LETTER

Body mass evolution and diversification within horses (family Equidae)

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Abstract

Horses (family Equidae) are a classic example of adaptive radiation, exhibiting a nearly 60-fold increase in maximum body mass and a peak taxonomic diversity of nearly 100 species across four continents. Such patterns are commonly attributed to niche competition, in which increased taxonomic diversity drives increased size disparity. However, neutral processes, such as macroevolutionary 'diffusion', can produce similar increases in disparity without increased diversity. Using a comprehensive database of Equidae species size estimates and a common mathematical framework, we measure the contributions of diversity-driven and diffusion-driven mechanisms for increased disparity during the Equidae radiation. We find that more than 90% of changes in size disparity are attributable to diffusion alone. These results clarify the role of species competition in body size evolution, indicate that morphological disparity and species diversity may be only weakly coupled in general, and demonstrate that large species may evolve from neutral macroevolutionary diffusion processes alone.

Keywords

Adaptive radiation, body mass distributions, Equidae, macroevolution, mathematical models, size disparity.

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INTRODUCTION

Horses (family Equidae) are a classic example of adaptive radiation. First appearing 56 million years ago (Ma) in Holarctica, horses underwent a dramatic diversification in the late Oligocene and early-to-mid Miocene. By the end of this period, Equidae included nearly 100 contemporaneous species, spread across four continents, in sizes ranging from approximately 10–1200 kg (Hulbert, 1993; Eisenmann, 2003). Although the biological mechanism driving this dramatic size disparity remains unclear, insights would inform both the evolutionary and ecological history of horses (MacFadden, 1992; Janis, 2007) and shed light on the general processes that shape morphological, taxonomic and ecological diversity in mammals (Stanley, 1973; Brown, 1995).

Many characteristics of horses changed during their radiation including body size, hoof shape, diet and molar characteristics (MacFadden, 1992; Janis, 2007). Here, we focus on species body mass or size, a fundamental biological variable that correlates strongly with ecological traits, including habitat preference, diet, range, life span, gestation period, metabolic rate and population size (Brown, 1995; West et al., 2002; Smith et al. 2002; Cardillo et al. 2005), as well as trophic level and niche position in food webs (Williams et al., 2010). For these reasons, size is an easy-to-measure proxy (Lucas et al., 2008) for studying and modelling species characteristics, ecosystem structure and ecological niches, even across evolutionary time (Gittleman, 1985). Moreover, the distribution of species sizes within a taxonomic group is an effective summary of species characteristics.

Among major animal lineages, including mammals, birds, fish and insects, this distribution often exhibits a canonical right-skewed pattern (McShea, 1994; Kozwski and Gawelczyk 2002; Clauset et al., 2009; Smith & Lyons, 2011). For example, the most common size of a terrestrial mammal is roughly 40 g (like the common Pacific Rat, *Rattus exulans*), while both larger and smaller species are less common, but asymmetrically so: the largest, like the African Elephant (*Loxodonta africana*, 4×10^6 g), are orders of magnitude larger, while the smallest, like Remy's Pygmy Shrew (*Suncus remyi*, 2 g), are only slightly smaller.

The origin of this ubiquitous pattern is commonly attributed to one of two biological mechanisms: asymmetric dispersion, produced by macroecological competition for niches, around a preferred or optimal body size (Maurer et al., 1992; Smith et al., 2010), or constrained macroevolutionary 'diffusion' (Table 1) in the presence of a hard limit at the lower end, due to physiological constraints, and a soft limit at the upper end, caused by extinction rates that gently increase with body size (Stanley, 1973; Clauset & Erwin, 2008). Traditionally, the evidence for these two mechanisms has been documented separately, and relatively little work has compared them directly using data. Crucially, these explanations make distinct predictions about the relationship between diversity and disparity during the expansion of a taxonomic group: the macroecology explanation predicts that increases in

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Table 1 Terminology used in this manuscript

Body size distribution	Relative frequencies of species body masses within a taxonomic group
Diversity	Number of species in a taxonomic group
Size disparity	Difference in body mass between the largest and smallest species in a group
Diffusion	Aggregate result of many individuals following, possibly constrained, random-walk-like trajectories through a fixed or evolving space
CESR model	Mathematical model of a species size distribution, in which individual species sizes follow a constrained, branching (cladogenetic) multiplicative random walk
Diversity-driven disparity	Mechanism for increased size disparity, in which interspecific competition drives new species into larger bodied, unoccupied niches
Diffusion-driven disparity	Mechanism for increased size disparity, in which species sizes vary independently of nearby niche occupation, as in diffusion
Cope's rule	Average multiplicative change between an ancestor A's and descendant species D's mass, $\langle \ln \lambda \rangle = \langle \ln (M_D/M_A) \rangle$ (While there are two common definitions of Cope's Rule, we use Alroy's, which lends itself to quantitative analysis.) (Alroy, 1998)

size disparity are driven directly by increases in species diversity or number, while the macroevolution explanation predicts that disparity can increase without a concurrent increase in diversity.

The Equidae family is well suited for investigating this question: it is an ecologically important monophyletic family and has a well resolved fossil record with reliable size estimates for hundreds of species over its duration. Furthermore, horses exhibit many of the patterns associated with adaptive radiations (Gavrilets & Losos, 2009): over the past 56 millions of years (Myr) but particularly from 24 to 20 Ma, both size disparity and the number of species increased dramatically, horse morphology diversified considerably, with many lineages switching from grazing to browsing and increasing their geographical ranges (MacFadden & Hulbert, 1988), new species arose from nonallopatric speciation, and mostly small phenotypic changes occurred after the main diversification period. The concurrent increases in diversity and disparity presents a simple but fundamental question: was the increase in disparity driven by increased diversity or not?

We investigate this question using a clade-level mathematical model that captures the distinct predictions of the two explanations for species body size distributions. Although still other explanations are possible, we focus on these two general hypotheses. Both hypotheses have extensive associated literatures and examine factors within a given clade that are hypothesised to contribute to expansion of body size. By using the same mathematical model to capture both mechanisms, we control the impact of auxiliary assumptions and place the hypotheses on equal footing, allowing for a self-contained pairwise comparison. We then use this model to measure the relative importance of each mechanism for explaining the observed increase in Equidae maximum size.

The first mechanism, which we call the diversity-driven model (Foote, 1993; Erwin, 2007), assumes a fixed set of available niches that are unequal in their attractiveness to species, e.g. due to different associated reproductive rates (Maurer et al., 1992; Brown, 1995). When the number of niches at a particular size is small, increasing diversity implies the occupation of progressively less attractive niches, via interspecific competition. When competition is strong, a fixed number of n species will occupy the n niches closest to the optimal or most attractive size, and as new species are added, niches are occupied in decreasing order of their

attractiveness. The result is that most or every available niche at a given size will be filled before many niches at more extreme sizes are filled (Maurer et al. 1992; Foote, 1993; Erwin 2007), and when no more niches are available, a saturating maximum body size is observed (Smith et al. 2010). Thus, under this hypothesis, disparity increases only from increasing diversity.

The second mechanism, which we call the diffusion-driven model, assumes that ecological pressures or selective effects on species body size are not dependent on the occupation status of nearby niches, and instead vary randomly both in direction and magnitude over evolutionary time, across a taxonomic group (Stanley, 1973; McShea, 1994, Clauset and Erwin 2008). The aggregate result of such pressures is a macroevolutionary diffusion process (Raup, 1977; Hunt, 2007) in which species body size varies like a random walk from ancestor to descendant. For a fixed number of species, individual lineages are occasionally pushed into larger bodied niches as the result of these uncorrelated selective pressures, causing size disparity to increase over time without the addition of new species. Heterogenous ecological variables like interspecific competition, life history and habitat play secondary roles in this type of mechanism, being aggregated across large spatial and temporal scales. Instead, the governing variables are those specifying the distribution of size changes at each step of the random walk and any constraints on the range of possible sizes (Clauset & Erwin, 2008). Under this mechanism, niche space remains sparsely occupied (in contrast to the diversity-driven model), species sizes may change independently of the occupation of niches at smaller sizes, and disparity can increase without increased diversity.

We first construct a comprehensive database of size data for Equidae over the past 56 Myr and then formalise the two hypotheses within a single quantitative framework. The mathematical form of this framework makes precise statements about both the theoretical structure of the one-dimensional body size morphospace as well as its species occupation number, without needing to model individuals or population dynamics. Using this model, we can predict both body size distribution and the increase in disparity through time. We apply this framework to our horse data to measure the relative importance of the two mechanisms for explaining Equidae's nearly 60-fold increase in maximum size.

MATERIALS AND METHODS

Family Equidae

Horses (family Equidae) consist of 246 known fossil species from 43 genera, which are found in North America, Europe, Asia, and South America (Janis, 2007). The family originated in Europe 56 Ma (MacFadden, 1992), and is a subclade of order Perissodactyla, or odd-toed ungulates (Janis, 2007). Over the course of Equidae evolution, horses have ranged in size from roughly 10 kg to over 1200 kg. The horse family is well-represented in the paleontological and paleobiological literatures, making it an ideal group for the study of body size evolution within mammalian taxonomic subgroups. In general, estimates of fossil horse species size are made from molar measurements, using standard techniques (MacFadden, 1986).

The earliest horses belonged to *Hyracotherium* (56 Ma), which had small hooves, a footpad, and molars with low crowns for crushing leaves, berries, and other fibrous vegetation (Janis, 2007). The subsequent expansion of the Equidae family is divided into three subfamilies, the Hyracotheriinae (Eocene), the Anchitheriinae (Eocene to Miocene) and the Equinae (Miocene to present) (Janis, 2007). The first subfamily, the Hyracotheriinae, found in North America and Europe, were relatively small, forest-dwelling horses with a fibrous diet that emphasised leaves (Janis, 2007).

In comparison, the second subfamily, the Anchitheriinae, developed more specialised hooves and molars, and exhibited three-toes and longer limbs that were more efficient for locomotion (Janis, 2007). Their teeth shape and microwear indicates a specialised diet of leaves, now from a temperate rather than tropical forest. From 24 to 20 Ma, Equidae exhibited enormous taxonomic diversification, increasing from less than 20 to nearly 100 known species, forming three distinct Equidae lineages (Fig. 1), exhibiting a broad range of body masses (Fig. 2).

The third subfamily, the Equinae, shifted to a relatively fibrous or grassy diet, just as grasslands expanded at the expense of tropical broadleaf forests, and included the first 'grazing horse,' *Merychippus*, in North America. Corresponding skeletal evolution includes an elongation of the face and a deepening of the lower jaw. Equinae lost footpads and late Equinae members exhibit the single toe characteristics of modern horses (Janis, 2007).

Equidae species mass data

We constructed a database of species body mass estimates that covers 225 (91%) of the 246 known Equidae species, which is nearly four times larger than previous databases (MacFadden, 1986) (see Table S1 in Supporting Information). Only plausibly independent, scientifically derived estimates were included (Hay, 1917; Sachs, 1967; Radinsky, 1978; Janis, 1982; Hulbert, 1985; MacFadden, 1986; Legendre & Roth, 1988; Damuth & MacFadden, 1990; Gingerich, 1991; MacFadden, 1992; Hulbert, 1993; Storer & Bryant, 1993; Janis *et al.*, 1994; MacFadden and Ceding 1994; Alberdi *et al.*, 1995; Silva and Downing 1995; Azzaroli, 1998; Blondel, 1998; MacFadden, 1998; Eisenmann & Sondaar, 1998; MacFadden *et al.*, 1999; MacFadden, 2001; Forsten, 2002; Mustoe, 2002;
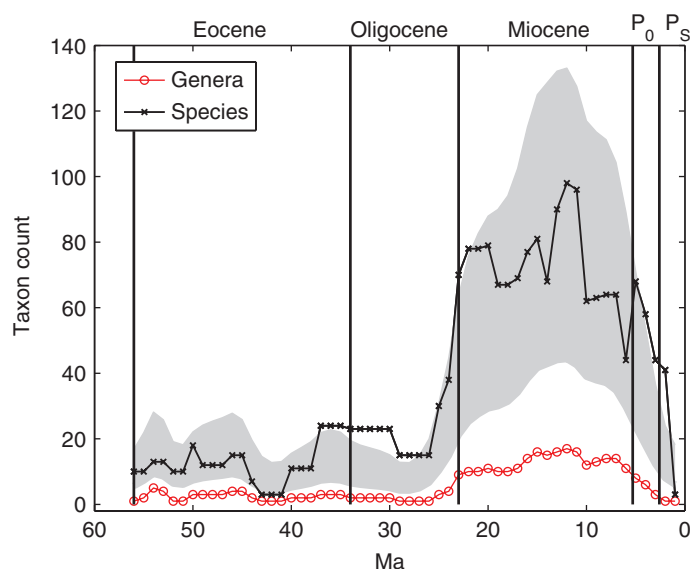
Figure 1 Equidae diversity over time, showing species- and genera-level counts from our database of 246 species and the estimated diversity range (shaded region) based on extrapolating high and low species counts from genera diversity. P_O, Pliocene epoch; P_S, Pleistocene.
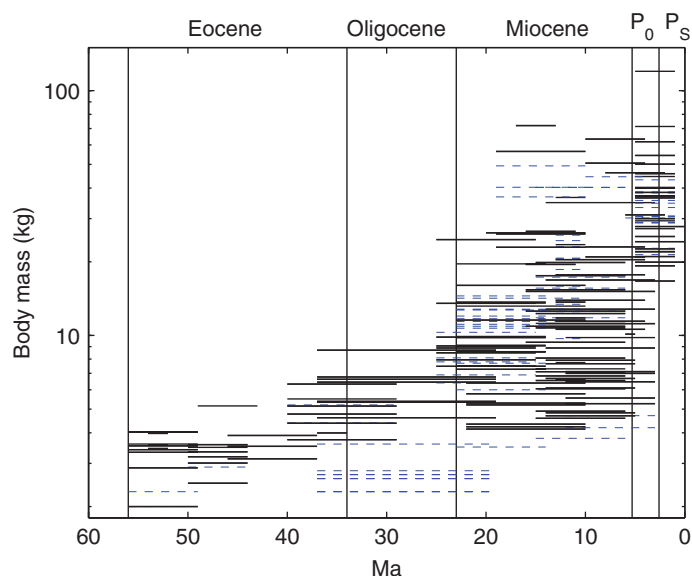
Figure 2 Equidae body masses over time for 225 species. Each line gives the estimated body mass of a single species and spans that species' known duration. Solid lines indicate estimates from molar or length measurements; dashed lines indicate estimates from genera-level ranges (see text).

Eisenmann, 2003; Ting *et al.*, 2003; Gould & MacFadden, 2004; Scott and Maga 2005; Mendoza *et al.*, 2006; Lambert, 2006; Pesquero *et al.*, 2006; Janis, 2007; Paleobiology Database, 2012). Species body masses were estimated using one of four methods, depending on the data available for a species (see Appendix S1 in Supporting Information for further details). In the first case, a species' body mass estimate was

previously published in the literature; these estimates were included without modification.

Following MacFadden's approach (MacFadden, 1986) for the second method, we converted upper first molar measurements, found in the literature, into head-body length estimates, using MacFadden's linear model. We then converted head-body length measurements into species body mass estimates using MacFadden's exponential model (MacFadden, 1986) (Appendix S1). Although this method slightly overestimates the sizes of smaller, earlier Equidae species, it is widely used and well accepted. We employ it here to maintain consistency with other studies. Furthermore, overestimating small sizes decreases size disparity for our study, providing a conservative framework for our analysis.

Modifying the above approach (MacFadden, 1986) for the third method, we converted lower first molar measurements into head-body length estimates, again using a linear model (Appendix S1). This model was estimated using a dataset of lower molar measurements and body size estimates from methods one or two (see Figure S1 in Supporting Information). Subsequently, this model was used to estimate body sizes when lower first molar measurements were available but no body mass data was found in the literature. Estimates of body mass from head-body length used the exponential model described for method 2 (MacFadden, 1986).

If a body mass estimate could be derived using several of the methods, the different results were averaged. Estimates produced by these methods cover 152 (62%) of 246 Equidae species listed in the Paleobiology Database by December 2011.

Finally, for an additional 73 species (30%), only a genus-level size range was known. Here, we estimated a species mass by aligning a normal distribution's 5 and 95% quantiles with the reported upper and lower values, and then drawing an estimated size from this distribution (a method similar to the convention in paleontology of taking the mid-point of the range). These species included none of the maximum sizes in any part of our study period, but included many of the smaller species, close to the lower end of the Equidae size distribution.

Modelling species mass distributions

Our mathematical model for the species body mass distribution takes two forms, one for the diversity-driven hypothesis and one for the diffusion-driven hypothesis. For mathematical consistency, we require that the long-term behaviour of both forms converge on the same final species mass distribution.

Relatively few mathematical models provide stationary and dynamical models of these distributions that are a good fit to the observed data. Here, we use the model developed by Clauset, Erwin, Schwab and Redner (CESR model) (Clauset & Erwin, 2008; Clauset et al. 2009, Clauset & Redner, 2009), which satisfies these requirements and can be fitted to our data on horse body sizes.

Under the diversity-driven model, the allowed distribution of species masses is fixed, representing a stable set of body-mass niches. The number of species is then increased over time, following the empirical diversity data. As new species are added, niches become occupied in proportion to their rela-

tive frequencies within the background distribution, which represents a weak assumption on the strength of interspecific competition for more attractive niches. As species are added, niches closer to the modal or most preferred size in the background distribution tend to be filled before niches farther away, and the maximum size increases steadily until no more niches are available. Under this formalisation, disparity increases faster than if all niches at some size were filled before any at more extremal sizes, either larger or smaller – as in the case of strong interspecific competition. Thus, this approach provides a conservative upper-bound on the rate of disparity increase across a range of strengths for interspecific competition.

Under the diffusion-driven model, niches are occupied without regard to the occupation status of other niches, and the distribution's evolution is driven instead by stochastic selective pressures on species sizes. The specification for this model is mathematically more complicated as it defines precisely how the species body mass distribution itself changes over time, even while the number of species remains fixed.

A detailed mathematical derivation of the CESR model may be found in the existing literature (Clauset et al., 2009; Clauset & Redner, 2009). Here, we summarise the model's basic assumptions and sketch the derivation of the equations that specify the background distributions used in the diversity- and diffusion-driven models. The CESR model assumes only macroevolutionary 'neutral' processes (Hubbell, 2001): speciation, extinction, size variation, a minimum viable size, and all species in the taxonomic group obey a common set of governing equations and constraints, while individualizing variables, e.g. predation relationships, life history, habitat and geography, are omitted.

In the CESR model, a species of mass M produces descendant species with masses λM, where λ is a random variable drawn from a fixed distribution that represents the net pressures with different magnitudes and directions. The value of a particular λ summarises all selective pressures on this species' size at the time of speciation (Fig. 3), e.g. environmental gradients, interspecific competition and resource constraints. Anagenetic variation, or changes in size between speciation events, need not be modelled separately as their impact is implicitly captured by the λ associated with each speciation event.

The resulting multiplicative random walk model (Raup, 1977; Hunt, 2007) is constrained at the lower end of sizes by physiological limits that induce a minimum viable size for every species. The minimum for Equidae is set to $M_{\min} = 20$ kg based on empirical data.

On the upper end, the probability of species extinction rises with increasing size (Liow et al., 2008; Davidson et al., 2012), which compactly summarises risk contributions from all sources, including energetic requirements (McNab, 2009) smaller populations (White et al., 2007), longer generation times (Martin & Palumbi, 1993) and demographic stochasticity (Jeppsson & Forslund, 2012). The net effect is a soft upper boundary on species sizes, in contrast to the hard limits typically derived from energetic constraints alone.

The resulting species mass distribution may be simulated directly (Clauset & Erwin, 2008) or approximated analytically
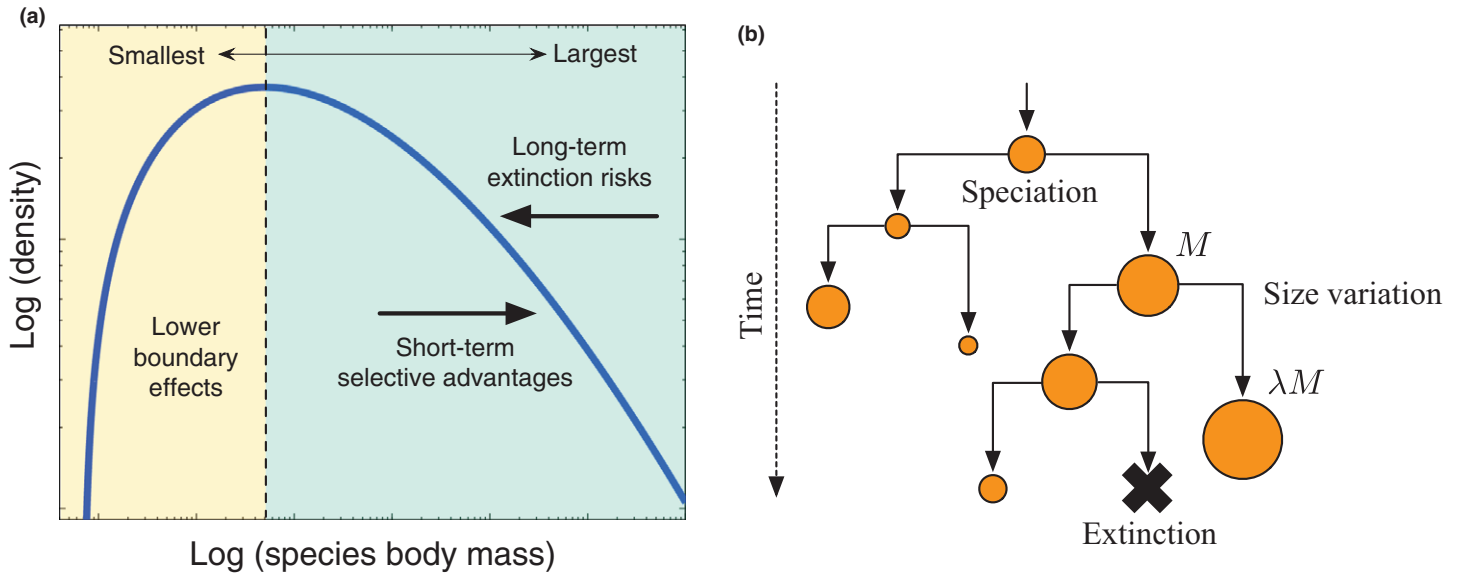
Figure 3 Schematic of body mass distribution model. Depicted in (a) are the three factors affecting body mass distribution through time, a lower boundary effect, short-term selective advantages, and long-term risk of extinction; (b) shows the cladogenetic model depiction of species body mass evolution, in which an ancestor species of mass M gives rise to descendant species of mass λM, where λ is a random variable. Species masses are constrained to be at least some minimum viable size M_{min} and species extinction increases with larger mass.

as the stationary or time-evolving solution to a constrained convection-reaction-diffusion equation (Clauset *et al.*, 2009; Clauset & Redner, 2009). Here, we use the analytic solution, which has a clean mathematical form and a small number of parameters that can be estimated directly from data.

We now sketch the main mathematical results of the CESR model that are necessary to conduct our comparison of the diversity and diffusion models in Equidae. Let $c(x, t)$ denote the fraction or density of observed species with mass $x = \ln M$ at time t. (We choose $\ln M$ rather than M to reflect the multiplicative variability of body masses.) The value of $c(x, t)$ is then modelled using a modified form of the standard convection-diffusion-reaction equation (Berg, 1993; Krapivsky *et al.*, 2010):

$$\frac{\partial c}{\partial t} + v\frac{\partial c}{\partial x} = D\frac{\partial^2 c}{\partial x^2} + (k - A - Bx)c. \qquad (1)$$

On the left-hand side, the first term models the density's time dynamics, while the second models the impact of the average change in size from ancestor to descendant, i.e. the strength of Cope's rule, represented by $v = \langle \ln \lambda \rangle$. On the right, the first term models the impact of the variability in size changes from ancestor to descendant, quantified by $D = \langle (\ln \lambda)^2 \rangle$, while the second models the changes in density due to extinction and speciation; k denotes the mean speciation rate, A the background or size-independent extinction rate ($k - A$ is the net background speciation rate) and B quantifies how quickly the extinction rate increases with size (Clauset *et al.*, 2009; Clauset & Redner, 2009).

We may then rewrite eqn 1 in the form of Airy's differential equation (Abramowitz & Stegun, 1972) by changing variables to $\beta = B/D$, $\mu = v/D$, and $\alpha = (k - A)/D$, which normalises these parameters by the variance of size changes. We then

impose a boundary condition on the solution by requiring the density go through zero $c(x, t) = 0$ at the minimum viable size $x = x_{min} = \ln M_{min}$. The steady-state solution can then be shown to be

$$c(x) \propto e^{\mu x/2}\text{Ai}\left[\beta^{1/3}(x - x_{min}) + z_0\right], \qquad (2)$$

where Ai[.] is the Airy function and $z_0 = -2.3381\ldots$ is the location of its first zero (Clauset *et al.*, 2009).

The full time-evolving solution can also be derived from eqn 1, using an eigenfunction expansion. The resulting solution is a sum of eigenmodes

$$c(x, t) = \sum_i C_i(x_0)C_i(x)e^{-\gamma_i t}, \qquad (3)$$

where each eigenmode $C_i(x)$ has the form of eqn 2 with z_0 replaced by $z_i = z_0 - \gamma_i/D\beta^{2/3}$, where γ_i denotes the decay rate for the ith eigenmode of the series, and where $x_0 = \ln M_0$ is the size of the taxonomic group's founder species (Clauset & Redner, 2009). The rates γ_i form an increasing sequence so that higher terms decay more quickly with time. In the long-time limit, all of the decaying eigenmodes with $i > 0$ become negligible and the species mass distribution converges to the steady state in eqn 2. (Note: the parameter α is eliminated in both solutions by normalisation.)

Given choices for parameters μ, β, and x_{min}, eqn 2 fully specifies a steady-state species mass distribution. With the additional choice of $x_0 = x_{min}$, eqn 3 fully specifies a time-evolving distribution. Previous studies using this model estimated $\mu \approx 0.2$ and $\beta \approx 0.08$ for terrestrial mammals (Clauset & Redner, 2009), and we use these values here. The lower end of the empirical horse size distribution remained close to the size of *Hyracotherium*, which has a mean estimated size of

20 kg (across multiple estimates found in the literature), until approximately 5 Ma. We choose this value for M_{min}.

Finally, this model is a deterministic approximation of an explicitly stochastic model (Clauset & Erwin, 2008). The predicted distribution, however, agrees well with extant data for all terrestrial mammals (Clauset & Erwin, 2008), all birds (Clauset *et al.*, 2009) and all cetaceans (Clauset, 2013). Furthermore, its temporal dynamics agree well with the expansion of terrestrial mammals as a whole in the late Cretaceous and early Paleogene (Clauset & Redner, 2009). It thus provides a well-motivated and empirically reasonable mathematical framework by which to formalise the diversity- and diffusion-driven mechanisms.

Model evaluation

The key period for evaluating these mechanisms is the rapid diversification around 24 Ma, during which both the species number and their maximum size increased dramatically. This period includes the expansion of browsing horses (*Parahippus, Anchitherium, Hypohippus, Anchitherium and Archaeohippus*) at 24 Ma and the expansion of grazing horses in North America between 18 and 15 Ma (MacFadden & Hulbert, 1988). We define the period before 24 Ma as 'pre-diversification' and the period after as 'post-diversification'.

We measure the extent to which each model correctly predicts the empirically observed increase in maximum size over 56 Myr (Fig. 2). Each model produces a probability distribution $c(x)$ for Equidae species masses at each time point. For any such distribution, the expected maximum species size M_* for n species is given mathematically by $1 - F(\ln M_*) = 1/n$, where $1 - F(M_*) = \int_{\ln M_*}^{\infty} c(x)dx$, i.e. where the complementary cumulative distribution function (ccdf) crosses the horizontal line $1/n$. For a fixed distribution and increasing n, or for fixed n and a distribution with a lengthening right tail, the location of this intersection will shift towards larger sizes.

For the diversity-driven model, we fix the species mass distribution $c(x)$ and let n vary according to the empirically observed species counts over time (Fig. 1). We control the impact of distribution variance – niche space 'width' – by testing two choices of $c(x)$: one fitted to the pre-diversification empirical mass distribution and one fitted to the broader post-diversification distribution. For the diffusion-driven model, we fix the number of species n and let $c(x)$ evolve over time, reflecting the empirically observed expanding size distribution (Fig. 2). We control the impact of species diversity by testing two choices of n, corresponding to the pre-and post-diversification species counts. For each model, the predicted maximum body mass was extracted for each 5 Myr period starting at 56 Ma and then compared to the observed maximum in the same period.

RESULTS

Data summary

From 56 to 24 Ma, horse diversity remained relative low (less than 30 species, up to 4 genera; Fig. 1), and the maximum mass only approached 100 kg towards the end of this period.

However, during the early Miocene (24–12 Ma), both diversity and disparity increased dramatically, reaching a peak of 98 species with maximum mass of nearly 800 kg (Fig. 2). This increase in diversity represented the appearance of many new genera, with genus diversity growing to 17 distinct groups by 12 Ma.

Subsequently, however, both species and genus counts decreased dramatically. This trend continued into the Pleistocene extinction, reflecting the broader loss of diversity seen across mammals (Owen-Smith, 1987; Guthrie, 2006), during which roughly half of all mammalian genera with body masses over 5 kg became extinct. For Equidae, this loss of diversity impacted mainly smaller bodied species, rather than larger ones, as is typically expected (Liow *et al.*, 2008). We observe no tendency for these emptied niches to be refilled from larger bodied lineages, as we would expect from the reproductive-power hypothesis. In contrast, the broad extinction of small-bodied lineages suggests high-level and long-term selection, possibly related to changing climate or reorganising ecosystems, with better adapted species groups expanding into niche-space previously filled by Equidae.

The expansion of Equidae's body mass distribution was thus highly asymmetric, but consistent with expansion from minimum viable size (Stanley, 1973, McShea, 1994) at roughly 20 kg. This pattern suggests the existence of a stable, and previously unidentified, physiological constraint at the lower end of the horse mass distribution. Furthermore, statistical tests indicate little evidence for either sampling bias in diversity data or non-stationary processes in the variation of body sizes over the study period (see Appendix S2 in Supporting Information).

Diversity or diffusion?

To extract the necessary distributions for our tests, we first fix the model parameters μ, β and x_{min}, as described above. For diversity-driven models, we divided the mass data into pre- and post-diversification periods from which we estimate the corresponding background mass distributions. The diversity data were then converted into a time series of eleven 5 Myr periods, starting at 56 Ma. For diffusion-driven models, mass data were divided into the same sequence of 5 Myr periods, and pre- and post-diversification species averages were fixed at $n_{pre} = 15$ and $n_{post} = 69$, respectively. (Modest variations in the division date yield similar results in both cases.)

For each of the two model types, we fitted the time-evolving model to the respective sequence of distributions using the nonparametric method of Clauset and Redner (2009), which chooses a mapping of model-time to real-time that minimises the distributional distances between the evolving distribution and the sequence of empirical distributions. This approach yields good agreement with the empirical pattern (Fig. 4).

For each 5 Myr period, we calculated the predicted maximum mass M_* under each model, which we compared to the observed maximum, smoothed using an exponential kernel. In both diversity-driven models, the empirical diversification pattern failed to produce a large increase in disparity (Fig. 5a), even when the background distribution itself was broad. To quantify a model's prediction accuracy, we computed the sum
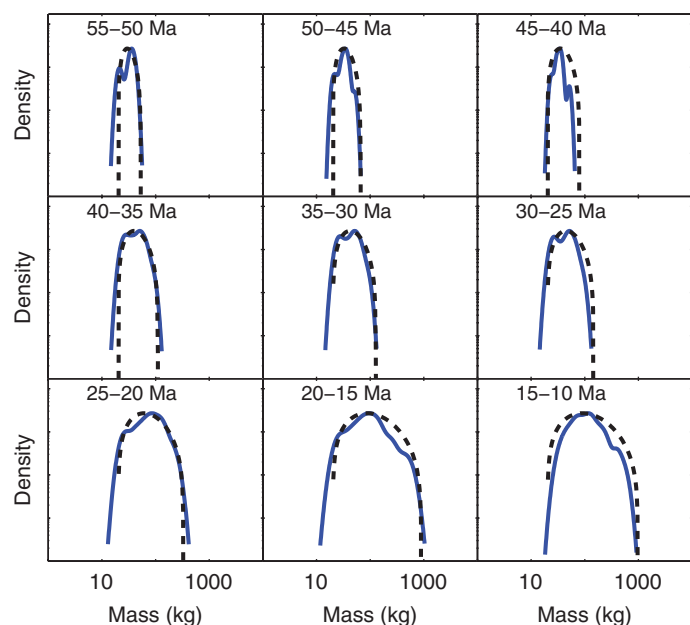
Figure 4 Comparison of empirical (blue; smoothed with a Gaussian kernel) and model-based (dashed, black) Equidae body mass distributions, in 5-million-year increments, showing good agreement.

of squared errors (SSE) between the diversity-driven prediction for ln M_* and the observed values. The pre-diversification diversity-driven model yielded the largest SSE across all models, with $R_{div,\ pre} = 35.43$, and failed to produce any species larger than 50 kg. The post-diversification model yielded a small improvement, with $R_{div,\ post} = 22.05$, but this model dramati-

cally overestimated the initial size disparity and produced very little increase in disparity over 50 Myr.

In contrast, both diffusion-driven models accurately predict the observed increase in disparity (Fig. 5b), with the post-diversification model performing slightly better over the last 20 Myr. The SSE for the pre-diversification diffusion prediction was $R_{diff,\ pre} = 1.29$, or about 27 times closer than $R_{div,\ pre}$, while the post-diversification model yielded $R_{diff,\ post} = 0.18$, or about 118 times closer. Overall, the post-diversification diffusion model (with $n = 69$) succeeds in explaining 92% of the observed increase in maximum size, from 39 kg to 1200 kg, over the 56 Myr expansion of Equidae.

DISCUSSION

Previous studies (Stanley, 1973; Maurer *et al.*, 1992; Clauset & Erwin, 2008; Smith *et al.*, 2010) have advanced specific mechanistic explanations for the body size distributions within large taxonomic groups, particularly mammals. Here, we investigated the ability of two general hypotheses, formalised within a common mathematical framework, to explain the common pattern of increased disparity in an expanding lineage. Using family Equidae as a model system, we found that macroevolutionary 'diffusion', in which selective effects on species body size vary independently of the occupation status of nearby niches, explains substantially more of the observed changes in the Equidae body mass distribution over 56 Myr (Fig. 5) than does a diversity-driven mechanism, in which niches closer to a preferred or optimal size are filled before less attractive and larger bodied niches are filled. These results suggest that increases in disparity are not necessarily driven by macroecological competition for niches, as is
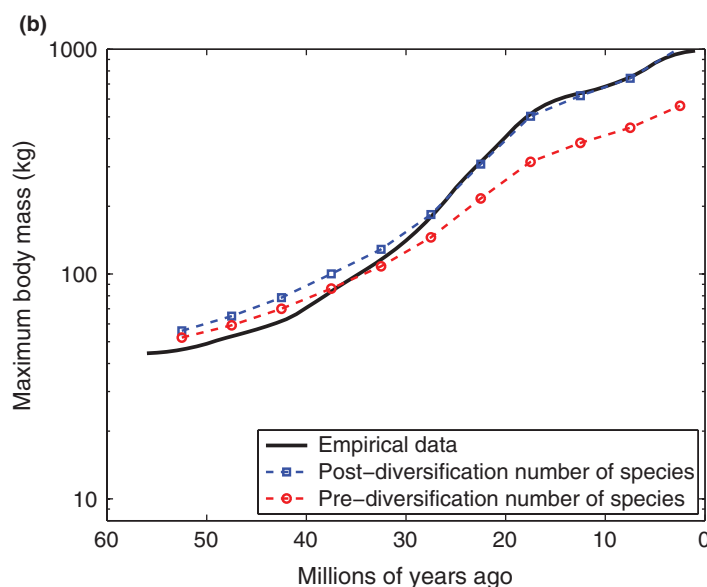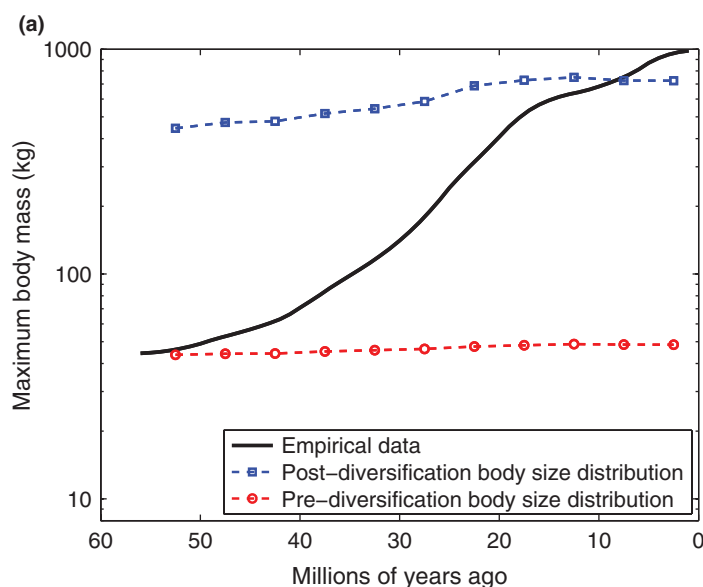
Figure 5 Evolution of species mass disparity in the Equidae lineage over 56 Ma, showing the empirical trend (bold line) and the predicted maximum sizes from (a) diversity-driven models, with background distributions fitted to pre- and post-diversification data, and (b) the diffusion-driven models, with a time-evolving distribution containing a number of species fixed at pre- or post-diversification levels. All models predict an increase in disparity, but diversity-driven disparity models show only modest increases, regardless of what background distribution is used, while diffusion-driven disparity accounts for 92% of the observed increase over this period, regardless of the number of species assumed.

commonly assumed. Instead, disparity may increase from neutral diffusion effects alone, even when small-sized niches are available and the niche space is sparsely occupied.

While some studies (Allen et al., 2002; Secord et al., 2012) have suggested a coupling between global temperatures and species body sizes, we found no such correlation with horse body sizes. However, global temperatures do appear to correlate with Equidae taxonomic diversity, which achieves its highest point during warm periods and low points during glaciation and cooler global temperatures (Fig. 1). For instance, the first member of Equidae appeared at 56 Ma, during a thermal maximum. From 56 to 42 Ma, ^{18}O isotope data show that average global temperatures were relatively cool (Zachos et al., 2001), and our data show that during this period both species and genera counts were low, with fewer than 30 species and four genera. Taxonomic counts increased substantially from 24 to 21 Ma and reached their peak during the global warming period spanning the Oligocene-Miocene boundary to the mid-Miocene (Fig. 1), which generated a loss of Antarctic ice and warmer deep water temperatures (Zachos et al., 2001).

This pattern suggests a climate-diversity coupling for Equidae in particular, and this pattern may also hold for other lineages. Although the evolutionary and ecological causes of the Equidae adaptive radiation remain unclear, the climatic connection provides a novel hypothesis, in which a warming climate drove changes in flora and the expansion of grassland ecosystems, which expanded the distribution of unoccupied niches, allowing for the evolution of grazing horses and the corresponding increase in diversity (MacFadden & Hulbert, 1988). Regardless of the cause of the radiation, our results suggest that Equidae disparity would have increased without any increase in species counts, and whatever mechanism caused the increase in diversity played only a minor role in the simultaneous increase in body size disparity.

The success of the diffusion-driven model in matching the observed tempo and magnitude of size disparity in Equidae over 56 Myr suggests that morphological disparity may generally be driven at the clade-level by diffusive processes rather than diversification processes. Such macroevolutionary diffusion is the natural consequence of randomly varying selective pressures on species sizes within fixed constraints on size (Clauset & Erwin, 2008), and is entirely consistent with an expanding space of niches (Odling-Smee et al., 1996). For horses in particular, although both the distribution and diversity expanded during their adaptive radiation, diffusion appears to have played the dominant role in producing increasingly large-bodied species (Fig. 5b), a point that is reinforced by the steady expansion of the mass distribution even with a roughly stable species number prior to 24 Ma (Figs 1 and 2).

A large role for diffusion does not undermine the general ecological importance of competition, but rather clarifies its role in generating broad-scale patterns for horses in particular, and for evolving systems in general. Macroevolutionary diffusion is an effective large-scale description of many roughly independent ecological interactions and evolutionary constraints on species size variation. Short-term selective effects on size for a particular species can stem from any number of specific mechanisms,

including but not limited to competition over ecological niches. So long as the magnitude and direction of these effects, as defined at the species-level, are roughly independent across the taxonomic group, the large-scale pattern will be well described by diffusion. Ecological competition may thus be crucial for individual species, but its effects are more diffuse at the large scale because competition is typically a local process.

In the body mass evolution and diversification of horses, competition between Equidae species appears to have played a minor role in driving the dramatic and sometimes rapid changes in species morphology observed over 56 My. Future work in which among-clade dynamics are modelled could shed additional light on the relative roles of interclade (e.g. competition or predation) vs. within-clade (e.g. diversification or diffusion) processes in structuring changes in the Equidae body-size distributions through time. Furthermore, understanding the ecological or evolutionary reason for the apparent coupling of climate and Equidae diversity and the apparent minimum viable size at roughly 20 kg, both identified here, may shed new light on Equidae evolution. Finally, diffusion-driven and diversity-independent increases in disparity may hold beyond Equidae, given the strong support for diffusion-type models in explaining the shape and dynamics of other species size distributions (Stanley, 1973; McShea, 1994; Clauset & Erwin, 2008; Clauset & Redner, 2009; Clauset, 2013). Determining the generality of this pattern is an important direction for future work.

AUTHORSHIP

LS and AC designed the research, performed modelling work and wrote the manuscript. LS collected data and analysed the results.

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