

Shallow size–density relations within mammal clades suggest greater intra-guild ecological impact of large-bodied species

Rasmus Østergaard Pedersen¹  | Søren Faurby^{1,2,3,4} | Jens-Christian Svenning¹

¹Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Aarhus C, Denmark

²Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain

³Department of Biological and Environmental Sciences, University of Gothenburg, Göteborg, Sweden

⁴Gothenburg Global Biodiversity Centre, Göteborg, Sweden

Correspondence

Rasmus Østergaard Pedersen
Email: rasmus.pedersen@bios.au.dk

Funding information

Carlsbergfondet, Grant/Award Number: CF16-0005; Natur og Univers, Det Frie Forskningsråd, Grant/Award Number: 4090-00227; European Research Council, Grant/Award Number: ERC-2012-StG-310886-HISTFUNC

Handling Editor: Shai Meiri

Abstract

1. Population densities of species have a predictable relationship with their body mass on a global scale. This relationship is known as the size–density relationship (SDR). The relationship was originally found to be directly opposite of metabolic rate scaling, which led to the hypothesis of energetic equivalence. However, recent studies have suggested that the SDR varies between clades. Specifically, the SDR for certain mammal clades has been found to be less negative than the relationship across all mammals.
2. The aim of the present study is to estimate phylogenetic variation in the scaling relationship, using a data-driven identification of natural phylogenetic substructure in the body size–density relation, and discuss its potential drivers. The classic model is often used to estimate natural population densities, and a further, practical aim is to improve it by incorporating variability among phylogenetic groups.
3. We expand the model for the SDR relation of mammals to include clade-specific variation. We used a dataset with population and body mass estimates of 924 terrestrial mammal species, covering 97 families, and applied an algorithm identifying group-specific changes in the relationship across a family-level phylogeny.
4. We show increased performance in species density estimation is achieved by incorporating clade-specific changes in the relationship compared to the classic model (increasing r^2 from .56 to .74 and $\Delta AIC_c = 466$). While the global SDR across clades was confirmed to be similar to previous findings ($r = -.74$), the relationship within all sub-clades was less negative than the overall trend.
5. Our results show that data-driven identification of phylogenetic substructure in the size–density relation substantially improves predictive accuracy of the model. The less negative relationship within clades compared to the overall trend and compared to within clade metabolic scaling suggest that the energetic equivalence rule does not hold. This relationship shows that large species within clades use proportionally more energy than smaller species. Therefore, our results are consistent with a greater intra-guild ecological impact of large-bodied species via partial monopolisation of resources by the largest species of a given guild, and hence size-asymmetric intra-guild competition.

KEYWORDS

allometry, body size, Cope's rule, energetic equivalence, evolution, intra-guild competition, mammals

1 | INTRODUCTION

Population densities of terrestrial mammals are negatively related to body mass, a relationship which has been found repeatedly across several phyla in the animal kingdom (Damuth, 1987; Peters, 1983). Notably, studies have found that the population density, D , of a species relates to mean body mass, M , as $\log D = a + b \log M$, with the slope b close to -0.75 , independent of habitat and dietary class (Damuth, 1981, 1987). The relationship is noisy though and densities vary about two orders of magnitude to either side of the overall trend (Damuth, 1981, 1987, 2007). Further, subsequent studies have questioned the generality of the relation within clades (e.g. Brown & Maurer, 1986; Munn, Dunne, Müller, & Clauss, 2013; Nee, Read, Greenwood, & Harvey, 1991).

In this study, we aim to contribute to an improved understanding of the so-called *global size-density relationship* (SDR), the relationship between the average body mass and the average population density for species around the globe unrelated of community or habitat (White, Ernest, Kerkhoff, & Enquist, 2007). Across large scales, broad body mass spans, and broad taxonomic levels, the *global SDR* is generally accepted to have a relationship of $b = -0.75$ (Damuth, 1987; Hayward, Kolasa, & Stone, 2010). On smaller scales and for narrower taxonomic groups, there is much more variation in the observed relationship, usually with less steep slopes (Hayward et al., 2010; Isaac, Storch, & Carbone, 2013). While increased variation of the slope estimates found within narrower taxonomic groups has been claimed to be a statistical artefact of modelling on a smaller range of body masses, it does not account for the one-sided bias in most studies towards shallower slopes (Hayward et al., 2010). The general tendency of the relationship is that guilds with low mean body mass (e.g. rodents) are often found to have near zero slopes or even positive slopes, while guilds with medium to heavy body mass have slopes that are closer to -0.75 or have even steeper slopes (Brown & Maurer, 1986; Nee et al., 1991; Robinson & Redford, 1986), and closely related groups tend to show shallower relationships than the overall pattern (e.g. it has been shown to be only around -0.37 in Australian marsupials, Munn et al., 2013). A mechanistic model framework shows that SDR is dependent on how the food resources scale with the consumer body mass, giving markedly different expectations for the relationship between herbivores and carnivores (Carbone, Rowcliffe, Cowlshaw, & Isaac, 2007). The carnivore SDR tends to be steeper than herbivore SDR, since larger predators take larger prey and larger prey tends to be distributed less evenly, which makes prey scarcer for larger carnivores (Carbone et al., 2007). Further, we expect carnivorous to be generally offset to lower population densities than herbivores at any given body mass due to the drop of available energy higher in the food chain (Lindeman, 1942).

Since both basal and field metabolic rate was found to be increasing with body mass (Kleiber, 1947) inversely proportional to population density, Damuth (1981) concluded that population-level metabolic rate was independent of body mass [now known as the energetic equivalence rule (EER)]. Later studies have shown that metabolism does not scale universally with a body mass slope of 0.75, but is scale dependent, and is often different from 0.75 within phylogenetic

clades (Agutter & Wheatley, 2004; Isaac & Carbone, 2010; Nagy, 2005; Sieg et al., 2009), calling the EER into question. The scaling exponent of metabolic rate has been found to vary between taxonomic groups (White, Cassey, & Blackburn, 2007; White & Kearney, 2014), which under the assumption of the EER would lead us to expect that the SDR of related groups should vary as well.

In simulations, Isaac et al. (2013) have shown that under the assumption that density is energy limited, a strong density-mass relationship is to be expected, and therefore we should consider EER a null model to be tested. Another simulation study has shown how the scaling coefficient can arise through small evolutionary steps driven by an increased extinction risk for species in energetic disequilibrium compared to their expected density given a specific metabolic scaling (Damuth, 2007). When slopes diverge from the null expectation of EER, then partitioning of resources is no longer invariant of body mass. A slope more negative than the general SDR means that smaller bodied species in a clade take a relatively larger share of the resource pool, while less negative slope signifies that bigger species tend to claim a larger part of the resource pool (Hayward et al., 2010). Several studies have shown energetic in-equivalence where population densities scale more weakly with body mass than metabolism does and bigger species therefore use a disproportionate amount of the available resources than expected under the EER (DeLong, 2011; Ehnes et al., 2014; Munn et al., 2013; Russo, Robinson, & Terborgh, 2003). Under EER, we would expect the SDR of clades to mirror their metabolic rate increase with body mass, and even lower slopes if bigger species do use a disproportionate amount of resources.

One of the most used methods in predicting species densities is the allometric SDR. Accurate estimates of population densities are important for analyses of fauna ecosystem effects (Dirzo et al., 2014; Galetti & Dirzo, 2013), e.g. in relation to the impacts of past, current and future defaunation on ecosystem function and dynamics (Donlan et al., 2006; Doughty, Wolf, & Malhi, 2013; Galetti & Dirzo, 2013; Ripple et al., 2014, 2015; Turvey & Fritz, 2011; Wolf, Doughty, & Malhi, 2013). The SDR usually employed to predict density assumes a constant relationship across all clades, which we know not to be true; therefore, a model that includes this knowledge would be beneficial. It is increasingly clear that humans have had large impacts on mammal species diversity and local communities across the globe not just in recent times, but also during prehistory, especially for the megafauna (Faurby & Svenning, 2015b; Sandom, Faurby, Sandel, & Svenning, 2014; Turvey & Fritz, 2011). With a better model for population densities, we could supplement these studies with better estimates of potential population densities.

Here, we re-assess the generality of -0.75 scaling rule for the size-density relation in mammals, incorporating phylogenetic relatedness in a new approach that allows a data-driven identification of phylogenetic substructure in the density-body size relation (cf. Ehnes et al., 2014). By doing this, we indirectly investigate phylogenetically structured traits that may cause groups to deviate from an overall trend. Other studies have done this by including a priori known traits such as diet (Damuth, 1987; Ehnes et al., 2014; Wolf et al., 2013), where e.g. carnivores tend to have steeper slopes and lower intercepts than

herbivores. Other studies have also shown that a better fit can be achieved if the availability of prey biomass is taken into consideration (Carbone & Gittleman, 2002). In contrast to this approach, we here fit a model on phylogeny alone with an iterative framework searching for groups with distinct slopes, without any a priori assumption on which traits might distinguish them from one another. Since many potentially important traits tend to be phylogenetically structured (Macdonald & Norris, 2001), we expect that our approach will be able to detect most of the important trait-related variation in the SDR of mammalian groups, and not just that for known traits, but also that associated with unrecognized but influential traits. Overall, we expect our approach to provide a more accurate model of population densities of species for which we know little of their ecology, and sometimes merely their taxonomic placement and body mass.

In this study, we assess the following specific study hypotheses for the size–density relation in mammals: While we expect the relation to hold up across all mammals, we hypothesize that there will be a phylogenetic substructure, where groups of more closely related species will exhibit a shallower decline in density with body mass, consistent with a disproportionate capture of resources by the larger species within groups of ecologically similar species. Further, we expect that carnivorous groups scale the steepest and are offset to overall lower population densities than all other clades due to their high trophic level.

2 | MATERIALS AND METHODS

2.1 | Data

First, we created a dataset where we assigned each family of mammals to all the monophyletic clades it is part of. For example, the family Felidae belongs to the suborder Feliformia, the order Carnivora, the cohort Placentalia, and in the end the class Mammalia, as well as a number of monophyletic unnamed clades in between. By using a phylogeny of all mammalian families, we could assign each family to all clades it belongs to by all dichotomies above it in the tree. The phylogeny used is by Meredith et al. (2011) and we added the few non-sampled families according to Faurby and Svenning (2015a). The dataset PanTHERIA (Jones et al., 2009) is a database which have recorded a number of average traits for each species of mammal. In the database, population density and body mass is provided for 947 mammal species. For family affiliation of the species, we followed Wilson and Reeder (2005), except primate families where we followed Perelman et al. (2011). By combining the datasets, we end up with a dataset that provides body mass, population density, and a number of binomial variables indicating which monophyletic clades each species belongs to. We excluded all non-terrestrial species (Orders: Cetacea and Sirenia; Families: Odobenidae, Otariidae, and Phocidae; Species: *Lontra felina*, *Enhydra lutris*, and *Ursus maritimus*) and bats (Order: Chiroptera) from our dataset. To avoid overfitting, we did not include monophyletic clades of less than 10 species, since standard GLM approaches recommend not fitting factor levels with less than 10 data points (Ryan, 2008). Our final dataset included 924 species belonging to 110 distinct monophyletic groups.

2.2 | Analysis

First, we fitted the simple allometric relation, \log_{10} -population density as a function of \log_{10} -body mass. Then, we iterated a model building procedure until we found no significant improvement. The iterations were stopped when there was no further improvement of the model of a ΔAIC_c of more than 4 (Burnham & Anderson, 2002). Each iteration consisted of adding a unique slope or intercept terms for all members of a specific clade by including the clade as a binomial factor in the model either as a main effect (intercept change) or as an interaction term (slope change). We fitted these as individual models for all clades and kept the model giving the highest improvement based on ΔAIC_c (Figure 1) as a new base. We then removed any terms that were no longer leading to improvements of ΔAIC_c of more than 4. The process was repeated with a new iteration expanding the model. The cut-off value of 4 was chosen as this value has been used previously in the macro-evolutionary program MEDUSA (Alfaro et al., 2009), which iteratively identifies monophyletic clades that behave differently from the remaining clades, these potentially being paraphyletic assemblages. Further, models that have a $\Delta AIC_c > 4$ are generally considered to have considerably less support than the lower scoring models (Burnham & Anderson, 2002).

An underlying assumption explicitly fitting clades alone is that shifts in the hypothesised SDR are instant between clades, which

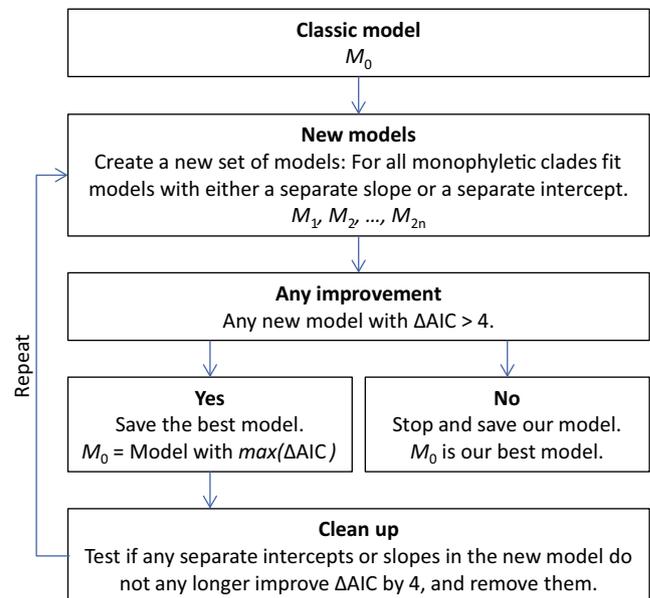


FIGURE 1 Model selection framework. We start out by the base model, and incrementally add new phylogenetic groups as either interaction (changing the specific clades slope) or main effect (changing the specific clades intercept), and keep whichever model improves AIC_c most (at least by 4). After this, we remove any previous term from the model which no longer improves the model AIC_c by at least 4. When no additions further improve the model it is terminated, and this is considered our final model

may not always be true. Many extant clades have, however, exhibited point-like changes in traits, such as carnivory, flight and digestion (Macdonald & Norris, 2001; Van Valkenburgh, 2004).

To validate our results, we used leave-half-out cross-validation, repeated 1,000 times. In other words, we fitted parameter estimates for both our final model and the base model on a random selection of half the dataset, calculated r^2 using linear regression between predicted and the remaining data, and estimated ΔAIC_c between the two models. This procedure was repeated with 1,000 random sample permutations. This method does not validate our final model against all possible models, but it does validate its stability and performance against the traditional model (Table S3).

The estimated SDR could be affected by body mass-specific biases of the density estimates. A bias such as this could arise either because there is a bias in how affected the actual density is by human influence, or if there is a bias in how the density is estimated based on body mass. We assume that any bias in the data linked to human influence of the actual density would be bias towards underestimates of natural population densities of large species, since extinctions linked to humans have a mass bias in that direction (Faurby & Svenning, 2015b, 2016). Further, we analysed a dataset containing information on both densities and sampled area and found a weak, but statistically significant trend towards underestimations of the densities for larger bodied species as a consequence of them generally being measured in a larger area (Appendix S1). From this, we conclude that if there was a bias in the population density estimates it would be underestimations of larger bodied species. If this bias existed in the data, it should have made the estimated slopes steeper. However, they were in reality shallower than expected, making conclusions based on the shallow slopes robust.

For all data handling, graphics and statistical analysis we used R v. 3.2.3 (R Core Team 2015). For working with the phylogenetic data, we used the packages 'ape' v. 3.4 (Paradis, Claude, & Strimmer, 2004),

'phytools' v. 0.5.10 (Revell, 2012) and 'geiger' v. 2.0.6 (Harmon, Weir, Brock, Glor, & Challenger, 2008). For statistical analysis, we used methods inspired by MEDUSA (Alfaro et al., 2009) and 'AICcmodavg' v. 2.0.3 (Mazerolle, 2015). For data handling, we used 'dplyr' v. 0.4.3 (Wickham & Francois, 2015), 'R.utils' v. 2.2.0 (Bengtsson, 2015) and 'stringr' v. 1.0.0 (Wickham, 2015); while 'raster' v. 2.5.2 (Hijmans, 2015) and 'rgdal' v. 1.1.3 (Bivand, Keitt, & Rowlingson, 2015) were used for spatial data. Graphics were made using 'ggplot2' v. 2.0.0 (Wickham, 2009).

3 | RESULTS

Across a wide sample of all mammalian species spanning six orders magnitude of body mass, we found that the overall relationship of \log_{10} -body mass to \log_{10} -density had a slope of $b = -0.74$ ($SE = 0.021$, $p < 2 \times 10^{-16}$), no different from the null expectation -0.75 (Figure 2).

Within mammalian clades, population density did not conform to a single overall trend, however. Rather the relationship between population densities and species body mass changed several times across the phylogeny (Table 1, Figures 2 and 3), but all coefficients were less negative than the overall trend.

The simple model prediction with a uniform relationship across all mammals performed substantially worse than a best-fit phylogenetic model improving r^2 from .56 to .74 with $\Delta AIC_c = 466$. Virtually identical improvement in the fit was found when comparing the original and the full phylogenetic model in our leave-half-out cross-validation (Table S3).

Our results showed that taxonomic groups with relatively heavier body masses have steeper slopes than lighter bodied groups in a linear model of group slope as a function of mean \log_{10} body mass ($r = -.31$, $p = .0011$). The body mass range of a group had no effect on slope in a linear model of group slope as a function of range width of \log_{10} body

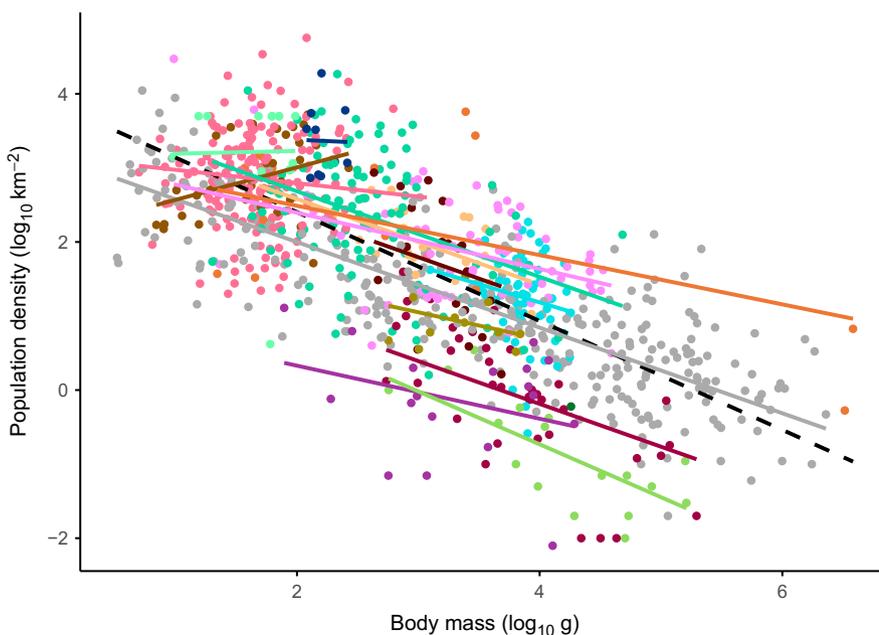


FIGURE 2 The size–density relationship of mammalian species on a \log_{10} – \log_{10} scale. The black dashed line indicates the general trend across all taxa, while the coloured lines indicate all the fits for the phylogenetic model. The 16 colours for the lines and points indicate different fit clades (For a coloured taxonomic reference see Figure S1)

TABLE 1 Allometric model fit for species' population density vs. average adult body mass for terrestrial mammals. This table shows the resulting size–density relationship for families, orders or larger well-defined monophyletic groups for an interpretable overview of our results. The relationships shown here are based on the 10 distinct slopes and six distinct intercepts we found strongly supported, based on $\Delta AIC_c > 4$, see Tables S1 and S2 for full model and AIC_c levels. An overall fit of all mammals without clade-specific variation led to an intercept of 3.87 and slope of -0.74

Clade	Intercept	Slope
Monotremata*	3.15	-0.58
Marsupialia		
Didelphimorphia	3.15	-0.58
Paucituberculata*	3.15	-0.58
Dasyuromorphia	3.15	-0.58
Diprotodontia	3.15	-0.38
Microbiotheria*	3.15	-0.58
Notoryctemorphia*	3.15	-0.58
Peramelemorphia*	3.15	-0.58
Afrotheria	3.15	-0.33
Xenarthra	3.15	-0.58
Euarchontoglires		
Dermoptera*	3.15	-0.58
Lagomorpha: Leporidae	3.53	-0.58
Lagomorpha: Ochotonidae	3.53	-0.07
Primates: Galagidae, Hominidae, Hylobatidae, Lorisidae, Tarsiidae, & Platyrrhini	3.15	-0.58
Primates: Cercopitheciae	3.15	-0.49
Primates: Daubentoniidae & Lemuriformes	3.74	-0.58
Rodentia: Castoridae*	2.13	-0.58
Rodentia: Geomyidae & Heteromyidae	2.13	0.44
Rodentia: Dipodidae* & Anomaluromorpha*	3.15	-0.58
Rodentia: Myomorpha	3.15	-0.18
Rodentia: Hystricomorpha & Sciuromorpha	3.84	-0.58
Scandentia*	3.15	-0.58
Laurasiatheria		
Artiodactyla	3.15	-0.58
Carnivora: Mustelidae	1.05	-0.36
Carnivora: Felidae & Viverridae	2.13	-0.71
Carnivora: Canidae, Eupleridae, Herpestidae, Hyaenidae, Nandiniidae, & Ursidae	2.13	-0.58
Carnivora: Ailuridae, Mephitidae, & Procyonidae	2.13	-0.36
Erinaceomorpha*	3.15	-0.58
Perissodactyla	3.15	-0.58
Pholidota*	3.15	-0.58

(continues)

TABLE 1 (continued)

Clade	Intercept	Slope
Soricomorpha: Solenodontidae & Soricidae	3.15	-0.58
Soricomorpha: Talpidae	3.15	0.04

Marked (*) groups where we only had density estimates from less than 10 species and unique slopes or intercept for the group therefore were not allowed. Intercepts and slopes marked with bold are from groups with distinct values different from the paraphyletic assemblage containing the remaining species. The value for the paraphyletic assemblage is repeated multiple times for monophyletic subparts to make the values for individual clades easier recoverable from the table.

mass ($r = -.087, p = .17$). Within the main carnivorous mammal clade (Carnivora), we saw slopes ranging from one of the steepest to some of the weakest (-0.36 to -0.71). Therefore, we saw no clear simple overall trophic explanation for differences in the SDR. Still, we did find the steepest slope of all the mammal clades for the most purely carnivorous subgroup of Carnivora, Felidae and Viverridae, while the Carnivora clades with the weakest slopes Ailuridae, Mephitidae, Mustelidae and Procyonidae have much more mixed diets, including many omnivorous or even herbivorous species (Wilson & Mittermeier, 2009).

Within the Carnivora clades, we saw a general downward shift in intercepts, resulting in lower population density estimates for this group than according to the classical model. Within the respective mass spans of the four different Carnivora groups, we saw that the predicted densities for Mephitidae and Procyonidae were 2–5 times lower than what they were modelled with the same model for all species (i.e. the null model with a slope of -0.74). Mustelidae had predicted densities that are 16–130 lower, Felidae and Viverridae have 44–49 times lower predicted densities while the rest of the Carnivora (Canidae, Eupleridae, Herpestidae, Hyaenidae, Nandiniidae and Ursidae) have predicted densities 8–21 times lower than predicted by the classical model.

4 | DISCUSSION

We found the *global SDR* across all mammals to be consistent with previous findings (Damuth, 1987; Nee et al., 1991; White, Ernest et al., 2007). However, when applying our approach by using a data-driven identification of natural phylogenetic substructure in the density–body size relation, other trends arose. We showed that within clades the global trend is broken, as has previously been shown for other organism groups (Damuth, 1991; Ehnes et al., 2014; Nee et al., 1991), and that all within-group slopes are weaker than the overall relationship. Similar results have been found within specific taxonomic groups of mammals before; we demonstrate here for the first time that clade-specific variation in the body SDR for all sub-clades is less negative than the SDR across Mammalia.

The pattern across all Mammalia as a whole shows that EER could be considered valid since the SDR scales inversely to overall mean metabolism (Isaac & Carbone, 2010). When we see that within groups

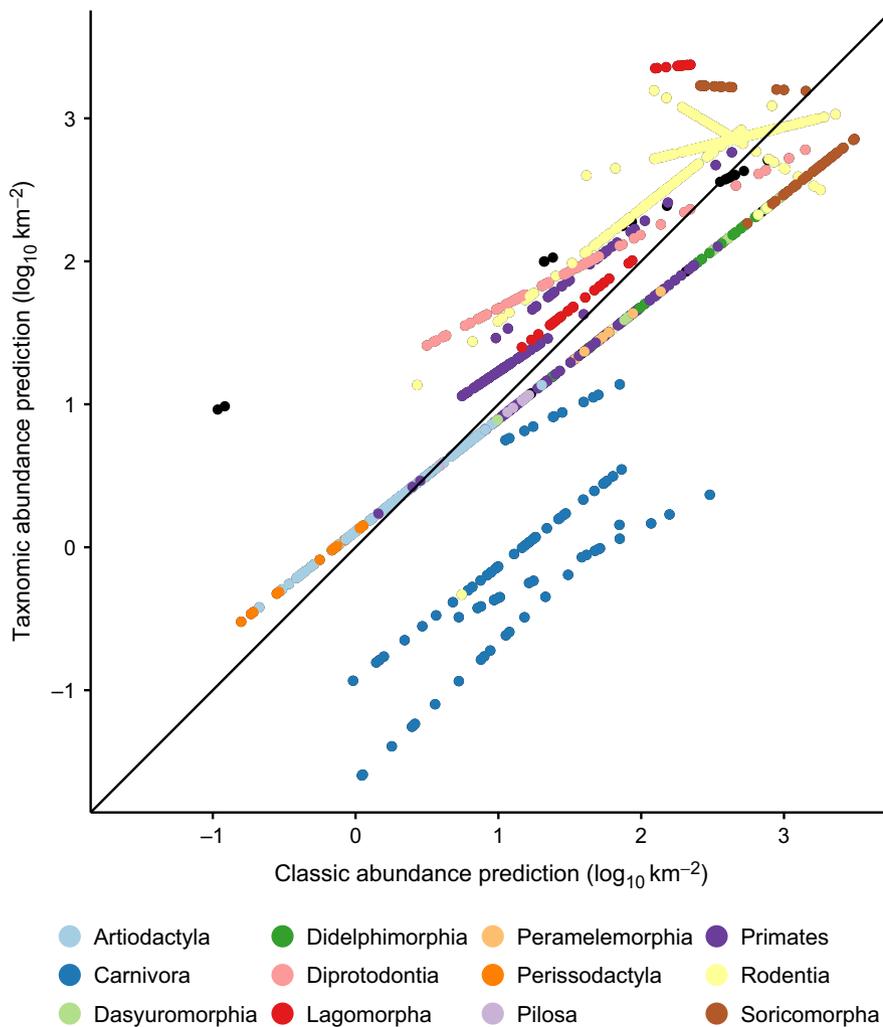


FIGURE 3 The estimated population density per species for the classical model and the phylogenetically structured model on a \log_{10} - \log_{10} scale. Points above the black line are species with densities predicted to be larger than predicted in the classic model, while points under the line are species with lower predicted densities than the classic model. For clarity, only orders with more than 10 species sampled are displayed in colour; the rest are black

the SDR is shallower than across all species combined, it indicates that either EER is flawed, or that metabolic scaling within groups is also less steep. Research on metabolic scaling within clades has shown variability in slopes from low slopes of 0.53–0.55 in soricids and rodents to as high as 0.87 in chiropterans, but show that most groups fall around 0.75 (Sieg et al., 2009), consistent with what others have found across a broader range of animal orders (Isaac & Carbone, 2010). We found that the SDR was less steep than that for most clades. This indicates an asymmetry in population-level energy use, where larger bodied species within clades succeed in acquiring more energy than the smaller bodied species. Munn et al. (2013) demonstrated this phenomenon in Australian marsupials, where metabolism (both field and basal metabolic rate) scales more steeply than density with body mass leading the total energy flux to be positively scaled with body mass.

A simulation study has shown how such a pattern could arise because smaller bodied species can maintain larger populations on less energy than larger bodied species (Damuth, 2007). When the slope is steeper than EER, of which we saw no indication, larger bodied species populations are living on the lower total energy use than smaller species. Extinction of the larger species is therefore more likely, and such extinctions will eventually drive the relationship back towards EER. In

contrast, slopes which are less steep than expected by the EER, as we found, indicate that smaller bodied species populations are using relatively less total energy. Since smaller bodied species populations can survive on far less energy than is required for a viable population of large species, it is possible to drive relationship towards a more positive relationship than the EER states (Damuth, 2007). Other studies point to the importance of size-structured competition in real communities, where large-bodied species take relatively more of the resource pool than populations of small-bodied species (DeLong, 2011; Hayward et al., 2010).

That larger species take a larger part of the energy pool could be an explanation for Cope's rule, which states that species within clades tend to increase in size through evolution (Stanley, 1973). This has been observed in mammals e.g. in Carnivora (Van Valkenburgh, 2004), where the mean and maximum body mass within clades increases through time. The within-group relations documented by our study imply that larger species do in fact occupy a larger part of the resource pool within clades. In the literature, there are plenty of examples of larger species outcompeting smaller species within guilds. In carnivores, we have an abundance of evidence of intra-guild competition and killing (Donadio & Buskirk, 2006; Palomares & Caro, 1999). For

example, grey wolves (*Canis lupus*) limit the density of coyotes (*Canis latrans*) through intra-guild predation and predation (Berger & Gese, 2007), which in turn limit the density and distribution of grey foxes (*Urocyon cinereoargenteus*) due to both greater ecological generalism and direct killing (Fedriani, Fuller, Sauvajot, & York, 2000). Intra-guild killing has also been shown in Eurasian lynx (*Lynx lynx*) killing red foxes (*Vulpes vulpes*), unrelated to feeding (Sunde, Overskaug, & Kvam, 1999). There is also a growing body of evidence for mesopredator (*V. vulpes* and *Felis catus*) regulation by top predators (*C. lupus* ssp. *dingo*) in Australia (Glen, Dickman, Soulé, & Mackey, 2007). Within rodents, there are several experimental examples on competitive suppression or exclusion by the larger species, e.g. a removal experiment shows an asymmetrical result where the smaller bank vole (*Myodes glareolus*) increased in density when the larger wood mouse (*Apodemus sylvaticus*) was removed, while no effect was found when the smaller species was removed (Fasola & Canova, 2000). Another experiment showed overall fitness decrease of bank voles due to the suppression by larger field voles (*Microtus agrestis*) (Eccard & Ylonen, 2002). Further, intrinsic species traits can also affect how larger species within a clade has a competitive advantage over smaller species without interaction: e.g. larger species are less susceptible to carnivore attacks and can therefore use areas not available to smaller species, and larger ruminants can also utilize more abundant low-quality food due larger guts and slower gut passage time (Demment & Van Soest, 1985; Hopcraft, Anderson, Pérez-Vila, Mayemba, & Olff, 2012).

The SDR did not become steeper with body mass span of a given group, but we did see stronger negative relationships for groups with average larger body masses (Figure 2), as Damuth (1991) also points out could be expected. That groups of larger bodied species have SDR closer to EER shows that the benefit of being large decreases with body mass. This might be explained by their larger home ranges, which are less easily defended and therefore have larger resource loss to neighbours (Jetz, 2004).

There was almost no difference throughout the phylogeny in the intercept of the SDR, with some notable exceptions. All members of the order Carnivora have population densities, several orders of magnitude below most other species irrespective of body mass. This follows expectation from their high trophic level, which could explain a factor 10–100 drop in available energy for any given body mass compared lower levels in the food chain (Lindeman, 1942). In general we did not see that population density of carnivorous groups scaled more steeply with body mass than in herbivorous groups, as other studies have found (Carbone & Gittleman, 2002; DeLong & Vasseur, 2012; Robinson & Redford, 1986). We do, however, see a trend potentially linked to diet variation within the carnivores. The order Carnivora has three distinct slopes, where the least carnivorous group had the least negative slope, whereas the most carnivorous has the most negative slope. This is consistent with mechanistic models which show that carnivory leads to a steeper SDR (Carbone et al., 2007). Further, the SDR of Carnivora has been accurately explained by Lotka–Volterra consumer–resource models (DeLong & Vasseur, 2012).

We can here conclude that there is good reason to use a clade-specific model in studies that wish to estimate population densities of

mammals from body mass, as have been suggested for other animal phyla. For example, studies using allometric relationships across phylogenetic groups could improve fit and predictions by incorporating phylogenetic differences in the relationship of their fit. Studies such as these focus primarily on megafauna effects since megafauna may have greater impacts on nutrient cycling because of their larger movement ranges and gut passage times (Doughty et al., 2013; Wolf et al., 2013). Models that do not account for phylogenetically varying relations neglect the effect of larger biomass consumption rates of larger species, since the nutrient flux in the classical size–density model will be offset by lower population densities. Our findings suggest an even larger impact with increasing body mass, possibly because larger species monopolise proportionally more of the energy in a system (Brown & Maurer, 1986).

Our conclusion that species-level population energy use increases with body mass is similar to what has previously been found in invertebrate communities (Ehnes et al., 2014), and support suggestions that the loss of larger predators can have greater ecosystem impacts than the loss of smaller species (DeLong et al., 2015). Our results therefore also support the use of a scaling coefficient of -0.58 for estimating population densities from body mass, lower than the classical -0.75 (e.g. used in Doughty et al., 2013). Therefore, studies that aim to estimate the impacts of megafauna loss using the classic Damuth model must be overly conservative in their estimates, since Damuth's model underestimates population sizes of large species. Our model provides a new method of relevancy for all studies predicting species densities on large scales. Our multi-level and -slope model is a substantial improvement over a single-slope model, where even the existence of predictive power has been questioned (Isaac et al., 2013). We encourage future studies to not assume a single slope across all mammals, but rather to use appropriate slopes for the specific clades, as our results show these to have better predictive ability. The same may well apply to other organism groups. Models for better estimates of natural population densities are vital for our understanding on global change in ecosystem function; our model here is a good first step. In future studies, further improvement of predictive ability could be made by including other important factors, e.g. energy availability (Carbone & Gittleman, 2002).

5 | SUMMARY

Classic models for estimating population density from body mass on a global scale often overlook important internal structure to this relationship. The relationship varies among phylogenetic groups, and notably is consistently shallower within phylogenetic groups. Overall, this pattern is inconsistent with the EER, but also suggests size-asymmetric monopolization of resources within groups, thereby also offering an explanation for Cope's rule (Rensch, 1948), the evolutionary tendency towards larger body mass within phylogenetic lineages. Further, our study shows that the use of group-specific density estimates should be used in studies that estimate densities from body mass, and that earlier studies likely have underestimated the densities of large-bodied species and thus their ecological effects.

ACKNOWLEDGEMENTS

R.Ø.P. and J.C.S. were supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC). S.F. was supported by the Danish Natural Science Research Council (#4090-00227). J.C.S. further sees this work as a contribution to his Carlsberg Foundation Semper Ardens project MegaPast2Future (CF16-0005). We thank the associate editor Shai Meiri, the reviewers John DeLong and Adam Munn, and two anonymous reviewers for helpful suggestions to an earlier version of the manuscript which substantially improved the paper.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; R.Ø.P. compiled the data; R.Ø.P. and S.F. analysed the data; R.Ø.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

DNA-based phylogeny data are available from <https://treebase.org/treebase-web/search/study/trees.html?id=11872> (Meredith et al., 2011) with additional families from <http://bios.au.dk/en/about-bioscience/organisation/ecoinformatics-and-biodiversity/data/#c303890> (Faurby & Svenning, 2015a). Species-level data on population density and body mass are available from PanTHERIA <http://esapubs.org/archive/ecol/e090/184/>, Jones et al., 2009), where family affiliation followed Wilson and Reeder (2005), except primate families where we followed Perelman et al. (2011). Results from individual families are available in Table S4, and can be used as exemplified in Appendix S2.

REFERENCES

- Agutter, P. S., & Wheatley, D. N. (2004). Metabolic scaling: Consensus or controversy? *Theoretical Biology & Medical Modelling*, 1, 13.
- Alfaro, M. E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D. L., ... Harmon, L. J. (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 13410–13414.
- Bengtsson, H. (2015). R.utils: Various Programming Utilities. Retrieved from <https://cran.r-project.org/package=R.utils>
- Berger, K. M., & Gese, E. M. (2007). Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology*, 76, 1075–1085.
- Bivand, R., Keitt, T., & Rowlingson, B. (2015). rgdal: Bindings for the Geospatial Data Abstraction Library. Retrieved from <https://cran.r-project.org/package=rgdal>
- Brown, J. H., & Maurer, B. A. (1986). Body size, ecological dominance and Cope's rule. *Nature*, 324, 248–250.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd ed. New York, NY: Springer-Verlag.
- Carbone, C., & Gittleman, J. L. (2002). A common rule for the scaling of carnivore density. *Science*, 295, 2273–2276.
- Carbone, C., Rowcliffe, J. M., Cowlshaw, G., & Isaac, N. J. B. (2007). The scaling of abundance in consumers and their resources: Implications for the energy equivalence rule. *The American Naturalist*, 170, 479–484.
- Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290, 699–700.
- Damuth, J. (1987). Interspecific allometry of population density in mammals and other animals: The independence of body mass and population energy-use. *Biological Journal of the Linnean Society*, 31, 193–246.
- Damuth, J. (1991). Of size and abundance. *Nature*, 351, 268–269.
- Damuth, J. (2007). A macroevolutionary explanation for energy equivalence in the scaling of body size and population density. *The American Naturalist*, 169, 621–631.
- DeLong, J. P. (2011). Energetic inequivalence in eusocial insect colonies. *Biology Letters*, 7, 611–614.
- DeLong, J. P., Gilbert, B., Shurin, J. B., Savage, V. M., Barton, B. T., Clements, C. F., ... O'Connor, M. I. (2015). The body size dependence of trophic cascades. *The American Naturalist*, 185, 354–366.
- DeLong, J. P., & Vasseur, D. A. (2012). A dynamic explanation of size-density scaling in carnivores. *Ecology*, 93, 470–476.
- Demment, M. W., & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, 125, 641–672.
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, 345, 401–406.
- Donadio, E., & Buskirk, S. W. (2006). Diet, morphology, and interspecific killing in carnivora. *The American Naturalist*, 167, 524–536.
- Donlan, J., Berger, J., Bock, C. E., Bock, J. H., Burney, D. A., Estes, J. A., ... Greene, H. W. (2006). Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *The American Naturalist*, 168, 660–681.
- Doughty, C. E., Wolf, A., & Malhi, Y. (2013). The legacy of the Pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geoscience*, 6, 761–764.
- Eccard, J. A., & Ylonen, H. (2002). Direct interference or indirect exploitation? An experimental study of fitness costs of interspecific competition in voles. *Oikos*, 99, 580–590.
- Ehnes, R. B., Pollierer, M. M., Erdmann, G., Klärner, B., Eitzinger, B., Digel, C., ... Brose, U. (2014). Lack of energetic equivalence in forest soil invertebrates. *Ecology*, 95, 527–537.
- Fasola, M., & Canova, L. (2000). Asymmetrical competition between the bank vole and the wood mouse, a removal experiment. *Acta Theriologica*, 45, 353–365.
- Faurby, S., & Svenning, J.-C. (2015a). A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Molecular Phylogenetics and Evolution*, 84, 14–26.
- Faurby, S., & Svenning, J.-C. (2015b). Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns (ed G Stevens). *Diversity and Distributions*, 21, 1155–1166.
- Faurby, S., & Svenning, J.-C. (2016). Resurrection of the Island rule: Human-driven extinctions have obscured a basic evolutionary pattern. *The American Naturalist*, 187, 812–820.
- Fedriani, J., Fuller, T., Sauvajot, R., & York, E. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia*, 125, 258–270.
- Galetti, M., & Dirzo, R. (2013). Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation*, 163, 1–6.
- Glen, A. S., Dickman, C. R., Soule, M. E., & Mackey, B. G. (2007). Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. *Austral Ecology*, 32, 492–501.
- Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER: Investigating evolutionary radiations. *Bioinformatics*, 24, 129–131.
- Hayward, A., Kolasa, J., & Stone, J. R. (2010). The scale-dependence of population density-body mass allometry: Statistical artefact or biological mechanism? *Ecological Complexity*, 7, 115–124.
- Hijmans, R. J. (2015). raster: Geographic data analysis and modeling. Retrieved from <http://cran.r-project.org/package=raster>

- Hopcraft, J. G. C., Anderson, T. M., Pérez-Vila, S., Mayemba, E., & Olf, H. (2012). Body size and the division of niche space: Food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, 81, 201–213.
- Isaac, N. J. B., & Carbone, C. (2010). Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecology Letters*, 13, 728–735.
- Isaac, N. J. B., Storch, D., & Carbone, C. (2013). The paradox of energy equivalence. *Global Ecology and Biogeography*, 22, 1–5.
- Jetz, W. (2004). The scaling of animal space use. *Science*, 306, 266–268.
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., ... Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648–2648.
- Kleiber, M. (1947). Body size and metabolic rate. *Physiological Reviews*, 27, 511–541.
- Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399–417.
- Macdonald, D. W., & Norris, S. (Eds.) (2001). *The new encyclopedia of mammals*. Oxford, UK: Oxford University Press.
- Mazerolle, M. J. (2015). AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). Retrieved from <http://cran.r-project.org/package=AICcmodavg>
- Meredith, R. W., Janecka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., ... Murphy, W. J. (2011). Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science*, 334, 521–524.
- Munn, A. J., Dunne, C., Müller, D. W. H., & Clauss, M. (2013). Energy inequivalence in Australian marsupials: Evidence for disruption of the continent's mammal assemblage, or are rules meant to be broken? *PLoS ONE*, 8, 1–5.
- Nagy, K. A. (2005). Field metabolic rate and body size. *Journal of Experimental Biology*, 208, 1621–1625.
- Nee, S., Read, A. F., Greenwood, J. J. D., & Harvey, P. H. (1991). The relationship between abundance and body size in British birds. *Nature*, 351, 312–313.
- Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, 153, 492–508.
- Paradis, E., Claude, J., & Strimmer, K. (2004). A[PE]: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.
- Perelman, P., Johnson, W. E., Roos, C., Seuánez, H. N., Horvath, J. E., Moreira, M. A. M., ... Pecon-Slattery, J. (2011). A molecular phylogeny of living primates. *PLoS Genetics*, 7, e1001342.
- Peters, R. H. (1983). *The ecological implications of body size*. Cambridge, UK: Cambridge University Press.
- R Core Team. (2015). R: A language and environment for statistical computing. Vienna, Austria. Retrieved from <http://www.r-project.org/>
- Rensch, B. (1948). Histological changes correlated with evolutionary changes of body size. *Evolution*, 2, 218.
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.
- Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., ... Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, 1, e1400103.
- Robinson, J. G., & Redford, K. H. (1986). Body size, diet, and population density of neotropical forest mammals. *The American Naturalist*, 128, 665–680.
- Russo, S. E., Robinson, S. K., & Terborgh, J. (2003). Size-abundance relationships in an Amazonian bird community: Implications for the energetic equivalence rule. *The American Naturalist*, 161, 267–283.
- Ryan, T. P. (2008). *Modern regression methods*, 2nd ed. New York, NY: John Wiley & Sons.
- Sandom, C., Faurby, S., Sandel, B., & Svenning, J.-C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133254.
- Sieg, A. E., O'Connor, M. P., McNair, J. N., Grant, B. W., Agosta, S. J., & Dunham, A. E. (2009). Mammalian metabolic allometry: Do intraspecific variation, phylogeny, and regression models matter? *The American Naturalist*, 174, 720–733.
- Stanley, S. (1973). An explanation for Cope's rule. *Evolution*, 27, 1–26.
- Sunde, P., Overskaug, K., & Kvam, T. (1999). Intraguild predation of lynxes on foxes: Evidence of interference competition? *Ecography*, 22, 521–523.
- Turvey, S. T., & Fritz, S. A. (2011). The ghosts of mammals past: Biological and geographical patterns of global mammalian extinction across the Holocene. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366, 2564–2576.
- Van Valkenburgh, B. (2004). Cope's rule, hypercarnivory, and extinction in North American canids. *Science*, 306, 101–104.
- White, C. R., Cassey, P., & Blackburn, T. M. (2007). Allometric exponents do not support a universal metabolic allometry. *Ecology*, 88, 315–323.
- White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology & Evolution*, 22, 323–330.
- White, C. R., & Kearney, M. R. (2014). Metabolic scaling in animals: Methods, empirical results, and theoretical explanations. *Comprehensive Physiology*, 4, 231–256.
- Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York, NY: Springer.
- Wickham, H. (2015). stringr: Simple, consistent wrappers for common string operations. Retrieved from <https://cran.r-project.org/package=stringr>
- Wickham, H., & Francois, R. (2015). dplyr: A grammar of data manipulation. Retrieved from <https://cran.r-project.org/package=dplyr>
- Wilson, D. E., & Mittermeier, R. A. (Eds.) (2009). *Handbook of the mammals of the world - volume 1 carnivores*. Barcelona, Spain: Lynx Edicions.
- Wilson, D., & Reeder, D. (2005). *Mammal species of the world: A taxonomic and geographic reference*, 3rd ed. Baltimore, MD: Johns Hopkins University Press.
- Wolf, A., Doughty, C. E., & Malhi, Y. (2013). Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. *PLoS ONE*, 8, e71352.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Pedersen RØ, Faurby S, Svenning J-C. Shallow size–density relations within mammal clades suggest greater intra-guild ecological impact of large-bodied species. *J Anim Ecol*. 2017;00:1–9. <https://doi.org/10.1111/1365-2656.12701>