Ecological modelling, size distributions and taphonomic size bias in dinosaur faunas: a comment on Codron et al. (2012)

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1. Introduction
Codron et al. [1] invoke an ecological model of size-specific competition in dinosaurs to explain an apparent bimodal distribution within Dinosauria, and find ‘intermediate-sized taxa’ (1–1000 kg) are prone to extinction. Although the authors take an interesting approach, we argue that the model is not an adequate analogue of ecological systems, ignores fundamental ecological interactions, and the raw data chosen to represent dinosaur size distribution are size-biased, not reflecting true dinosaurian faunas. Our concerns are discussed in the following sections.

2. Model
First, the predicted size distributions could not emerge from the proposed mechanisms if the model is put in a more realistic dynamical context. The model assumes constant survivorship schedules and fecundity for each species, and competition is only interspecific. Under these assumptions, a population would either grow exponentially or decline towards extinction, owing to the absence of intraspecific regulation. Persistent differences in growth rate between populations would lead to the complete domination by one species. The smallest would have probably benefited by its higher fecundity, while having no survival disadvantage as the survivorship functions were standardized across species [1]. The size distributions reported in Codron et al. [1] may look realistic, however, they were obtained from just one model iteration and cannot represent either equilibrium states or long-term averages, thereby questioning their ecological meaning.

Second, the model does not incorporate trophic differentiation (e.g. herbivores/carnivores), and treats competition as the only ecological interaction shaping abundances. Carnivores predominated in the intermediate-size bin (45%) relative to the more than 1000 kg bin (14%; p-value < 0.001), and would benefit from predation upon other species, instead of only suffering negative effects as assumed in a purely competitive model. Ecological models intending to explain the size distribution of such a large collection of taxa should incorporate the possibility of multiple trophic levels.

3. Size distribution
The size distribution is based on sparse sampling of globally distributed dinosaurs that span the entire Mesozoic (approx. 140 Ma). This violates the assumptions of the model; the sample is an incomplete, biased, multi-faunal composite that does not reflect true faunal-level size distributions, the ecological level simulated in the model. For example, a maximum of 20/123 dinosaur species included may have co-occurred in space and time (Morrison Formation), 65 per cent of formations sampled are represented by a single species, and the median and mode number...
of species per formation is 1 [2]. When examined at the faunal level, the best-sampled dinosaur assemblage (the Dinosaur Park Formation, DPF) shows higher diversity in the 1–1000 kg range than the more than 1000 kg range (figure 1a) [3].

If a holistic Mesozoic distribution, rather than faunal, is desired, the dataset is taxonomically and size-biased. The dataset is understandably restricted to published mass estimates; however, dinosaur mass estimation studies are generally biased towards large taxa. This bias is evident here, where approximately 30 per cent of sauropod genera (10/33) are multispecific, yet less than 3 per cent (1/42) of ornithischian genera are represented by more than one species, when approximately 40 per cent of these ornithischians are considered multispecific [2]. Essentially, the sample of Codron et al. [1] considers sauropods at the species level but ornithischians at genus level, thereby artificially increasing the diversity of larger taxa, resulting in a significant positive correlation between mass and generic diversity \((p\text{-value} = 0.016)\). Furthermore, smaller taxa are generally less complete than larger taxa [3], and the mass estimates used are largely based on volumetric reconstructions requiring complete skeletons, resulting in systematically under-sampling small taxa.

4. Taphonomy

Codron et al. [1] state that taphonomic biases could not account for the observed size distribution, and that increased sampling would not change the distribution. However, taphonomic biases play a major role. Recent work on the DPF [3] determined that body mass is significantly correlated with completeness, taphonomic mode, time to discovery/description and familial diversity. These correlations, and a negatively skewed size distribution, can be explained by strong preservational biases against small-bodied vertebrates within continental deposits [4]. Within assemblages, large taxa are generally found first and small taxa later [3], causing the skewness of the distribution to reduce through time (figure 1a,b), the condition required by Codron et al. [1] (see the electronic supplementary material, figure S6) to make the distribution positively skewed with increased sampling. Illustrating this, since 1971, the DPF assemblage has nearly doubled in diversity (increased 78%), with 92 per cent of these taxa being less than 1000 kg [3], similar to the 98 per cent Codron et al. [1] obtained by arbitrarily doubling the sample (a value that decreases with increased sampling). Finally, a mechanism of competition with mammals fails to explain the rarity of both articulated mammals and juveniles of large dinosaur taxa in dinosaur assemblages [3].

5. Conclusions

The application of ecological modelling to the fossil record is commendable, as it sheds light on ecosystem dynamics in a changing world, like we face today. However, these models must incorporate as much rigour as possible, and we urge caution against taking the fossil record at face value, especially when models infer no-analogue ecosystems/ecologies.

References