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Concern for megafauna is increasing among scientists and non-scientists. Many studies have emphasized that megafauna play prominent ecological roles and provide important ecosystem services to humanity. But, what precisely are "megafauna"? Here we critically assess the concept of megafauna and propose a goal-oriented framework for megafaunal research. First, we review definitions of megafauna and analyze associated terminology in the scientific literature. Second, we conduct a survey among ecologists and paleontologists to assess the species traits used to identify and define megafauna. Our review indicates that definitions are highly dependent on the study ecosystem and research question, and primarily rely on ad hoc size-related criteria. Our survey suggests that body size is crucial, but not necessarily sufficient, for addressing the different applications of the term megafauna. Thus, after discussing the pros and cons of existing definitions, we propose an additional approach by defining two function-oriented megafaunal concepts: "keystone megafauna" and "functional megafauna", with its variant "apex megafauna". Assessing megafauna from a functional perspective could challenge the perception that there may not be a unifying definition of megafauna that can be applied to all eco-evolutionary narratives. In addition, using functional definitions of megafauna could be especially conducive to cross-disciplinary understanding and cooperation, improvement of conservation policy and practice, and strengthening of public perception. As megafaunal research advances, we encourage scientists to unambiguously define how they use the term "megafauna" and to present the logic underpinning their definition.

Keywords:

apex predators, body size, etymology, functional traits, keystone species, large animals, megaherbivores

1. Introduction

Prehistoric art provides evidence that megafauna (literally, “large animals”; see Appendix S1 for the etymology and popular definitions of this term) have fascinated humans since our origins (e.g. [1]). The eminent nineteenth century naturalist Alfred Russel Wallace [2] referred to megafauna as “the hugest, and fiercest, and strangest forms”. A hundred and forty plus years later, however, megafaunal research still lacks a unifying framework for the use of this term, which has diverged in the development of disciplines as diverse as wildlife biology, oceanography, limnology, soil ecology, evolutionary biology, conservation biology, paleontology, and anthropology. Thus, definitions in the scientific literature include disparate combinations of species: from the smallest organisms readily visible in photographs to the largest vertebrates ever on earth (e.g. [3-5]; Fig. 1, Appendix S2). Given the great sociocultural significance of megafauna [6-7], the ubiquity of the megafauna concept in addressing profound and varied scientific questions [8-11], and the multiple threats that jeopardize large animals [12-14], a re-examination of the concept is warranted [15].

Here we review the concept of megafauna and propose a goal-oriented framework for megafauna research, which may support scientific endeavors, improve conservation policy and practice, and strengthen public perception. To do this, we adopt a two-pronged approach. First, we review the scientific literature to i) examine the different definitions of megafauna and ii) analyze the terminology commonly associated with the concept of megafauna. Second, we carry out a survey among ecologists and paleontologists to iii) assess the traits of the species they consider as megafauna and iv) identify the key criteria that should define megafauna. The goal of this survey is to enhance our understanding of how researchers working with megafauna conceptualize data that already exist in the scientific literature. Based on insights gained from the review and survey, we propose a working scheme for the use of the megafauna concept, discuss pros and cons of different definitions, and provide recommendations for advancing interdisciplinary megafaunal research.

2. Literature review

(a) Megafauna definitions

We conducted a systematic review of existing megafauna definitions in the scientific literature (276 articles reviewed; see Appendix S3 for a complete list of references and Appendix S4 for the searching methods). The majority of megafauna articles focused on terrestrial species (55% of the papers; mainly concerned with prehistorical times) and marine ecosystems (52%; mostly referencing recent times), with very few articles dealing with freshwater megafauna (1%; Figs. 2 and S1). Our search did not uncover any paper dealing with soil megafauna, although soil ecologists use this term as well [16].

When considering whether the reviewed papers provided definitions of the term megafauna and how such definitions were justified, strikingly, 74% of the identified articles did not provide an explicit definition of megafauna. Among the remaining 26% (i.e. the 71 articles using a definition), 45% did not provide any argument or reference to support the definition, whereas 25% provided references, 20% specified distinct arguments, and 10% offered both references and arguments (Fig. 2). Definitions, when provided, were somewhat idiosyncratic (i.e. varied according to the study system) and relied on *ad hoc* size-related criteria (see Table S1 and Fig. 1; for a complete list of definitions, see Table S2).

Definitions of the megafauna concept were primarily of two types. The first group used an explicit, albeit generally arbitrary, body-size threshold above which a species is considered megafauna. Among the definitions of this group, a distinction can be made between those that used a *mass*-based threshold and those that used a *length*-based threshold.

On the one hand, mass thresholds ranging from around10 kg to 2 tons have been widely used in a terrestrial context to define megafauna [5]. Paleontologists, for example, have often referred to the megafauna definition provided by Martin [4]: i.e. animals, usually mammals, over 100 pounds (c. 45 kg; e.g. [17-20]). Recently, this megafauna definition has also been applied to marine environments [21], and several authors have adopted a slightly lower threshold (30 kg) to define freshwater megafauna [14,22]. Some terrestrial megafauna studies (e.g. [23]) are based on the megaherbivore concept of Owen-Smith [24,25], restricted to herbivores exceeding 1,000 kg in adult body mass according to distinctions from smaller herbivores in a number of ecological features. Other authors have applied guild-dependent thresholds for terrestrial megafauna (e.g. ≥ 100 kg for herbivores and ≥15 kg for carnivores) [13]. Finally, Hansen and Galetti [26] emphasized the importance of taking into account the ecological context too: "one ecosystem's mesofauna is another ecosystem's megafauna". This means that relatively small species can also be considered megafauna, as long as they are, or were, among the largest species occurring in a given area.

On the other hand, papers in which the megafauna definition relies on body length are characterized by much smaller size thresholds. These studies have been common in the context of benthic and epibenthic environments, where marine megafauna are usually defined as animals visible on seabed photographs (normally over c. 1 cm) or caught by trawl nets (e.g. [3,27-29]). Furthermore, soil ecologists have used the term megafauna to encompass those species above 20 mm in length that exert strong influences on gross soil structure [16].

The second major group of papers included those that relied on body size only implicitly – i.e. considering megafauna as certain clades or groups of species that are relatively large-sized within the focal study system. These articles normally concerned aquatic environments. Several studies of marine benthic megafauna focused on particular taxonomic groups, such as decapods and fish [30,31]. In a marine pelagic context, some authors focused on the largest sea-dwelling species – i.e. marine mammals, sea turtles and seabirds (termed "air-breathing marine megafauna") [32], along with sharks, rays, and other predatory fish (e.g. [33-35]) and even polar bears and cephalopods [36]. In freshwater ecosystems, crustaceans, amphibians, and fish were classified as megafauna by some authors [37]. Other work has focused on particular functional groups, such as higher/apex marine predators [34,36]. It is noteworthy that the term megafauna has been virtually ignored for dinosaurs and, until recently, barely used for mammals other than those of the Late Pleistocene period. Instead, dinosaur experts and wildlife biologists prefer using the species, clade, or group name rather than the more general term megafauna (e.g. [38-41]).

(b) Terminology associated with megafauna research. As demonstrated above, the megafauna definition may differ according to the studied ecosystem. In this section, we highlight the fact that definitions also differ depending on the ecological and biological questions of the study. To this end, we created semantic networks based on the terms included in the title and abstract of the 276 reviewed articles, and identified thematic clusters based on co-occurrence of these terms (see Appendix S4 for methodological details). From this, we obtained three major megafauna research clusters (Figs. S1 and S2). The first cluster included articles on terrestrial megafauna and mainly corresponded to the study of the extinction of Pleistocene megafauna: its timing, causes, and impacts on ecosystems (e.g. [17,42,43]). The terms included in this terrestrial cluster were related to the megafauna definitions provided by Owen-Smith [24] and, mostly, by Martin [4]. The second cluster concerned extant benthic and epibenthic marine megafauna: the characterization of their communities [44-46], the environmental factors that determine their composition [47-49], and their ecological properties [9,30]. In general, the terms of this cluster were linked to definitions not specifying a body-size threshold [3,32]. The third cluster covered studies on the impacts of bycatch in fisheries, mainly on marine air-breathing vertebrates [12,32,50], as well as on strategies for their conservation [51,52].

These clusters were not totally disconnected, as Figure S2 reveals several bridging terms that have the potential to link different clusters in the network [53]. For example, terrestrial and pelagic clusters were recently connected by research on the conservation of threatened vertebrates in relation to global change [54-57]. In this case, important bridging terms were *impact*, *climate* and *review* (Figure S2). Similarly, benthic and pelagic clusters were interlinked by research on biodiversity conservation in marine environments [58], with *biodiversity*, *use*, and *fish* being bridging terms (Figure S2). Thus, our lexical analysis revealed a growing, albeit still weak, tendency to connect the different conceptual clusters that make up the main megafauna research network. Our findings indicate that the increasing concern about the causes and consequences of human impacts on the conservation of large animals has a promising potential to foster collaboration among researchers focusing on different ecosystems (e.g. [59]).

3. Survey of researchers

Given that the majority of the papers using the concept megafauna do not provide a definition of this term, we surveyed researchers working on megafauna to get a better understanding of how they understand the concept when using it.

(a) Species traits associated with megafauna. To understand the species traits (i.e. taxonomy, biology, ecology, behavior, conservation status and popularity; see Tables S3 and S4 for more details) that researchers associated with megafauna, we asked ecologists and paleontologists (n=93 respondents) to fill in a questionnaire that included photos of 120 animal species (Table S3). In the questionnaire, respondents had to specify which species they considered as megafauna. Then we ranked species traits according to their capacity to predict the probability that the respondents would classify these species as megafauna (see Appendix S4 and Tables S3-S5 for methodological details). We found that adult body mass was by far the most important trait, followed by taxonomic group; all other traits analyzed were of minor importance (Fig. S3a). According to a Generalized Linear Model (GLM), body mass and taxonomic group accurately predicted the probability that a species would be classified as megafauna ($F_{15,104}$=72.79, P<0.001, R^2=0.90). Larger species were more likely to be considered as megafauna, following a sigmoidal (logistic) relationship (Fig. 3a). However, the slope of this relationship varied among taxonomic groups, as reflected by the significance of the interaction coefficient ($F_{7,104}$=4.13, P<0.001; Fig. 3b). Mammals, birds and reptiles had steeper slopes, fish species had intermediate values, and amphibians and invertebrates exhibited shallower slopes (Fig. 3b). Thus, for a given body mass, the classification of a species as megafauna depended on its taxonomy, likely reflecting a bias arising from the prominence of terrestrial vertebrate species in scientific research or the general (average) size of the species in the different groups. These patterns were consistent despite variability in respondents' characteristics such as age and expertise (see Appendix S4 and Figs. S3b and S4).

(b) What criteria should define megafauna? We also used the questionnaire to assess researchers' recommendations for defining megafauna. We explicitly asked the respondents to choose among six criteria needed to define megafauna: body mass, taxonomy, ecological function, ecological context, life history traits, and extinction risk. Respondents could choose as many of them as they wanted and could also name additional criteria (see Appendix S4 for methodological details). Among the criteria provided, 92% of respondents identified body mass as the key criterion (Fig. S5). However, body mass was very often (86% of respondents) chosen in combination with other criteria (mean total number ±SD of criteria selected by respondents: 2.9±1.3). This suggests that body size alone is insufficient for defining megafauna. Extinction risk was rarely taken into account in defining megafauna, probably because respondents identified this criterion as a circular and extrinsic argument or because it cannot be applied to extinct taxa, which frequently contributed to megafauna research. The selection of criteria was again barely affected by respondents' characteristics (see Table S6, Figs. S6 and S7). Only 7% of the respondents suggested alternative criteria to define megafauna. These additional suggestions (namely species' volume, habitat requirements, "importance" within the food web, ecological "status", ecosystem and temporal context) were closely related to the six criteria already provided in the questionnaires.

4. Rethinking the megafauna concept

As evidenced in the literature, the term megafauna has been widely applied in ecological and paleontological research. However, our literature review revealed that researchers have been adopting a context-dependent use of the term, most often using operational definitions with varying and largely arbitrary body-size thresholds and taxonomic groups as proxies, depending on the study system and research question. Only a few studies have explicitly emphasized the functional importance of the largest species in a given ecosystem and over a specific period [16,24,26]. In addition, our survey of researchers provided consensus that body size (e.g. body mass) is a crucial descriptor, but not necessarily sufficient, for addressing the different applications of the term megafauna.

When rethinking the megafauna concept, the primary question that should arise is whether we need a threshold. As argued next, there are reasons that justify the search for non-arbitrary thresholds and that indicate that these are, in fact, achievable, at least in some cases. First, avoiding a threshold-based definition would make the use of the megafauna term largely impractical. Second, clear breakpoints in either body size or ecological features have been identified for some animal groups (see below). Thus, a follow-up agenda exploring whether corresponding thresholds do, or do not exist in different groups of organisms is needed.

Below, we reconsider the megafauna concept and propose a general working scheme for its use in various ecological and evolutionary contexts. These include either natural systems (i.e. before *Homo sapiens* began to defaunate them [26]) or systems that have been impacted by human-mediated extinctions and introductions of wild and domestic species [60].

(a) The largest. The central challenge in using a threshold concept to define megafauna – as is also the case for other popular ecological terms such as keystone, flagship or umbrella species (see [61]) – is how to empirically establish a metric (e.g. body mass, or body length) and a corresponding value above which an animal may be effectively regarded as megafauna. This value needs to be placed within a community or an ecosystem context to make any sense. We could circumvent this threshold concept by simply defining "megafauna" as *the subset of largest species in a community or an ecosystem*. To answer the critical question of what the threshold should be, we could follow two approaches. In its simplest form, we could refer to the *single* largest species. Going beyond this, a transparent definition of "subset" requires exploring the frequency distributions of body size (e.g. body mass) values within the community or ecosystem under study, and determining a breakpoint in body size. Although body size data are not available for all animal species within an ecosystem, this information is often biased towards larger species [62].

Another approach would be to focus on particular clades or guilds to restrict the species pool under consideration, facilitating the identification of megafauna. Thus, "clade- or guild-specific megafauna" would be *the subset of largest species of a given clade or guild in a community or an ecosystem*. This implies acknowledging that the megafauna within a clade or guild do not necessarily include the largest species in the ecosystem. Within phylogenetic lineages, body mass is skewed towards smaller sizes, with larger species being almost invariably rarer than smaller species [24,63,64]. For instance, >90% of sub-Saharan vertebrate herbivore species weigh <500 kg, while only ca. 5% of species has a body mass exceeding 1000 kg [24]. However, most animals, with the exceptions of birds and mammals, grow through prolonged ontogenetic stages. For instance, giant bluefin tuna (*Thunnus thynnus*) cover 5-6 orders of magnitude in mass from larvae to adult [65]. Whether scales of ontogenetic change cause taxa with long developmental changes in size to have a shallower slope than in cases where the break might be more obvious needs to be investigated.

(b) Operational definitions. We refer to operational definitions as those using specific body size criteria but that are not based on a body size distribution, namely most definitions enumerated in Tables S1 and S2. A prominent example is Martin's definition of megafauna (c. 45 kg [4]), which can be seen as a human-centered perspective, partitioning animals similar or larger in size than humans from those smaller. These definitions have been the core of the megafauna scientific literature, most likely because of their obvious practical advantages. For instance, they facilitate data processing and analysis, and they may normally apply to both extant and extinct species.

A main feature of operational definitions is their strong dependence on the research discipline, which makes them highly applicable to conduct comparisons within disciplines but strongly limits their trans-disciplinary use. However, some attempts have recently been made to move certain operational definitions beyond the original research context. In particular, the application or adaptation of Martin's megafauna standard [4] to aquatic environments [14,21,22] represents a connection among terrestrial, marine pelagic, and freshwater megafauna research. In addition, soil and marine benthos megafauna research, which is concerned with communities characterized by relatively small-sized species, may be closely linked because they use similar – body length-based – definitions. However, a weak connection between terrestrial/pelagic/freshwater and soil/benthos megafauna research is anticipated due to their very different conceptions of "mega" (see Fig. 1). Nevertheless, while operational definitions could seem conducive to multidisciplinary coordination and collaboration in megafauna research (e.g. to undertake biodiversity inventories and conservation status assessments), the application of operational thresholds to different disciplines relies on the unrealistic assumption that body mass (and functional traits; see below) distributions are comparable among different communities or ecosystems. Thus, operational definitions, which are inherently arbitrary, are at risk of including or ignoring species that respectively should or should not be considered as megafauna, in both intra- and cross-disciplinary approaches.

(c) Functional definitions: looking for a new approach. While some existing definitions go beyond body size (e.g. [16,26]), we largely lack a conceptual definition of megafauna that integrates the ecological function and functional traits of a species along with its size (e.g. represented by body mass; but see 24; see Fig. 4). In this section, we present a function-oriented framework for the use of the megafauna concept, therefore responding to the general perception of researchers that body size alone is an incomplete descriptor of megafauna (see above). Here, unlike previous definitions, which were primarily based on body size, breakpoints are associated with biological and ecological features/qualities that vary with body size. These functional concepts can be applied to different communities and ecosystems, from terrestrial and soil to marine and freshwater systems, and are, at least *a priori*, not biased towards vertebrates or invertebrates.

The first concept, which combines a body-size based megafauna definition with the keystone species concept [66], assumes that the largest species in an ecosystem generally have disproportionally large effects in the structure and functioning of their communities and ecosystems, both in magnitude and in the spatial and temporal heterogeneity they create [67]. In line with this concept, a disproportionate increase in energy use (e.g. represented by population biomass) in relation to body mass increases has been identified in many vertebrate [24,63] and invertebrate phylogenetic groups [64]. Accordingly, "keystone megafauna" would be *the subset of animals among the largest in size that have consistently strong effects on the structure or functioning of a community or an ecosystem*. Smaller animals would exhibit high variation in relation to the effects that they exert on their ecosystems, from very weak to very strong (Fig. 4a). All species that have a strong influence on their ecosystems, in general stronger than expected by their abundance or biomass, may be regarded as keystone species [61,66,68-70], but only those with relatively large body size should be termed as keystone megafauna (Fig. 4b). In practice, this concept of megafauna may require extensive ecological knowledge of the biotic communities and their functioning [68], which would encourage a research agenda to better understand the ecological roles of large species [61,68]. However, the use of proxies for ecological effects, such as size-density relationships [63], could greatly simplify the identification of keystone megafauna within different clades or guilds, including extinct fauna. Comparing the magnitude, variability and skewness, as well as related breakpoints, of these relationships (see Fig. 4a for a general formulation) among different animal groups seems an exciting avenue for future megafauna research.

The second functional concept for megafauna is referred to as "functional megafauna", which can be defined as *the subset of largest species of a given clade or guild that have distinctive functional traits* (*sensu* [71]). An important practical advantage of this concept is that the identification of megafauna could be relatively easily accomplished because it only needs a basic ecological knowledge. Ideally, studies should focus on traits with high inter-specific variation, that may be easily measurable and, therefore, comparable among the members of a given animal group. For instance, within terrestrial mammals, megaherbivores differ from smaller herbivores in almost all ecological and life history aspects (e.g. age at first conception, birth interval and gestation time [24]). Also in terrestrial mammals, there is a functional transition associated with a number of life history traits between carnivores exceeding an average mass of 13-16 kg and those carnivores of smaller size [72]. In other, less studied cases, the key question is, of course, to define the subset of functional traits to be explored.

A feasible variant of the functional megafauna concept would be "apex megafauna": *animals so large that they have escaped most non-anthropogenic predation as adults*. This concept is related to the megaherbivore and apex predator concepts [24,25,72] and can be applied to humans too. In Africa, herbivores larger than 150 kg are subject to reduced predation rates than smaller mammalian prey in some areas [73], but only for herbivores exceeding 1000 kg predation is a consistently negligible cause of adult mortality [24,73,74]. Within the order Carnivora, an average mass of c. 15 kg corresponds to the transition between extrinsic- and self-regulation [72].

5. Conclusions

Our comprehensive literature review and survey of researchers point to a dichotomy between the need to establish operational body-size thresholds and a more functional definition of megafauna. This confirms that the concept of megafauna is far from simple, and, probably, it should not be simplified either. However, we highlight that assessing megafauna from a functional perspective could challenge the perception that there may not be a unifying definition of megafauna that can be applied to all eco-evolutionary contexts and scientific approaches. The functional framework we present, which arises from the perception of megafauna researchers that body size is insufficient to capture the varied eco-evolutionary ramifications of megafauna, could help to reach ecological generality and to minimize the arbitrariness of operational and other non-functional definitions, which present ambiguity problems even at the within-discipline level. This requires exploring thresholds in ecological functions and functional traits of animals pertaining to different clades, guilds, communities and ecosystems. Addressing this challenge could help to broaden out megafauna research, and provides an opportunity to increase our biological understanding of megafauna too. Interestingly, important advances have already been made in terrestrial mammalian systems, so that herbivores exceeding 1000 kg and carnivores above an average body mass of c. 15 kg could be considered as paradigmatic examples of both functional and apex megafauna. Until studies exploring other animal groups and ecosystems are available, we encourage scientists to define megafauna unambiguously and clearly present the distinct logic behind their definition in every megafaunal study. Only by being explicit and appropriately contextualizing the concept will we be able to reach the needed conceptual disambiguation.

We found that cross-disciplinary investigations of megafauna are virtually non-existent (but see e.g. [59]), which may be due, in part, to the fact that most megafauna definitions in the scientific literature are strongly context-dependent. The existence of recurrent topics among megafauna researchers concerned with different animal taxa and ecosystems, such as the conservation of threatened megafauna, compels the search for unifying tools. Using functional, rather than arbitrary, operational definitions, would facilitate understanding and cooperation among wildlife, evolutionary and conservation biologists, marine and soil ecologists, limnologists and paleontologists, and eventually promote cutting-edge research across systems, disciplines, and geographic boundaries [75,76].

Data accessibility. Data and code to replicate analyses are available on Dryad Digital Repository: https://doi.org/10.5061/dryad.dv41ns1v3.

Authors' contributions. M.M., J.A.S.Z., J.A.D., E.R. and K.T. conceived and designed the study; M.M. made the literature review and collected data; M.M. and Z.M.R. created the databases; M.M., C.G.C. and B.M.L. conducted the semantic and statistical analyses, with critical inputs from all co-authors; M.M. drafted the manuscript; all authors participated in discussions, contributed critically to data interpretation and manuscript reviewing, and gave final approval for publication.

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References

1. Gunn RG, Douglas LC, Whear RL. 2011. What bird is that? Identifying a probable painting of *Genyornis newtoni* in western Arnhem Land. Australian Archaeology 73: 1-12.
2. Wallace AR. 1876. The Geographical Distribution of Animals. Harper.
3. Grassle JF, Sanders HL, Hessler RR, Rowe GT, McLellan T. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible *Alvin*. Deep-Sea Research 22: 457-481.
4. Martin PS. 1967. Prehistoric overkill. Pages 75-120 in Martin PS, Wright HE, eds. Pleistocene extinctions: The search for a cause. Yale Univ. Press.
5. Wroe S, Field JH, Archer M, Grayson DK, Price GJ, Louys J, Faith JT, Webb GE, Davidson I, Mooney SD. 2013. Climate change frames debate over the extinction of megafauna in Sahul (Pleistocene Australia-New Guinea). Proceedings of the National Academy of Sciences of the United States of America 110: 8777-8781.
6. Lindsey PA, Alexander R, Mills MGL, Romañach S, Woodroffe R 2007. Wildlife viewing preferences of visitors to protected areas in South Africa: Implications for the role of ecotourism in conservation. Journal of Ecotourism 6: 19-33.
7. Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Donázar JA, Owen-Smith N. 2014. Humans and scavengers: The evolution of interactions and ecosystem services. BioScience 64: 394-403.
8. Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB. 2004. Assessing the causes of Late Pleistocene extinctions on the Continents. Science 306: 70-75.
9. Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen DW, Caley MJ, Costa DP, Eguíluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton D, Ropert-Coudert Y, Sato K, Shaffer SA, Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M, Womble JN, Thums M. 2016. Key questions in marine megafauna movement ecology. Trends in Ecology and Evolution 31: 463-475.
10. Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning J-C, Terborgh JW. 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proceedings of the National Academy of Sciences of the United States of America 113: 838-846.
11. Galetti M, Moleón M, Jordano P, Pires MM, Guimarães PR Jr, Pape T, Nichols E, Hansen D, Olesen JM, Munk M, de Mattos JS, Schweiger AH, Owen-Smith N, Johnson CN, Marquis RJ, Svenning J-C. 2018. Ecological and evolutionary legacy of megafauna extinctions. Biological Reviews 93: 845-862.
12. Lewison RL, Crowder LB, Read AJ, Freeman SA. 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends in Ecology and Evolution 19: 598-604.
13. Ripple WJ, Chapron G, López-Bao JV, Durant SM, Macdonald DW, Lindsey PA, Bennett EL, Beschta RL, Bruskotter JT, Campos-Arceiz A, Corlett RT, Darimont CT, Dickman AJ, Dirzo R, Dublin HT, Estes JA, Everatt KT, Galetti M, Goswami VR, Hayward MW, Hedges S, Hoffmann M, Hunter LTB, Kerley GIH, Letnic M, Levi T, Maisels F, Morrison JC, Nelson MP, Newsome TM, Painter L, Pringle RM, Sandom CJ,

Terborgh J, Treves A, Van Valkenburgh B, Vucetich JA, Wirsing AJ, Wallach AD, Wolf C, Woodroffe R, Young H, Zhang L. 2016. Conserving the world's terrestrial megafauna. BioScience 66: 807-812.

14. He F, Zarfl C, Bremerich V, Henshaw A, Darwall W, Tockner K, Jähnig SC. 2017. Disappearing giants: a review of threats to freshwater megafauna. WIREs Water 4: e1208.
15. Price GJ, Louys J, Faith JT, Lorenzen E, Westaway MC. 2018. Big data little help in megafauna mysteries. Nature 558: 23-25.
16. Coleman DC, Crossley D Jr 2004. Fundamentals of Soil Ecology. 2nd Ed. Elsevier Academic Press.
17. Roberts RG, Flannery TF, Ayliffe LK, Yoshida H, Olley JM, Prideaux GJ, Laslett GM, Baynes A, Smith MA, Jones R, Smith BL. 2001. New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. Science 292: 1888-1892.
18. Barnosky AD. 2008. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. Proceedings of the National Academy of Sciences of the United States of America 105: 11543-11548.
19. Boulanger MT, Lyman RL. 2014. Northeastern North American Pleistocene megafauna chronologically overlapped minimally with Paleoindians. Quaternary Science Reviews 85: 35-46.
20. Villavicencio NA, Lindsey EL, Martin FM, Borrero LA, Moreno PI, Marshall CR, Barnosky AD. 2016. Combination of humans, climate, and vegetation change triggered Late Quaternary megafauna extinction in the Última Esperanza region, southern Patagonia, Chile. Ecography 39: 125-140.
21. Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B. 2016. Megafaunal impacts on structure and function of ocean ecosystems. Annual Review of Environment and Resources 41: 83-116.
22. Carrizo SF, Jähnig SC, Bremerich V, Freyhof J, Harrison I, He F, Langhans SD, Tockner K, Zarfl C, Darwall W. 2017. Freshwater megafauna: flagships for freshwater biodiversity under threat. BioScience 67: 919-927.
23. Doughty CE, Faurby S, Svenning J-C. 2016. The impact of the megafauna extinctions on savanna woody cover in South America. Ecography 39: 213-222.
24. Owen-Smith RN. 1988. Megaherbivores. The influence of very large body size on ecology. Cambridge Univ. Press.
25. Owen-Smith RN. 2013. Megaherbivores. Pages 223-239 in Levin SA, ed. Encyclopedia of Biodiversity, 2nd ed., Vol. 5. Academic Press.
26. Hansen DM, Galetti M. 2009. The forgotten megafauna. Science 324: 42-43.
27. Smith CR, Hamilton SC. 1983. Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep-Sea Research 30: 907-928.
28. Ruhl HA. 2007. Abundance and size distribution dynamics of abyssal epibenthic megafauna in the northeast Pacific. Ecology 88: 1250-1262.
29. Dunlop KM, Kuhnz LA, Ruhl HA, Huffard CL, Caress DW, Henthorn RG, Hobson BW, McGill P, Smith KL Jr 2015. An evaluation of deep-sea benthic megafauna length measurements obtained with laser and stereo camera methods. Deep-Sea Reearch Part I 96: 38-48.

30. Cartes JE, Fanelli E, Papiol V, Maynou F. 2010. Trophic relationships at intrannual spatial and temporal scales of macro and megafauna around a submarine canyon off the Catalonian coast (western Mediterranean). Journal of Sea Research 63: 180-190.
31. Papiol V, Cartes JE, Fanelli E, Rumolo P. 2013. Food web structure and seasonality of slope megafauna in the NW Mediterranean elucidated by stable isotopes: Relationship with available food sources. Journal of Sea Research 77: 53-69.
32. Lewison RL, Crowder LB, Wallace BP, Moore JE, Cox T, Zydelis R, McDonald S, DiMatteo A, Dunn DC, Kot CY, Bjorkland R, Kelez S, Soykan C, Stewart KR, Sims M, Boustany A, Read AJ, Halpin P, Nichols WJ, Safina C. 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. Proceedings of the National Academy of Sciences of the United States of America 111: 5271-5276.
33. Sleeman JC, Meekan MG, Wilson SG, Jenner CKS, Jenner MN, Boggs GS, Steinberg CC, Bradshaw CJ A. 2007. Biophysical correlates of relative abundances of marine megafauna at Ningaloo Reef, Western Australia. Marine and Freshwater Research 58: 608-623.
34. McClellan CM, Brereton T, Dell'Amico F, Johns DG, Cucknell A-C, Patrick SC, Penrose R, Ridoux V, Solandt J-L, Stephan E, Votier SC, Williams R, Godley BJ. 2014. Understanding the distribution of marine megafauna in the English Channel region: Identifying key habitats for conservation within the busiest seaway on Earth. PLoS ONE 9: e89720.
35. Teh LSL, Teh LCL, Hines E, Junchompoo C, Lewison RL. 2015. Contextualising the coupled socio-ecological conditions of marine megafauna bycatch. Ocean & Coastal Management 116: 449-465.
36. Hooker SK, Gerber LR. 2004. Marine reserves as a tool for ecosystem-based management: The potential importance of megafauna. BioScience 54: 27-39.
37. Vilella FS, Becker F, Hartz S, Barbieri G. 2004. Relation between environmental variables and aquatic megafauna in a first order stream of the Atlantic forest, southern Brazil. Hydrobiologia 528: 17-30.
38. West PM, Packer C. 2002. Sexual selection, temperature, and the lion's mane. Science 297, 1339-1343.
39. Prasad V, Strömberg CAE, Alimohammadian H, Sahni A. 2005. Dinosaur coprolites and the early evolution of grasses and grazers. Science 310: 1177-1180.
40. Wasser SK, Brown L, Mailand C, Mondol S, Clark W, Laurie C, Weir BS. 2015. Genetic assignment of large seizures of elephant ivory reveals Africa's major poaching hotspots. Science 349: 84-87.
41. Langer MC, Ezcurra MD, Rauhut OWM, Benton MJ, Knoll F, McPhee BW, Novas FE, Pol D, Brusatte SL. 2017. Untangling the dinosaur family tree. Nature 543: 501-506.
42. Kerr RA. 2003. Megafauna died from big kill, not big chill. Science 300: 885.
43. Johnson CN, Alroy J, Beeton NJ, Bird MI, Brook BW, Cooper A, Gillespie R, Herrando-Pérez S, Jacobs Z, Miller GH, Prideaux GJ, Roberts RG, Rodríguez-Rey M, Saltré F, Turney CSM, Bradshaw CJA. 2016. What caused extinction of the Pleistocene megafauna of Sahul? Proceedings of the Royal Society of London Series B-Biological Sciences 283: 20152399.

44. Piepenburg D, Schmid MK. 1997. A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: distribution, abundance, and estimates of biomass and organic carbon demand. Marine Ecology Progress Series 147: 63-75.
45. Nakajima R, Yamakita T, Watanabe H, Fujikura K, Tanaka K, Yamamoto H, Shirayama Y. 2014. Species richness and community structure of benthic macrofauna and megafauna in the deep-sea chemosynthetic ecosystems around the Japanese archipelago: an attempt to identify priority areas for conservation. Diversity and Distributions 20: 1160-1172.
46. Yesson C, Simon P, Chemshirova I, Gorham T, Turner CJ, Hammeken Arboe N, Blicher ME, Kemp KM. 2015. Community composition of epibenthic megafauna on the West Greenland Shelf. Polar Biology 38: 2085-2096.
47. D'Onghia G, Maiorano P, Sion L, Giove A, Capezzuto F, Carlucci R, Tursi A. 2010. Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. Deep-Sea Research Part II 57: 397-411.
48. Podowski EL, Ma S, Luther GW III, Wardrop D, Fisher CR. 2010. Biotic and abiotic factors affecting distributions of megafauna in diffuse flow on andesite and basalt along the Eastern Lau Spreading Center, Tonga. Marine Ecology Progress Series 418: 25-45.
49. Mosch T. Sommer S, Dengler M, Noffke A, Bohlen L, Pfannkuche O, Liebetrau V, Wallmann K. 2012. Factors influencing the distribution of epibenthic megafauna across the Peruvian oxygen minimum zone. Deep-Sea Research Part I 68: 123-135.
50. Capietto A, Escalle L, Chavance P, Dubroca L, Delgado de Molina A, Murua H, Floch L, Damiano A, Rowat D, Merigot B. 2014. Mortality of marine megafauna induced by fisheries: Insights from the whale shark, the world's largest fish. Biological Conservation 174: 147-151.
51. Moore JE, Curtis KA, Lewison RL, Dillingham PW. 2013. Evaluating sustainability of fisheries bycatch mortality for marine megafauna: a review of conservation reference points for data-limited populations. Environmental Conservation 40: 329-344.
52. Fuentes MMPB, Blackwood J, Jones B, Kim M, Leis B, Limpus CJ, Marsh H, Mitchell J, Pouzols FM, Pressey RL, Visconti P. 2015. A decision framework for prioritizing multiple management actions for threatened marine megafauna. Ecological Applications 25: 200-214.
53. Horcea-Milcu AI, Martín-López B, Lam D, Lang D. 2020. Research pathways to foster transformation: linking sustainability science and social-ecological systems research. Ecology & Society.
54. Singh HS, Gibson L. 2011. A conservation success story in the otherwise dire megafauna extinction crisis: The Asiatic lion (*Panthera leo persica*) of Gir forest. Biological Conservation 144: 1753-1757.
55. Edwards HH. 2013. Potential impacts of climate change on warmwater megafauna: the Florida manatee example (*Trichechus manatus latirostris*). Climatic Change 121: 727-738.
56. Durant SM, Wacher T, Bashir S, Woodroffe R, De Ornellas P, Ransom C, Newby J, Abáigar T, Abdelgadir M, El Alqamy H, Baillie J, Beddiaf M, Belbachir F, Belbachir-Bazi A, Berbash AA, Bemadjim NE, Beudels-Jamar R, Boitani L, Breitenmoser C, Cano M, Chardonnet P, Collen B, Cornforth WA, Cuzin F, Gerngross P, Haddane B, Hadjeloum M, Jacobson A, Jebali A, Lamarque F, Mallon D, Minkowski K, Monfort S,

Ndoassal B, Niagate B, Purchase G, Samaïla S, Samna AK, Sillero-Zubiri C, Soultan AE, Stanley Price MR, Pettorelli N. 2014. Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. Diversity and Distributions 20: 114-122.

57. Kümpel NF, Grange S, Fennessy J. 2015. Giraffe and okapi: Africa's forgotten megafauna. African Journal of Ecology 53: 132-134.

58. Di Beneditto APM, Awabdi DR. 2014. How marine debris ingestion differs among megafauna species in a tropical coastal area. Marine Pollution Bulletin 88: 86-90.

59. McClenachan L, Cooper AB, Dulvy NK. 2016. Rethinking trade-driven extinction risk in marine and terrestrial megafauna. Current Biology 26: 1640-1646.

60. Wallach AD, Lundgren EJ, Ripple WJ, Ramp D. 2018. Invisible megafauna. Conservation Biology 32: 962-965.

61. Simberloff D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation 83: 247-257.

62. Kozłowski J, Gawelczyk A. 2002. Why are species' body size distributions usually skewed to the right? Functional Ecology 16: 419-432.

63. Pedersen RØ, Faurby S, Svenning J-C. 2017. Shallow size-density relations within mammal clades suggest intra-guild ecological impact of large-bodied species. Journal of Animal Ecology 86: 1205-1213.

64. Ehnes RB, Pollierer MM, Erdmann G, Klarner B, Eitzinger B, Digel C, Ott D, Maraun M, Scheu S, Brose U. 2014. Lack of energetic equivalence in forest soil invertebrates. Ecology 95: 527-537.

65. Rooker JR, Alvarado-Bremer JR, Block BA, Dewar H, de Metrio G, Corriero A, Kraus RT, Prince ED, Rodríguez-Marín E, Secor DH. 2007. Life history and stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). Reviews in Fisheries Science 15: 265-310.

66. Paine RT. 1969. A note on trophic complexity and community stability. The American Naturalist 103: 91-93.

67. Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH. 2005. Body size in ecological networks. Trends in Ecology and Evolution 20: 402-409.

68. Paine RT. 1995. A conversation on refining the concept of keystone species. Conservation Biology 9: 962-964.

69. Mills LS, Soulé ME, Doak DF. 1993. The keystone-species concept in ecology and conservation. BioScience 43: 219-224.

70. Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. 1996. Challenges in the quest for keystone. BioScience 46: 609-620.

71. McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21: 178-185.

72. Wallach AD, Izhaki I, Toms JD, Ripple WJ, Shanas U. 2015. What is an apex predator? Oikos 124: 1453-1461.

73. Sinclair ARE, Mduma S, Brashares JS. 2003. Patterns of predation in a diverse predator–prey community. Nature 425: 288-290.

74. Owen-Smith N, Mills MGL. 2003. Predator–prey size relationships in an African large-mammal food web. Journal of Animal Ecology 77: 173-183.
75. Bromham L, Dinnage R, Hua X. 2016. Interdisciplinary research has consistently lower funding success. Nature 534: 684-687.
76. Stephan P, Veugelers R, Wang J. 2017. Blinkered by bibliometrics. Nature 544: 411-412.

Figure legends:

Figure 1. A representation of several examples of megafauna according to explicit-size-based-threshold definitions that are commonly found in the scientific literature (see Table S1). Mass-based definitions are typically used in vertebrate studies in terrestrial, pelagic marine and freshwater ecosystems, while length-based definitions are typically used in invertebrate studies in benthic marine and soil ecosystems. A list of the species represented and photograph credits is provided in Appendix S2.

Figure 2. Number of megafauna publications according to ecosystem (terrestrial, marine, and freshwater) and period (historical and prehistorical). For each pathway, we indicate in parentheses the number and percentage of the total reviewed articles (n=276) that provide a definition of megafauna and those that do not provide any definition; in the former case, we indicate if the definition is supported by citations, arguments, both or none. Line width is proportional to the number of studies. When an article referred to more than one ecosystem and/or period – 6% of cases – we depicted as many lines as needed. Note that some "terrestrial" studies do not explain in detail the species considered and may include also freshwater-dwelling species. Only articles with the term "megafauna" in the title were considered for this purpose.

Figure 3. Relationship between species body mass and the proportion of respondents to the questionnaire that classified the showed species as megafauna, either for the whole set of species (a) or broken down by taxonomic group (b). Solid lines represent the fitted values of the model including only body mass as predictor (for panel a: $F_{1,118}$=510.3, P<0.001; R^2=0.81). According to a regression tree analysis (see Appendix S4), the species included in the questionnaires with body mass ≥ 61 kg (vertical dotted line) had the highest probability of being classified as megafauna (probability ≥ 0.69; horizontal dotted line).

Figure 4. A general, conceptual definition of megafauna based on body size and its coupling to the effect of the species population on ecosystems. (a) The largest animals exert strong, consistently high impacts on local ecosystems. In contrast, the effect of small animals on local ecosystems is highly variable, with

different species having low or high effects. The empirical challenge is to identify the shape of the size-effect relationship. (b) Qualitative distribution of animal species in the two-dimensional space defined by body size and ecosystem effects. Animals exerting high effects are defined as keystone species [61,68-70], but only the largest keystone species are considered as megafauna. Note that large animals exerting low/medium effects are rare.

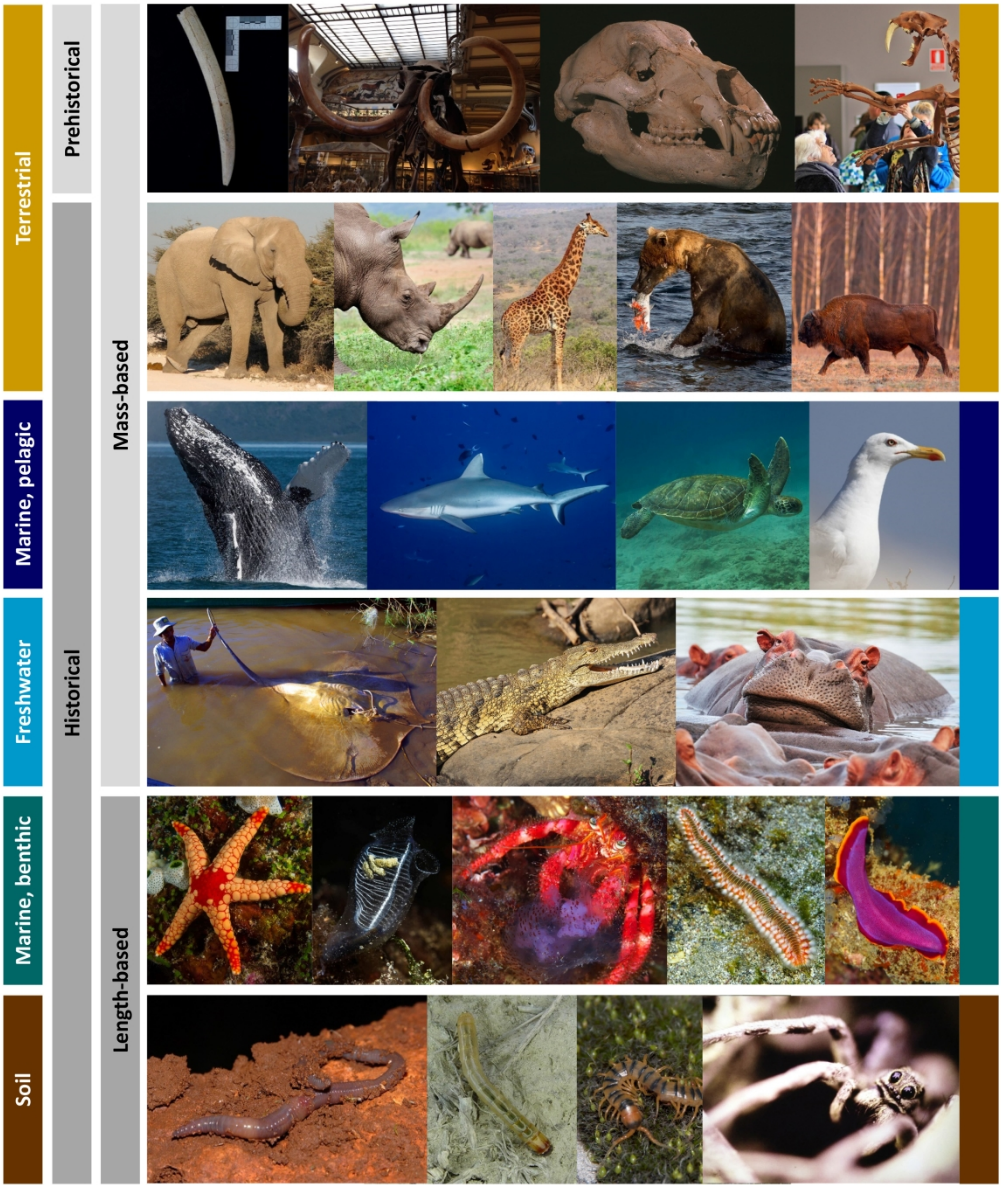

Figure 1

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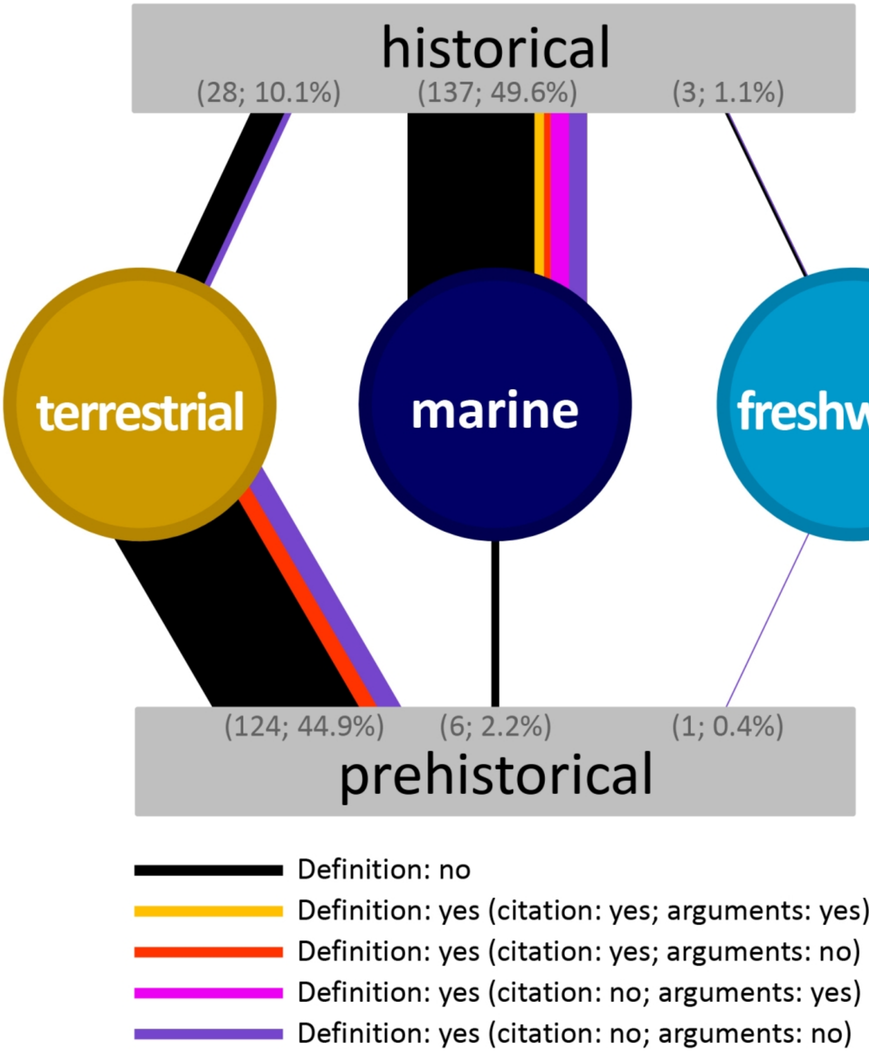

Figure 2

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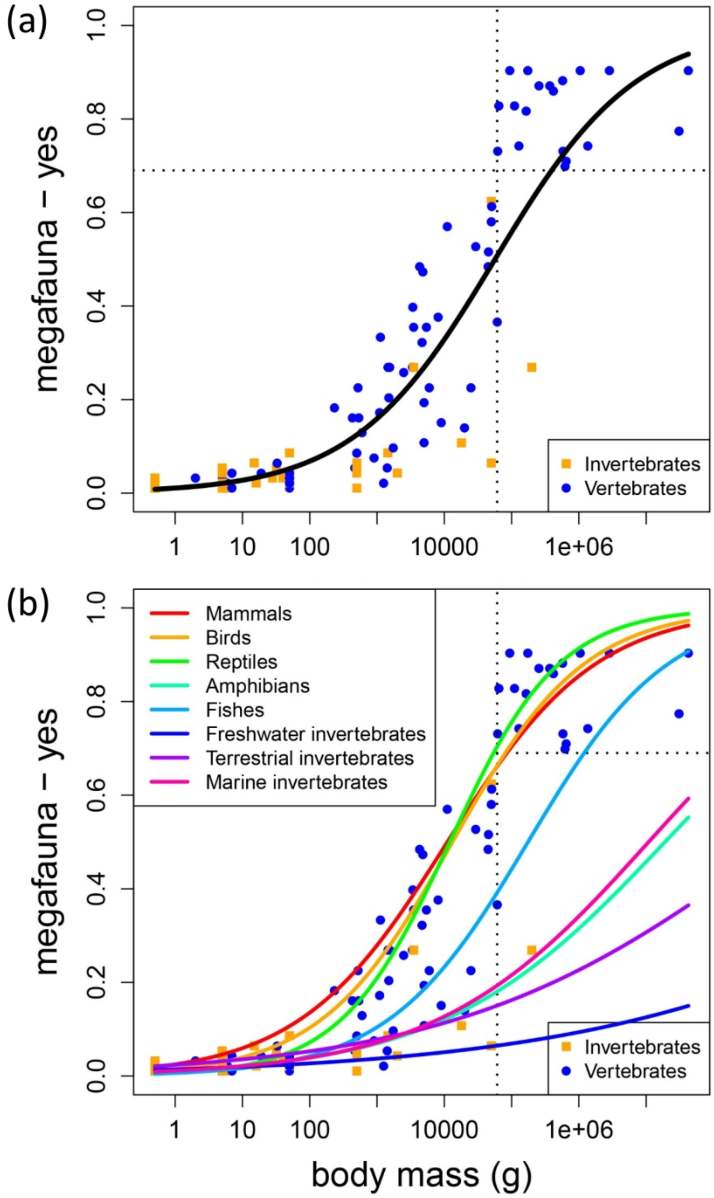

Figure 3

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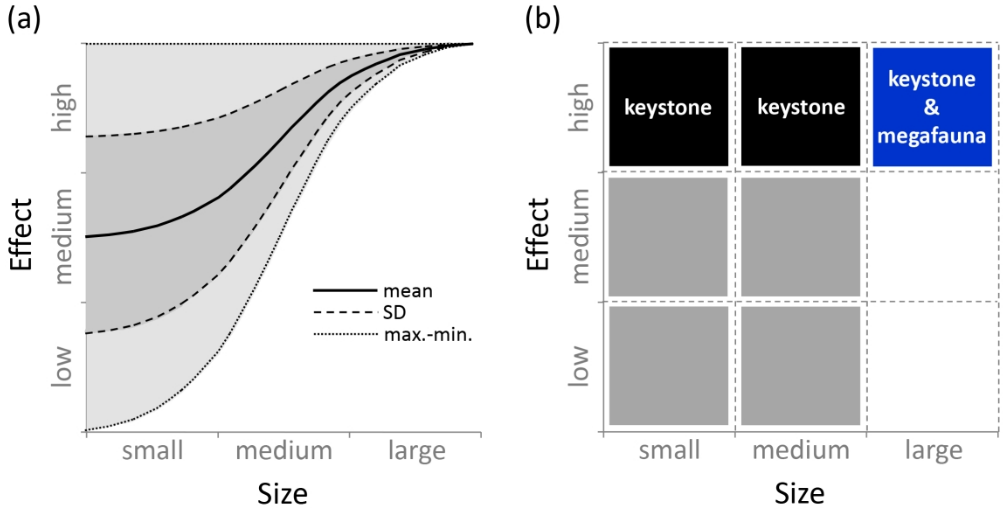

Figure 4

193x99mm (300 x 300 DPI)