of the inspiration for this thesis and other works like it has come from the ideas about evolution proposed by Simpson (1944; 1953). He defined the terms tempo and mode in the context of evolution and importantly tied these ideas together with those concerning evolutionary radiations, ecological opportunities, adaptive landscapes and importantly, somewhat calmed the battle between palaeontologists and evolutionary biologists about stasis in the fossil record. In facing the question of how diversity arises, Simpson proposed that different rates of evolution fall into two distinct categories – 'normal' evolution (which could occur at rates ranging from slow to fast) and 'quantum' evolution, a different beast altogether. Quantum evolution was used to describe the type of evolution that happened along branches of a phylogeny to facilitate organisms shifting between adaptive zones. Examples of such shifts might be the leap taken by bats to become small bodied and volant, unlike their terrestrial ancestors and similarly, the reverse in terrestrial birds which mostly increased in body size and lost the ability to fly. Chapter 3 reveals that exceptional evolutionary changes contributed to facilitating such major evolutionary transitions, thus, they may be interpreted as episodes of quantum evolution as Simpson defined it. Simpson's world was one where to jump between distant adaptive peaks by making a quantum leap, would be the equivalent of getting out of a standard car and getting into a Ferrari. The findings of this thesis however suggest that evolution is always driving a Ferrari. Mostly, it's driven at only a few miles per hour – a fairly bewildering concept given the far flung places it can get to at this pace - but sometimes it can rev up and reach speeds of over 200 miles per hour, all using the same car, the same engine and the same driver. Essentially the characterisation presented in this thesis of a fat tailed, or stable, distribution encompasses Simpson's regular and quantum changes in one, single framework; they are continuous with each other, with quantum changes merely being the result of evolution working at its extremes.

Frequently within the course of this thesis, the concept of an adaptive landscape is turned to as a theoretical environment within which to envisage how evolution has worked and continues to work to generate and fine-tune the organisms in the fossil record and those alive today. Such a landscape however is not necessarily considered here as in the literature concerning the Ornstein-Uhlenbeck (OU) process (Lande, 1976; Hansen, 1997) which frequently refers to an adaptive landscape framework but also emphasises the role of constraint in species' evolution (Lande, 1976; Hansen, 1997; Butler and King, 2004). Here, the landscape is one with peaks and with valleys between them, which species are able to move between over time, by and large without emphasis on constraint. An individual peak may represent a whole adaptive zone, in which case, niches within the zone should be thought of as little peaks on the surface of the zone's peak (akin to the structure of micro-villi and villi in the human intestine). Small jumps geographically or morphologically may represent improvements to an organism, population or species' fitness in its niche, or between niches as ecological opportunities arise to move or change. Alternatively, the same interpretation of small jumps can be formed from a landscape with peaks which represent niches and where clustered together represent those niches falling within the same adaptive zone. Major changes in location or phenotype however may occur owing to selection to evolve features required to exist in a niche outside of an organism's current adaptive zone, for example to become volant in the case of the bats. In addition, given that the physical environment is in a constant state of flux, this means that species' trajectories of increasing fitness are constantly changing with adaptive peaks or 'optima' sometimes referred to as 'moving targets' (Van Valen, 1973; Venditti *et al.*, 2010). Thus, the adaptive landscape as a whole never remains still; peaks rise, fall and shift about the landscape constantly, adding yet another layer of complexity to studying the evolution of diversity. If this is the normal state of nature, it is possible then to fully appreciate the scale of upheaval owing to the stochastic events such as those causing mass extinctions. Organisms can be faced with novel niche space or an entirely new adaptive zone either because they have undergone a morphological shift (e.g. Eastman *et al.,* 2013), evolved a key innovation (e.g. Dumont *et al.,* 2011), a niche was recently emptied by the extinction of another lineage (e.g. Meredith *et al.,* 2011) or because a new niche was created by some kind of environmental perturbation (Chen and Benton, 2012) . Such opportunity can give rise to patterns such as genetic and phenotypic change accompanied or followed by rapid speciation within the new adaptive zone, as is predicted to happen in an adaptive radiation (Osborn, 1900; Osborn, 1902; Simpson, 1953).

Ecology and evolutionary biology have myriad, complicated interfaces; they share concepts and terminologies and a history of being studied both together and in isolation. Such a history has lent itself to confusion and inconsistencies in how concepts bridge the gap between research in both subjects and how language is used and interpreted. In addition, scale of study both taxonomically and temporally has an impact on how historical ideas and modern quantitative research are reconciled. In this thesis theories regarding adaptive radiations, ecological opportunity, competition, character displacement, sympatric and allopatric modes of speciation, selection, niche filling or early burst patterns and late burst patterns of movement and trait evolution are all referred to but perhaps remain subtly disconnected. On one hand, the idea of exceptionally large, morphological changes facilitating shifts to new environments, opening up novel opportunities and subsequently enabling a lineage to rapidly multiply into many lineages after which evolutionary rates slow and plateau (as in Chapter 1). This implies two phases of evolution. Firstly, owing to the provision of ecological opportunity (given some biological innovation or environmental change) an ancestral group of organisms within a phylogeny widen the niche space they fill by quantum jumps in traits, simultaneously expanding the geographical space they are distributed across and thus speciating allopatrically. Secondly, as lineages diverge both physical and niche space become more densely populated and thus a 'niche packing' phase is entered, where intraspecific competition causes character displacement and thus *in situ* (sympatric) speciation. However, on the other hand, Chapters 2 and 3 suggest that morphological changes have increased in magnitude, or rate, as has also been found previously. How can both of these large scale trends be true? The answer perhaps lies with the fact that potentially, whilst all three chapters in this thesis are presented on a macroevolutionary scale, that Chapters 2 and 3 take an even wider framed view of evolution conceptually than Chapter 1's geographically global view and that signatures akin to that in Chapter 1 may be seen in the data used in Chapters 2 and 3. Cooney *et al.*, (2017) find a disconnect between patterns of change in avian beak morphology which imply an early burst phenomenon and rates of change in beak morphology which imply an increase in rate through time. They discuss this in the light of the idea that early burst patterns, or adaptive radiations may be features of individual clades within a phylogeny whereas on a larger "mega-evolutionary" scale, the trend across the tree as a whole carries a different signature. This perhaps explains how hypotheses about niche filling models can fit with those suggesting that biotic interactions and the environment change so constantly that niches are not fixed and thus not fillable. On smaller macroevolutionary levels, 'niche packing' can occur, producing slowdowns in evolutionary rates. However, taken holistically, on a global scale niches can be packed, but never filled. Niches within a single adaptive zone may be divided into increasingly narrower spaces in a fractal-like way but nature (the environment and organisms within it) will never stand still long enough that organisms can exhaust all possibilities.

This thesis has taken a wealth of biological data, phylogenetic trees and an evolutionary model which embraces the vast complexity of the evolutionary process and with these, uncovered the mode of evolution, highlighted factors that shape it and studied special features of it. The result has been to create a macroevolutionary picture of evolution acting to create diversity across the entire tree of life - a picture that itself is a mosaic of interconnecting, nuanced elements. In Chapter 1 an understanding of the roles that geographical movement and physical space play in how an ancestral population of organisms can give rise to an evolutionary radiation of diverse lineages is gained for the first time. This geographical model, here applied to the dinosaurs could similarly be used to understand these dynamics in phylogenies of other extant or extinct species, or those with a combination of the two. In addition, the flexibility to use such spatial data in association with variables beyond just speciation represents an exciting opportunity for future work. These variables may include ecological ones such as biological history and the environment that species evolve in, which are seen in Chapters 2 and 3 to influence morphological evolution in terms of which evolutionary paths species take and how the evolutionary process is shaped.

The central themes to this thesis are spatial distribution and movement, morphological evolution and speciation which are also the fundamental components of an adaptive radiation. The interactions of speciation with morphological evolution and speciation with geographical movement are all studied. Whilst major steps into unchartered territory have been taken in both these areas, moving forward it will be important to study these processes in a single, quantitative framework such that a unifying characterisation of evolution can be interpreted. Where speciation is currently included in the geographical model presented in Chapter 1 and similarly there is scope to include ecological variables that may impact how species move and spread across the globe, there too is the potential to include data regarding species' morphological evolution such as rates of morphological change. This would allow researchers to finally place previously disparate puzzle pieces together to understand the full picture of the dynamics underlying the millions of species that have arisen from evolutionary radiations. This picture is most certainly likely to be a vast and complicated web of interactions between spatial movements, speciation and morphological change but represents the only path to take. The picture can reveal the answers to long standing questions such as whether rates of morphological change are correlated with those of geographical movement and speciation when studied all together. Or whether speciation dynamics are governed by ecology, geography and morphology and if so, how. Researchers will be able to further understand the degree of similarity between ancestors and descendants and how, if at all, species are defined in nature, the presence and effects of interspecific competition, types of speciation, rates of speciation, morphological change and movement through time and the role of novel environments and key innovations in altering these processes. This research provides the foundation for a single framework encompassing realistic complexity at every level, combining the fundamental workings of both ecology and evolution. It paves the way to a new level of clarity in understanding diversity and nature.

With the bewildering scope for variation in the genetic code - evolution's fundamental biological building material - and the constant fluctuations in the physical and chemical properties of the environment, diversity seemingly has no bounds. Evolution works tirelessly in an unstoppable manner by taking the materials at hand and making something successful out of them. In a few billion years evolution has snowballed, generating millions of species from just the materials collected together in a single cell. Thus organisms, as with our ideas about them will continue to evolve in endless directions with variation being created, moulded and used all the time as new biological avenues are explored. Evolution perpetuates itself, like a beating heart at the centre of a vast living system and thus is a process with infinite potential for creating unimaginable diversity.

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"...I believe a leaf of grass is no less than the journey-work of the stars,
And the pismire is equally perfect, and a grain of sand, and the egg of the wren,
And the tree-toad is a chef-d'œuvre for the highest,
And the running blackberry would adorn the parlors of heaven,
And the narrowest hinge in my hand puts to scorn all machinery,
And the cow crunching with depress'd head surpasses any statue,
And a mouse is miracle enough to stagger sextillions of infidels...."

Walt Whitman, (1892). 'Song of Myself', excerpt from Verse 31.

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