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Review and Synthesis

Megaherbivore impacts on ecosystem and Earth system functioning: the current state of the science

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Megaherbivores (adult body mass > 1000 kg) are suggested to disproportionately shape ecosystem and Earth system functioning. We systematically reviewed the empirical basis for this general thesis and for the more specific hypotheses that 1) megaherbivores have disproportionately larger effects on Earth system functioning than their smaller counterparts, 2) this is true for all extant megaherbivore species and 3) their effects vary along environmental gradients. We furthermore explored possible biases in our understanding of megaherbivore impacts. We found that there are too few studies to quantitatively evaluate the general thesis or any of the hypotheses for all but the African savanna elephant. Following this finding, we performed a qualitative vote counting analysis. Our synthesis of this analysis suggests that megaherbivores can elicit strong impacts on, for example, vegetation structure and biodiversity, and all the elephant species promote seed dispersal. We were, however, unable to evaluate whether these effects are disproportionate to smaller large herbivores. Although environmental conditions can mediate megaherbivore impact, few studies quantified the effect of rainfall or soil fertility on megaherbivore impacts, precluding prediction of megaherbivore effects on the Earth system, particularly under future climates. Moreover, our review highlights major taxonomic, thematic and geographic biases in our understanding of megaherbivore effects. Most of the studies focused on African savanna elephant impacts on vegetation structure and biodiversity, with other megaherbivores and Earth system functions comparatively neglected. Studies were also biased towards semi-arid and relatively fertile systems, with the arid, high-rainfall and/or nutrient-poor parts of the megaherbivores' distribution ranges largely unrepresented. Our findings highlight that the empirical basis of our understanding of the ecological effects of extant megaherbivores is still limited for all species, except the African savanna elephant, and that our current understanding is biased towards certain environmental and geographic areas. We further outline a detailed, urgently needed avenue for future research.

Keywords: Earth system functioning, ecosystem functioning, herbivore impact, megaherbivore



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Introduction

Large-bodied animals and Earth system functioning

The global climate and biodiversity crises highlight the growing urgency to better understand the connections and interactions between the different parts of the Earth system. The Earth system consists of different spheres, such as the atmosphere, geosphere, hydrosphere and biosphere, that are all interlinked by dynamic and complex processes (Kerényi and McIntosh 2020, Steffen et al. 2020). A major disruption in the processes within one sphere can influence processes in other spheres and, therefore, affect the entire Earth system. Here, we define 'Earth system function' as any process that is embedded in at least one of these spheres and that supports the structure and/or stability of the Earth system.

The Earth's biosphere has shaped the atmosphere and hydrosphere for at least 2.5 billion years, that is, since the Great Oxidation Event (Pufahl and Hiatt 2012). Large-bodied animals are increasingly recognized as playing important roles in the functioning of the biosphere and thus the Earth system (Cromsigt et al. 2018, Schmitz et al. 2018). Their prehistoric and historic dramatic loss (i.e. defaunation) has, therefore, been proposed as an underestimated driver of global change (Estes et al. 2011). A growing body of literature explores the effects of Pleistocene defaunation on various Earth system functions (Brault et al. 2013), including the distribution of biomes (Gill 2014, Doughty et al. 2016c, Dantas and Pausas 2020), biodiversity (Gill 2014), biogeochemistry (Doughty et al. 2016c), seed dispersal (Pires et al. 2018), fire regimes (Gill et al. 2009, Rule et al. 2012), surface energy fluxes (Doughty et al. 2010, Brault et al. 2013) and pathogen dispersal (Doughty et al. 2020). Simultaneously, there is an increasing interest in the ongoing effects of extant large-bodied animals on Earth system functioning (Smith et al. 2016, Cromsigt et al. 2018, Schmitz et al. 2018). For example, mammals, as prime dispersers of seeds of certain hardwood tree species, importantly contribute to the carbon sequestration potential of tropical forests (Bello et al. 2015). Thus, a disruption in seed dispersal (a biosphere process) by defaunation can lead to changes in carbon sequestration (a process that intersects the atmosphere, biosphere and geosphere). Other recent examples of how extant large-bodied animals shape Earth system functioning include reindeer *Rangifer tarandus* grazing and trampling reducing shrub cover in the arctic tundra, thereby increasing surface albedo (Te Beest et al. 2016) and beavers (*Castor* spp.) changing watershed chemistry and hydrology (Rosell et al. 2005, Nummi et al. 2018).

Environmental conditions shape the magnitude and direction of herbivore effects

Environmental conditions are known to mediate the magnitude and direction of the ecological impacts of large herbivores on, for example, vegetation structure, soil processes and fire regimes. For instance, Augustine and McNaughton (2006) found that the impacts of wild grazers on primary

productivity varied along rainfall and soil fertility gradients. They reported that increasing rainfall improved the above-ground productivity on relatively fertile soils while suppressing it on nutrient-poor soils, leading to different grazing impacts. Similarly, Waldram et al. (2008) found that white rhino *Ceratotherium simum* impact on grassland structure and fire regimes was more pronounced in the higher rainfall areas of their study area compared to the lower rainfall areas.

Megaherbivore effects on Earth system functioning

Megaherbivores, as defined by Owen-Smith (1988) are plant-eating mammals that weigh > 1000 kg as adults. The term 'megaherbivore' differs from the increasingly popular term 'megafauna', which often refers to animals with adult body mass > 100 lbs (~45 kg), but the latter is not based on a functional distinction (Moleón et al. 2020). In contrast, their very large body size distinguishes megaherbivores functionally from smaller species. First, it renders them near-immune to non-human predation and top-down population control by large carnivores. Consequently, megaherbivores are bottom-up limited by food resources, exacerbating their impact on the environment (Caughley 1976). Second, owing to their size, megaherbivores require a large intake of forage, but their low mass-specific metabolic rate allows them to tolerate low-quality forage (Müller et al. 2013). As a result, they can consume more fibrous plant material than smaller species, which leads to impacts on a wider range of plant species and plant parts and potentially more homogenous space use. Third, their size enables megaherbivores to cover greater distances than smaller species, allowing them to move nutrients and seeds much further (Owen-Smith 1988, Doughty et al. 2016a). Because of these functional differences, megaherbivores are hypothesized to have disproportionately larger effects on ecosystems than their smaller counterparts (Owen-Smith 1988), thus eliciting stronger effects on ecosystem and Earth system functioning than smaller herbivore species, even when occurring at the same biomass density (Fig. 1).

Aims and scope of the study

Here, we systematically review published, peer-reviewed studies that presented empirical data on contemporary megaherbivore effects on ecosystem and Earth system functioning. While traditional reviews can be useful in summarizing the state of a scientific discourse, systematic reviews may reveal and reduce publication and selection bias by deploying a strict methodology that promotes transparency, objectivity and repeatability (Haddaway et al. 2015). We are unaware of any studies that have systematically reviewed the literature on the ecological and Earth system effects specifically of extant megaherbivore species. Our main aim was to evaluate the empirical basis for ecological impacts of megaherbivore species and for the thesis that megaherbivores shape the functioning of the biosphere (i.e. ecosystems) and the Earth system as a whole. We also test the more specific, generally assumed hypotheses that 1) megaherbivores have disproportionately

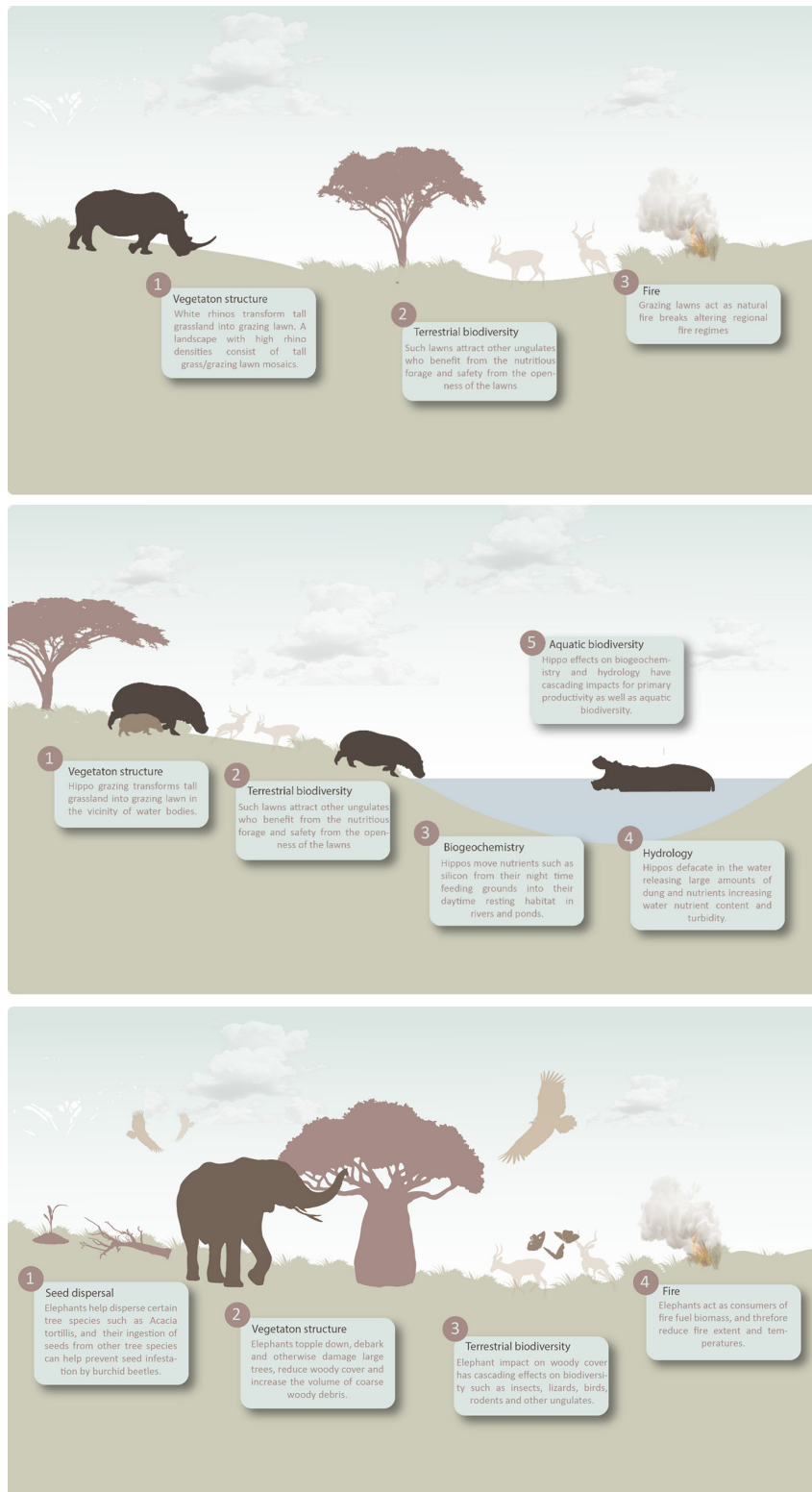


Figure 1. (A–C) Illustration of potential megaherbivore impacts on various aspects of Earth system functioning: (A) white rhino impact on vegetation structure, terrestrial biodiversity and fire, (B) hippo impact on vegetation structure, terrestrial biodiversity, biogeochemistry, hydrology and aquatic biodiversity and (C) African savanna elephant impact on seed dispersal, vegetation structure, terrestrial biodiversity and fire.

larger effects on Earth system functioning than their smaller counterparts, that 2) this is true for all megaherbivore species and that 3) their effects vary along environmental gradients. Our second aim was to synthesize the current-state-of-the-art of our understanding of megaherbivore impacts on the Earth system and to explore possible biases in our understanding. We evaluated studies that used megaherbivore density or presence/absence contrasts (hereafter ‘effect contrasts’) and that report effect sizes (therefore being eligible to be used in a quantitative meta-analysis) (here classified as type I studies). We also included more descriptive studies that did not meet the criteria for a formal quantitative meta-analysis, such as the reporting of effect sizes and confidence intervals (here classified as type II studies) (Supporting information). Following Owen-Smith’s (1988) definition, extant terrestrial megaherbivore species include African savanna elephant *Loxodonta africana*, African forest elephant *Loxodonta cyclotis*, Asian elephant *Elephas maximus*, white rhinoceros, black rhinoceros *Diceros bicornis*, greater one-horned rhinoceros *Rhinoceros unicornis*, Javan rhinoceros *Rhinoceros sondaicus*, common hippopotamus *Hippopotamus amphibius* as well as giraffe *Giraffa camelopardalis* and Sumatran rhinoceros *Dicerorhinus sumatrensis*. The latter two species marginally fit the definition as only some adult individuals exceed the 1000 kg threshold (Table 1).

Material and methods

Study design

We systematically reviewed peer-reviewed empirical studies on megaherbivore effects on ecosystem and Earth system functioning published between 1945 and 1 July 2020 following the widely used PRISMA guidelines. These guidelines describe the routines and criteria for systematic reviews and meta-analyses (Moher et al. 2009). We included all extant megaherbivores in this review (Table 1). We conducted the literature search 1 May 2019 on the Web of Science core collections database and updated the search 1 July 2020. The search string consisted of the common and scientific names of all the megaherbivore species and terms for effect (Supporting information).

Screening process

First, the search was narrowed by excluding studies not published in peer-reviewed journals and those not written in English. All the remaining studies were filtered through a stepwise screening based on pre-defined relevance and inclusion criteria (steps 1–3) and quality criteria (step 4) (Supporting information). Figure 2 gives more details on the criteria. In step 1, the titles of the publications were evaluated against criteria set 1, and all the titles deemed irrelevant were excluded from further analysis. Step 2 exclusions were based on abstracts evaluated against criteria set 2, and step 3 exclusions were based on the full-text evaluated against criteria set 3. In step 4, we categorized the remaining publications into type I and type II based on the reported methods and results, which we evaluated against criteria set 4. Type I publications consisted of studies that fit the criteria for formal quantitative meta-analyses (i.e. those that deployed effect contrasts, tested significance and reported measures of uncertainty) while type II publications did not have an effect contrast and/or did not test significance or report measures of uncertainty (i.e. type II publications were ineligible for quantitative meta-analyses). For steps 1–3, all studies were evaluated by two assessors independently. The lead author, O H, screened through all the search outputs while co-authors E D and R V each screened half of the search outputs for steps 1–3. The first half of the search output consisted of publications on the three elephant species, while the second half included the rest of the studied species. In case of a disagreement, all three afore-mentioned authors discussed the publication in question until an agreement about its inclusion or exclusion was reached. Step 4 was carried out solely by O H.

Data collection

For each publication that passed the full-text screening (both type I and type II studies), we recorded the authors, journal, year of publishing, study location(s), mean annual temperature, mean annual precipitation, a measure of soil fertility (cation exchange capacity), each megaherbivore species studied and each Earth system function studied. For type I studies, we further recorded the effect contrast type for each response variable at the detail reported in the study (i.e.

Table 1. Summary of megaherbivore characteristics. Adult body weight, feeding strategy and gut morphology are extracted from Owen-Smith (1988), while conservation status and population number are extracted from the IUCN red list (‘The IUCN Red List of Threatened Species’).

Megaherbivore	Adult body weight (kg)	Feeding strategy	Gut morphology	Conservation status	Population number
African savanna and forest elephants	2500–6000	mixed feeder	hind-gut fermenting	vulnerable	415 000
Asian elephant	2720–5400	mixed feeder	hind-gut fermenting	endangered	41 410–52 345
White rhino	1600–2300	grazer	hind-gut fermenting	near threatened	17 212–18 915
Black rhino	700–1300	browser	hind-gut fermenting	critically endangered	5630
Greater one-horned rhino	1600–2100	grazer	hind-gut fermenting	vulnerable	3588
Sumatran rhino	800	browser	hind-gut fermenting	critically endangered	80
Javan rhino	1300	browser	hind-gut fermenting	critically endangered	68
Giraffe	800–1200	browser	ruminant	vulnerable	97 562
Hippopotamus	1365–2600	grazer	hind-gut fermenting	vulnerable	115 000–130 000

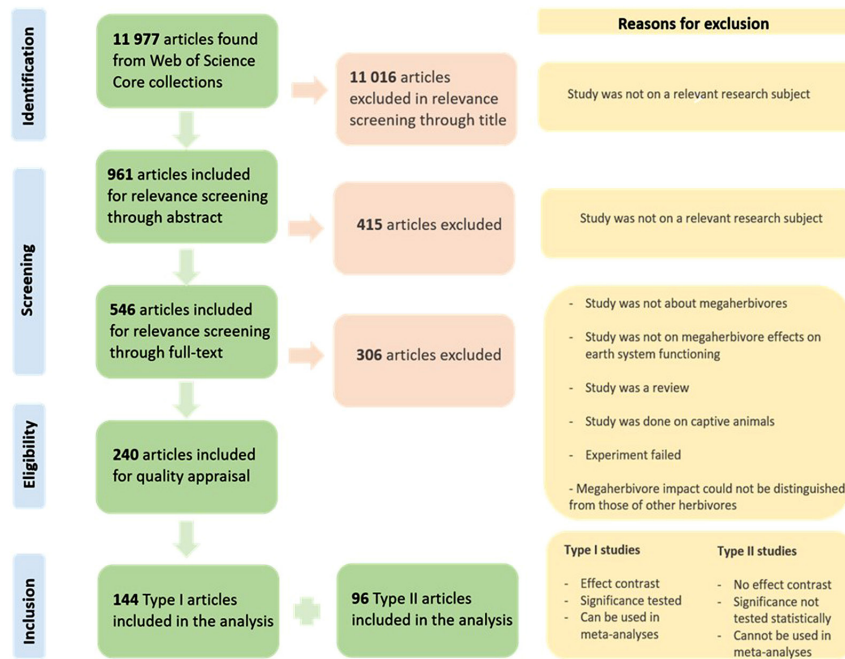


Figure 2. Prisma flow diagram of the systematic review process including identification, screening eligibility and inclusion of publications. Reasons for exclusion in each step and the characteristics of type I and type II papers are described in the yellow column on the right.

level 1 in Fig. 3, e.g. mortality of *Vachellia tortillis* < 2 m or concentration of total phosphorus in soil, etc.), whether the effect was significant or not based on p-values (significance cut-off < 0.05) and/or confidence intervals and the direction of the effect (whether increasing or decreasing) (Fig. 3, Supporting information). If the effect on the response variable was not significant, it was reported as such (i.e. ‘no significant effect’). For type II studies, we further recorded each measured response variable, but in slightly coarser categories than for type I studies (i.e. Level 2 in Fig. 3) (e.g. woody cover or nutrient concentration etc.), and the direction of effect if applicable. If there was no observed effect, it was reported as such (i.e. ‘no effect’) (Fig. 3).

Analysis of potential biases

We evaluated both type I and type II publications for taxonomic, thematic, geographic and environmental (temperature, precipitation and soil fertility) biases. For evaluating taxonomic and thematic biases, we compared the number of studies published on the different megaherbivore species and the different Earth system functions. For this purpose, we grouped all selected articles into the following seven general Earth system function categories: vegetation structure, biodiversity, biogeochemistry, seed dispersal, fire, hydrology as well as soil and geomorphology. For evaluating geographic bias, we first extracted the current and prehistoric distributions for

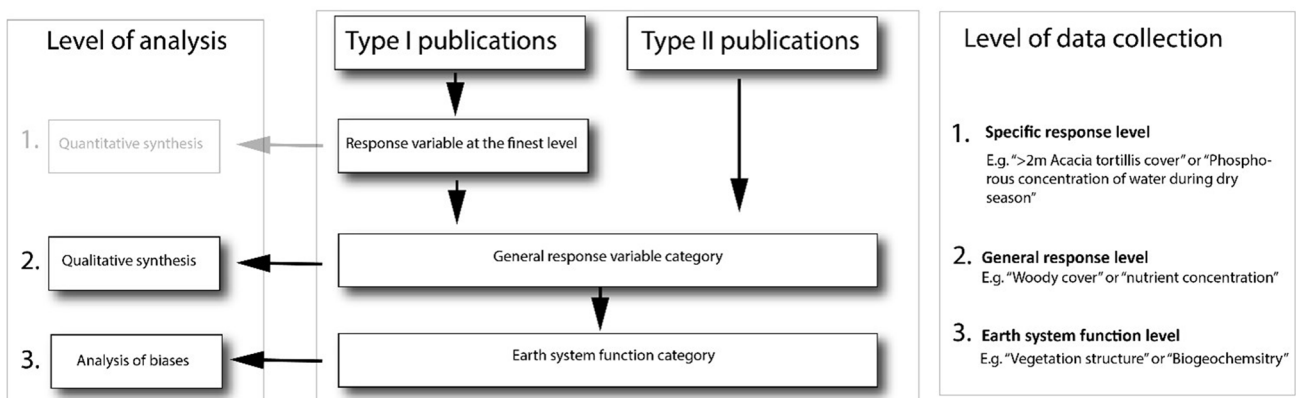


Figure 3. A schematic overview of the levels of data collection and analysis. For type I publications, we extracted each unique response variable at the finest level (level 1) and further categorized them into a general response variable category (level 2). For type II publications, we extracted response variables directly at level 2. We finally assigned each response from type I and type II publications into an Earth system function category at level 3. We performed our qualitative synthesis at level 2, and our analysis of biases at level 3.

each megaherbivore species from the Phylacine database (pre-historic distributions called ‘present natural’ in the database of origin (Faurby et al. 2020)). For current distributions, we only used records that were corroborated by the distribution estimates reported in Wilson and Reeder (2005) (Supporting information). We then mapped the publication study sites and evaluated their geographic locations relative to the current and prehistoric distributions of each megaherbivore species. To analyze environmental bias, we first extracted the climate (mean annual precipitation, mean annual temperature) and elevation data from WorldClim database at 10 min resolution (Fick and Hijmans 2017). We further derived the soil fertility data from ISRIC as mean soil cation exchange capacity at pH 7, 0–5 cm depth at 250 m spatial resolution (Hengl et al. 2015). We derived the climatic and soil fertility envelopes for the current distribution of each megaherbivore species by extracting values for mean annual precipitation, mean annual temperature and cation exchange capacity from 1000 random points throughout their current distribution ranges. We then plotted the study sites of the different species onto their respective climatic and soil fertility envelopes to identify areas of the envelopes that had not been studied. Early in our analysis, we noticed unusually high rainfall values for some of the random points on the Asian elephant, African savanna elephant and white and black rhinos current distribution ranges. Due to the low spatial resolution (96.5 km by 96.5 km at 30° north and 30° south) of the Phylacine data, high-altitude areas, potentially outside of the species’ current distribution ranges, overestimated the averaged values per pixel included in our analysis. While elephants have been recorded at high altitude (Yalden et al. 1986), they are unlikely to spend a significant amount of time at high altitude (Choudhury 1999), and thus we felt it justified to mask areas above 2000 m from the current distribution ranges in order to minimize this distortion due to high-elevation outlier rainfall and temperature values. This excluded part of the Himalayas as well as Ethiopian and Lesotho highlands. We finally analyzed the temporal trends in the publications per Earth system function studied and citation bias (citation counts extracted from Google Scholar on 20 July 2020) by evaluating the relative contribution of the different study sites to our understanding of the Earth system effects of each megaherbivore species separately.

Synthesis

With the initial intention of doing a quantitative meta-analysis of type I publications, we identified all relevant response variables within each type I publication at the finest level (level 1 in Fig. 3) and recorded the direction of effect per megaherbivore species, that is, ‘increasing’, ‘decreasing’ or ‘no significant’ effect. For a more inclusive qualitative analysis within which we could include both type I and type II publications, we further classified each response variable in each type I and type II study into a more general response variable category (level 2 in Fig. 3) and recorded the direction of effect at that level per megaherbivore species, that is, ‘increasing’, ‘decreasing’ or ‘no’

effect. We then qualitatively synthesized the reported megaherbivore effects on the level 2 response categories, across all type I and type II studies using the so-called ‘vote counting’ method. Using this method, we counted the number of statistically significant ‘increasing’ and ‘decreasing’ as well as ‘no (significant)’ effects per response category in order to evaluate the overall effect on that particular category (Vogel et al. 2021, Stewart 2010) (Fig. 3).

Results

Literature identification and screening

By specifying the publication type and language in Web of Science core collections, we first omitted 3202 symposium presentations, abstracts, newsletters, books and book chapters, postgraduate theses, reports and other grey literature as well as 622 peer-reviewed publications that were not written in English, before running the search. Our specified search query led to 11 977 peer-reviewed publications for the period from 1945 to 1 July 2020. We excluded 11 016 publications in the relevance screening of titles (step 1), 415 in the relevance screening of abstracts (step 2) and 306 in the relevance screening of full-text (step 3). After full text screening, 240 publications remained, which we subjected to a critical appraisal (step 4) during which we categorized each remaining study as either type I (144) or type II (96). In other words, only 3% of the 11 977 studies from the initial search were deemed relevant (i.e. studied megaherbivore ecological impacts). Moreover, just 46% of this 3% deployed appropriate methodology and/or reporting (i.e. use of effect contrasts, reporting of effect sizes and measures of uncertainty) to be eligible for a quantitative meta-analysis.

In the full-text screening (step 3), the most common reasons for exclusion were that the publication was not specifically focused on megaherbivore ecological impacts (82% of 306 excluded studies), megaherbivore impacts could not be distinguished from the impact of other herbivores and/or environmental variables (11% of 306 excluded studies), or that the publication was a review (5% of 306 excluded studies). In the critical appraisal (step 4), the most common reasons for classifying publications as type II (instead of type I) were the absence of effect contrast (61% of 96 type II studies), the absence of required test statistics (23% of 96 type II studies), insufficient quantitative data (11% of 96 type II studies) or that the publication was based on modelling without yielding novel data (5% of 96 type II studies) (Supporting information for a full list of excluded papers in step 3 with reasons for exclusion).

Characteristics of the peer-reviewed publications

The number of both type I and II studies increased strongly over the years and appeared in a wide diversity of journals (Supporting information). The vast majority of studies

(70%) was on African savanna elephants, followed by giraffe and hippo. The other seven species jointly made up about 10% of studies (Fig. 4). Studies on Asian megaherbivores were particularly rare, with only 16 on Asian elephant, one on the greater one-horned rhino and none on the other two rhino species. Only 10% (14) of the included type I publications and 7% (7) of type II publications looked at the effects of two or more megaherbivores in the same system, of which just one quantified the relative effect sizes for each species separately. From these initial results, we concluded that we could not perform rigorous formal quantitative meta-analyses for any of the species and Earth system functions, except for African savanna elephant effects on vegetation structure and biodiversity. The sample sizes for the other species were too small (<5 studies) to meaningfully perform a similar quantitative analysis for all species. Quantitative meta-analyses for African savanna elephant effects on vegetation structure and biodiversity have already been completed (Guldemond and Van Aarde 2008, Guldemond et al. 2017). Hence, instead of duplicating these studies on the savanna elephant, we focused our efforts on qualitative analyses where we were able to include more studies and all extant megaherbivore species. In terms of the Earth system functions, the vast majority of studies looked at vegetation structure (~65%) and biodiversity (~20%), with relatively few studies on biogeochemistry and seed dispersal and only a handful on the other Earth system functions (Fig. 4).

Geographic distribution of studies and potential environmental biases

The included type I and type II studies originated from 26 different countries (Supporting information) and 105 different study areas (Supporting information). The number of type I and type II publications per country ranged between 1 and 88, whereas the number of publications per study area ranged between 1 and 31 (Supporting information). Almost half of type I studies (40%) came from only five areas in three countries: Kruger National Park in South Africa (20), Mpala Research Centre in Kenya (18), Addo Elephant National Park in South Africa (9), Hluhluwe-iMfolozi Park in South Africa (8) and Hwange National Park in Zimbabwe (5), while the same proportion of type II studies (41%) came from ten areas in seven countries (Supporting information). Major parts of the extant distribution ranges of all megaherbivore species lacked any studies on their ecological impacts (Supporting information).

Collectively, the study sites represented only a fraction of the climate and soil fertility envelopes of the current distribution ranges of these megaherbivore species (Supporting information). Studies on African savanna elephant were strongly biased towards the arid and semi-arid parts of their distribution range, with 83% of the studies in areas that are below their distribution range's median rainfall (Supporting information). In contrast, Asian elephant studies were biased

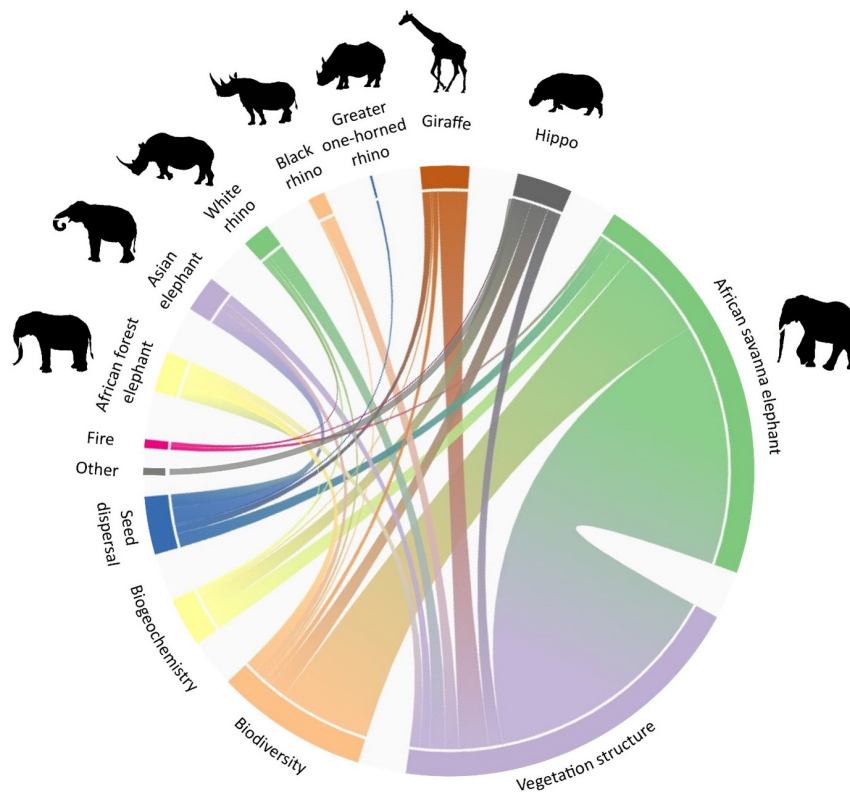


Figure 4. Chord diagram showing the proportion of studies published on the effects of the different megaherbivore species on each Earth system function category. The ‘other’ category includes hydrology as well as soil and geomorphology.

towards the mesic and very wet parts of their range (all studies coming from areas with mean annual precipitation > 1500 mm (Supporting information). White rhino effects were studied in only three locations, under semi-arid and mesic conditions, limited to the parts of their range with relatively high soil fertility (Supporting information). Studies on black rhino and giraffe were heavily biased towards relatively cool (17–18°C and 17–22°C, respectively) (Supporting information) and relatively fertile areas (Supporting information). All black rhino studies were performed under relatively similar rainfall conditions (mean annual precipitation of 506–760 mm), despite black rhinos occurring over a wide range of rainfall (Supporting information). Studies on hippo were concentrated in the drier and relatively more fertile parts of their range (Supporting information). One outlier study site was present at the high rainfall end of the hippo's range (at 2607 mm year⁻¹) but comes from outside of their natural distribution range (from South America where they were introduced) (Shurin et al. 2020).

Synthesis

We extracted 1259 and 99 responses at level 2 of data collection from type I and type II publications, respectively (Supporting information for a detailed overview per study), and further classified them into 26 vegetation structure categories, 47 biodiversity, 10 biogeochemistry, 4 seed dispersal and 4 other categories (Fig. 5).

1. Vegetation structure

Most studies dealt with the effects of African savanna elephants on woody species, in general concluding that they open up the landscape by either increasing woody damage or mortality or decreasing woody cover, density. Effects of the African forest and the Asian elephant species on woody communities were more mixed (votes more spread among 'increasing', 'decreasing' and/or 'no' effects), with much fewer response categories studied. Similar to the African savanna elephant, several studies on the browsers, black rhino and giraffe, found that they generally have negative effects on woody vegetation, with increased woody damage or mortality or reduced reproduction, height and abundance. Giraffes were often reported to have negligible effects on many woody response categories, therefore suggesting a lack of consensus on the direction of effect. The majority of studies on the grazers, hippo and white rhino, found them to increase grassland heterogeneity although the direction of their effects on herbaceous structure was less clear.

2. Biodiversity

Again, most studies on biodiversity impacts dealt with African savanna elephant impacts, suggesting that they have variable effects on most plant groups except succulents, for which there is a voting bias towards them decreasing species richness. Their impact on the diversity of other organisms varied widely, with most votes going to 'increasing' or 'no' effects. Notable exceptions are the vertebrate foraging behavior as

well as presence and richness indices, where the vote balance leaned towards 'decreasing' and 'no' effects. Studies on the biodiversity impacts of hippo also varied widely with a relatively equal spread of votes among 'increasing', 'decreasing' and 'no' effects or too low number of votes to draw meaningful conclusions about the direction of their effects. The number of votes for the biodiversity-related variables studied in the context of the other megaherbivore species were too few to make any general conclusions.

3. Biogeochemistry

Most publications on biogeochemistry studied hippo effects on nutrient content and concentration of water bodies, predominantly suggesting nutrient addition, that is, responses collectively leaning towards 'no' and 'increasing' effects (yet with substantial variation among studies and elements). Collectively, only three studies dealt with biogeochemical effects of white rhino and African savanna elephant, mostly showing them to promote soil carbon and lateral nutrient transport (most responses exhibiting 'no' and/or 'positive' effects). No studies were done on the effects on biogeochemistry by the other species.

4. Seed dispersal

Most studies on megaherbivore effects of seed dispersal have been done on elephants, particularly on African forest elephant and Asian elephant. Overall, these studies show elephants to increase germination success and decrease germination time (although a large proportion of studies did not find (significant) effects). For the three elephant species combined, there is a vote bias towards positive effects on seed dispersal.

5. Other

Only a handful of studies dealt with other response categories. African savanna elephants, white rhino and hippo reduced fire-related variables (five votes in total), and hippo reduced soil pore space while increasing geomorphology and hydrology-related variables (only one vote each).

Discussion

We concluded that the number of peer-reviewed, empirical, studies is still too small (<5 studies) to run formal quantitative meta-analyses for any of the megaherbivore species and Earth system functions, except for African savanna elephant impacts on vegetation structure and biodiversity. However, our qualitative synthesis suggests that megaherbivores can have a wide variety of impacts on the different Earth system functions. Yet, the empirical support for this varies substantially across ecosystem processes, species and systems, suggesting considerable contextual complexity that remains unexplored. Only a few studies directly quantified the effect of rainfall or soil fertility on megaherbivore impacts. Given the paucity of studies, we could not quantify the extent to which surviving megaherbivore species shape contemporary

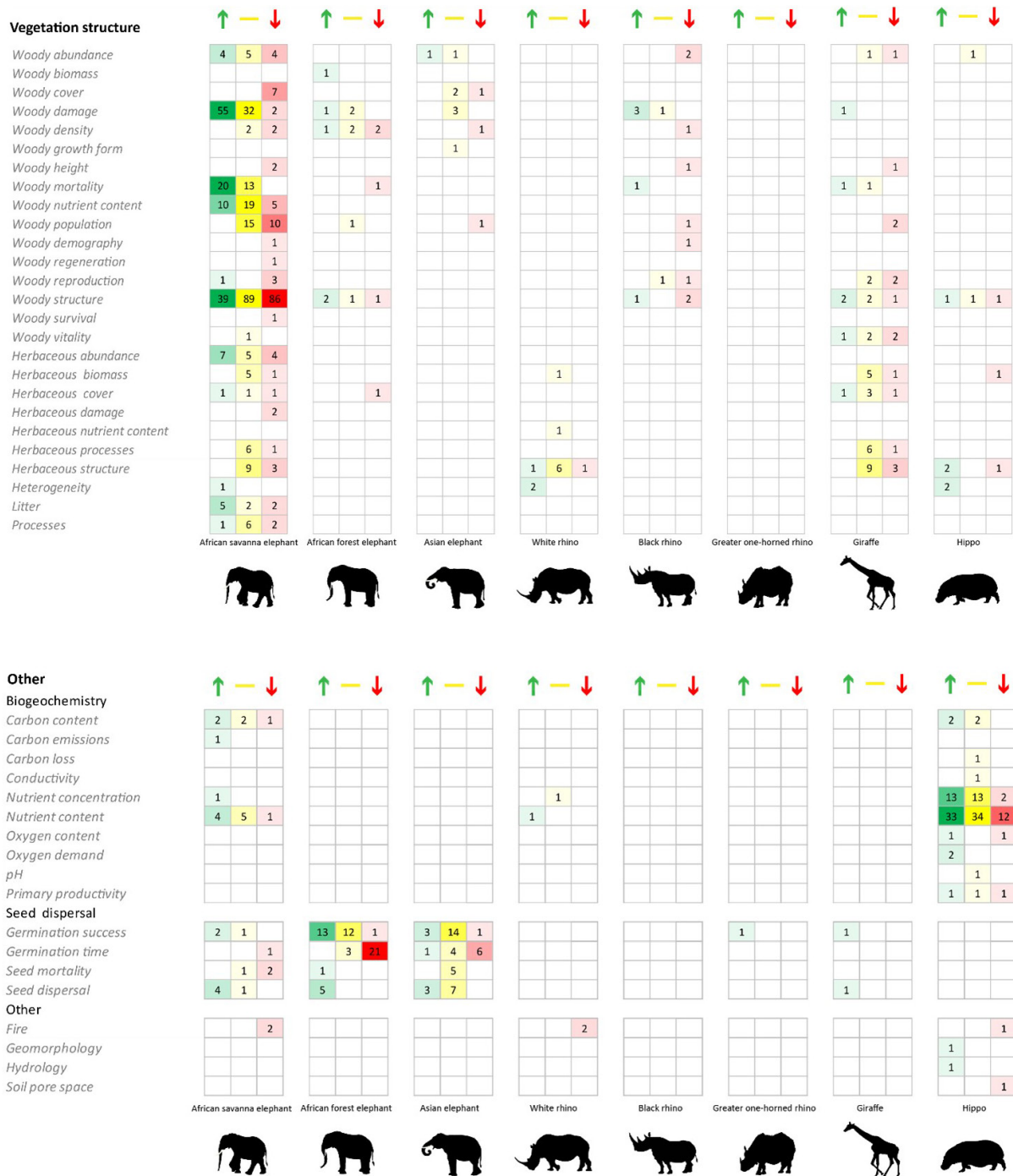


Figure 5. (A–C) Summary of the results of the vote counting per megaherbivore species. Green columns indicate increasing effect, yellow columns no (significant) effect and red columns decreasing effect. The intensity of the colour signifies the number of responses in that category, but does not necessarily reflect the number of studies in that category.

ecosystems and Earth system functioning or how this varies across environmental gradients. There was also insufficient evidence to evaluate one of the core hypotheses that megaherbivore effects are disproportionate to those of smaller herbivores. Moreover, almost half of all type I studies suitable for future meta-analyses, originated from only three study areas in South Africa, one in Kenya and one in Zimbabwe

potentially leading to major environmental biases in our current understanding.

Low inclusion rates

Most published research on non-elephant megaherbivore species focused on conservation-oriented topics, such as

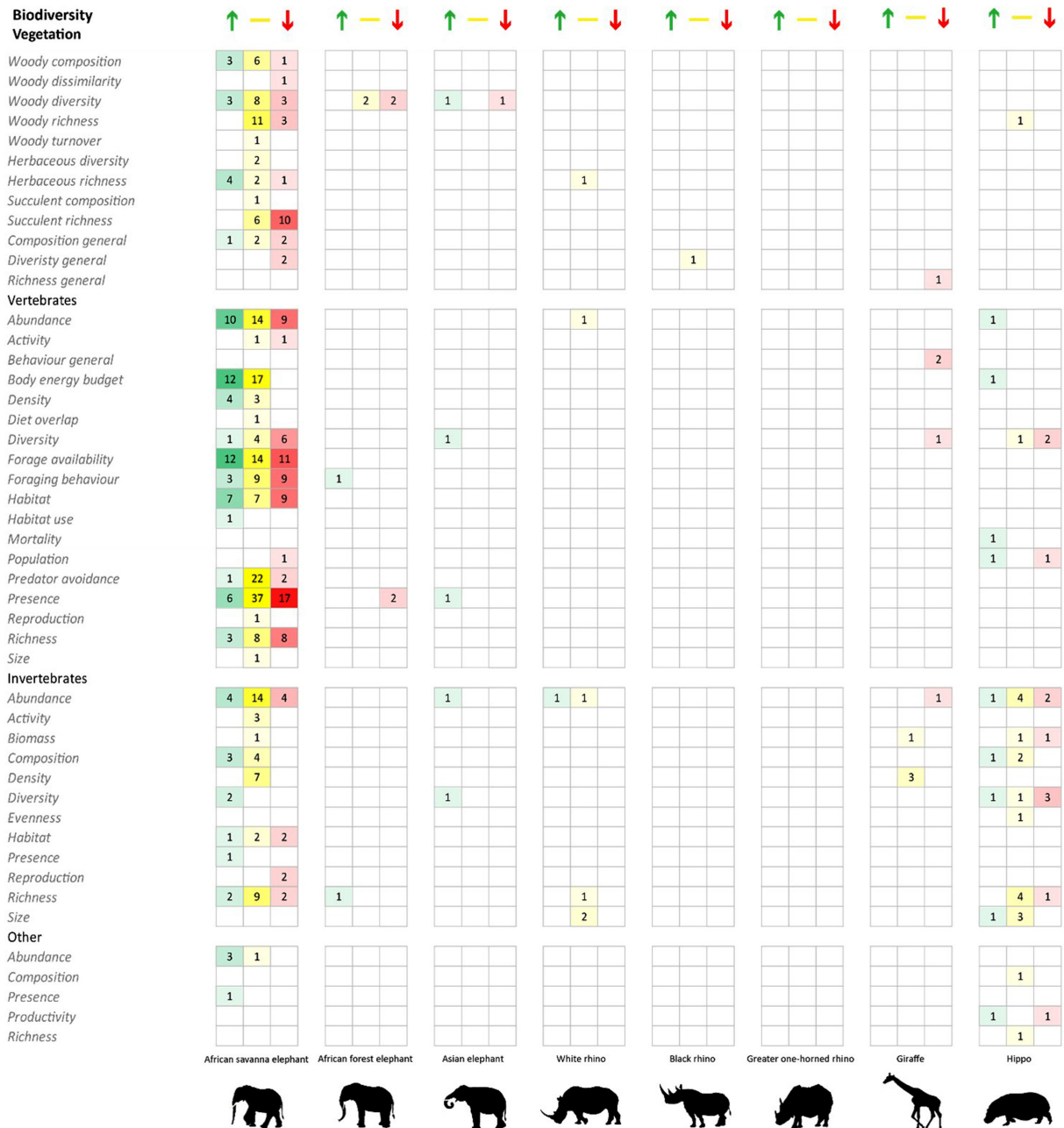


Figure 5. (Continued).

reproduction, habitat suitability and movement ecology rather than their ecological impacts. This may be a consequence of the conservation status and generally low population sizes of most of these species (Table 1), which promotes conservation management such as re-introduction and range expansion. As a result, research on these species focuses on aspects of their ecology that support these conservation actions. A second reason for the low inclusion rate of type I studies was methodological and reporting issues such as the lack of effect contrasts and/or missing effect sizes and measures of uncertainty. Therefore, we encourage researchers working on megaherbivore effects to invest in studies that use

a comparative approach (effect contrasts) and to report the essential statistics for inclusion in future quantitative meta-analyses. Relocation and range expansion programs provide fruitful opportunities to study megaherbivore impacts as they have clear 'effect contrasts' i.e. before versus after reintroduction or range expansion (Landman et al. 2014).

Many studies also failed to (or did not aim to) distinguish megaherbivore impacts from the impacts of smaller large herbivores. For example, exclusion experiment studies often separated the impact of small and medium-sized herbivores from that of large herbivores, while making no distinction between large- and megaherbivores (Dharani et al. 2009, Cassidy et al.

2013) (but see Ogada et al. 2008 and Charles et al. 2017). Future exclusion experiments, aimed specifically at discerning the impact of megaherbivores from the impact of other large herbivores, could benefit from examples, such as the Kenya Long-Term Exlosure Experiment (KLEE) at Mpala Research Centre (Young et al. 1997) and the, no longer standing, exlosure design at Hluhluwe-iMfolozi Park (Van der Plas et al. 2016). The studies that do discern impacts of megaherbivores from those of other large herbivores suggest that these two groups can elicit vastly different effects on vegetation structure (Van der Plas et al. 2016) and biodiversity (Ogada et al. 2008). If, in addition, the intention is to assess the disproportionality of megaherbivore impact, measures of biomass density must also be included (Van der Plas et al. 2016). Another approach is to carefully quantify the relative density of the different taxa and use statistical models to quantify their relative effects (Smit and Archibald 2019).

Taxonomic bias

We found strong taxonomic bias towards the African savanna elephant, with a complete absence of qualifying studies on Asian rhino species (apart from one type II study on greater one-horned rhino). This bias can be partly explained by the growing conservation management concerns about the impacts of confined, growing, African savanna elephant populations on vegetation structure and biodiversity, prompting research in these directions (Guldemond et al. 2017). When studies are solely motivated by concerns of extremely high or low megaherbivore population densities, their impacts may not be studied across their entire density range, but only at the extremes. This presents another potential bias. Most of the studies that report decreasing impacts of African savanna elephant on woody cover (Guldemond and Van Aarde 2008), for example, come from confined fenced areas with relatively high elephant population numbers. Although these findings robustly show that high densities of elephants can decrease woody cover, they do not necessarily demonstrate that such impacts are universal across population densities and environmental gradients (Guldemond and Van Aarde 2008, Guldemond et al. 2017 for extensive discussions).

The impact of megaherbivores other than African savanna elephant has generated less management concern, which may translate into less research focus on ecological impacts of these species (although see Heilmann et al. (2006) and Luske et al. (2009) for the discussion on the impact of black rhino on euphorbia trees). The lack of studies on ecological impacts by Asian rhino species may at least partly be explained by their extremely low population sizes and restricted ranges (and possibly by the English language restriction on this study). Management of these species is thus focused on enhancing their conservation status, stimulating research in directions such as population ecology and habitat selection, rather than ecological impacts. Furthermore, ecological impacts of a species occurring at extremely low population densities are difficult to study, and results of such studies would likely suffer from type II error (false negative). In other words,

megaherbivore effects studied at extremely low population densities do not necessarily reflect the effects they would elicit at higher densities. This point is particularly relevant for the Javan and Sumatran rhino. Asian elephant and greater one-horned rhino do occur in several areas in Asia at densities that would allow for studies on how they shape Earth system functions. We strongly encourage such studies and comparative work between Asian and African megaherbivores. Comparisons between African forest versus Asian elephant and white rhino versus the greater one-horned rhino seem to be particularly relevant as they seem functionally similar.

Only 10% of type I studies included in our systematic review dealt with more than one megaherbivore species in the same landscape, and only one of them was able to differentiate the relative impacts of the different species (Smit and Archibald 2019). Many studies for instance recorded herbivore damage on woody plants and associated the damage to a particular megaherbivore based on the physical attributes of the damage. Certain megaherbivore species, such as black rhino and savanna elephant, leave a unique fingerprint on the damage, making it relatively easy for the researcher to identify which species caused it. Such studies, however, often did not quantify the respective megaherbivore visitation rate, population density nor employ any other effect contrast (Birkett 2002, Muboko 2015). Exclusion studies, on the other hand, often combined different megaherbivore species as part of the same treatment, although without quantifying the relative species-specific impacts. For example, Charles et al. (2017) studied the impact of different groups of herbivores on various aspects of vegetation structure. While African savanna elephant and giraffe were both studied, they were included in the same treatment as ‘megaherbivores’ without teasing apart their relative impacts. Given this inability to compare between the impacts of different megaherbivore species and the taxonomic bias in studies mentioned above, extra caution should be taken when generalizing ‘megaherbivore impact’ across species. This is particularly relevant given the likely differences between the ecological impacts of grazers, such as white rhino and hippo, and browsers, such as black rhino and giraffe (Owen-Smith 1988).

Thematic (Earth system function) bias

Our analysis revealed clear thematic biases in the literature. Changes in vegetation structure and biodiversity were the most studied Earth system function response categories, particularly for African savanna elephant, with more emphasis placed on their impact on woody plants than on the herbaceous layer, despite a large proportion of their diet consisting of grasses (Codron et al. 2011). Strikingly, very few studies addressed the impact of megaherbivores on soils and soil microbes, even though their foraging, trampling and other disturbances are expected to have a large impact on them (Sitters and Andriuzzi 2019). Our understanding of how megaherbivores influence biogeochemistry is very limited, and most of our knowledge comes from studies on hippo’s role in nutrient transport in riverine systems (Stears et al.

2018, Schoelynck et al. 2019). Although megaherbivores have been also suggested to play major roles in terrestrial lateral nutrient transport and ecosystem carbon dynamics (Doughty et al. 2016a), very few have studied this for extant megaherbivore species (but see le Roux et al. (2018) and Veldhuis et al. (2018) for white rhino's role in nutrient transport, as well as Sitters et al. (2020), Wigley et al. (2020) for African savanna elephant's role in soil carbon storage). Megaherbivore effects on seed dispersal have only been studied in the context of the three elephant species, particularly for African forest elephant and Asian elephant (Babweteera et al. 2007, Granados et al. 2017) (although see Dinerstein (1991) for a description of the potential of greater one-horned rhino for seed dispersal). Giraffes might have an important role in pollination and seed dispersal, although their effects have been largely overlooked in the literature (but see Fleming et al. 2006). Although megaherbivores are frequently said to shape fire regimes (Gill et al. 2009, Rule et al. 2012), we found only three fire-related studies coming from Hluhluwe-iMfolozi Park (on white rhino (Waldram et al. 2008)), Kruger National Park (on African savanna elephant and hippo (Smit and Archibald 2019)) and Mpala Research Centre (on African savanna elephant (Kimuyu et al. 2014)). Furthermore, we found only one type I study on megaherbivore impacts on ecosystem hydrology (Dutton et al. 2018), and two type II studies on soil and geomorphology. No studies were found on surface energy fluxes, pathogen dispersal or any other Earth system function (although see Keesing et al. 2013).

Our findings reveal mismatches between literature on the Earth system effects of Pleistocene megaherbivore extinctions and the studies on modern effects of extant megaherbivores. First, the Pleistocene literature links megaherbivore extinctions to increases in fire extent and frequency (Gill et al. 2009, Rule et al. 2012), decreases in surface reflectance (Doughty et al. 2010, Brault et al. 2013) and pathogen dispersal (Doughty et al. 2020) as well as changes in lateral nutrient diffusion and carbon dynamics (Doughty et al. 2016b). These connections have not been solidly tested for the extant megaherbivores, although changes in surface energy fluxes (Te Beest et al. 2016) and pathogen dispersal (Berggoetz et al. 2014) have been linked to other large herbivores. Surviving megaherbivores, in turn, have been well linked to changes in vegetation structure, aspects of biodiversity and seed dispersal, with much weaker understanding of their effects on other aspects of earth system function, such as biogeochemistry, hydrology and fire. Second, the Pleistocene literature often upscales their findings to the biome or global scale, while studies on modern effects of extant megaherbivores mostly remain at the local to landscape scale. Few studies, however, have modelled the impact of other large-bodied herbivores on processes such as carbon emissions (Hempson et al. 2017) and surface energy fluxes (Te Beest et al. 2016) at a biome or global scale. Bridging these thematic and scale mismatches will strengthen the basis for our understanding of megaherbivore effects on Earth system functioning.

Geographic and environmental biases

We also found substantial geographic bias in the literature on megaherbivore effects with almost half of type I studies coming from only five African areas (i.e. Kruger National Park, Addo Elephant National Park and Hluhluwe-iMfolozi Park in South Africa and Mpala Research Centre, Kenya and Hwange National Park, Zimbabwe). These areas are internationally well-known for their excellent field research facilities, exemplifying the importance of governments and the private sector continuing to invest in long-term field facilities. Without the presence of such facilities in these five areas, our understanding of megaherbivore impacts would undoubtedly be much poorer. In contrast, a similar proportion of type II studies came from ten areas, including both African and Asian countries, demonstrating slightly smaller geographic bias compared to type I studies.

This enormous overall geographic bias, however, potentially leads to further environmental biases in our understanding of megaherbivore impacts. Our findings reveal, for all megaherbivore species, that current study areas only represent small parts of the climate and soil fertility envelopes of their current distribution ranges. Both type I and type II studies are generally biased towards semi-arid and relatively fertile systems, with a near absence of studies under arid, high rainfall and nutrient-poor conditions. Furthermore, less than a handful of studies directly quantified the effect of rainfall or soil fertility on megaherbivore impacts (Waldram et al. 2008, Goheen et al. 2013, Smit and Archibald 2019). Therefore, we do not know how megaherbivores shape ecosystems and Earth system processes for particularly the drier and wetter parts of their ranges, or how environmental drivers influence the direction and strength of their effects. The few studies that we have on megaherbivores and those on other large herbivores, however, suggest that environmental drivers do mediate herbivore impacts (Waldram et al. 2008). These limitations hinder our efforts to predict how future climates may influence the Earth system effects of megaherbivores.

Emerging trends in megaherbivore impact research

Although much of the research on modern megaherbivore impacts focus independently on either vegetation structure or biodiversity, some have recently studied their interactive effects on both vegetation structure and biodiversity (Ogada et al. 2008), therefore, incorporating a focus on ecological cascades. Although very few studies, in general, were on megaherbivore impacts on ecosystem biogeochemistry, two recent publications reported on the impact of white rhino on lateral nutrient transport, demonstrating their ability to move nutrients against fear-driven gradients (le Roux et al. 2018, Veldhuis et al. 2018). There is an increasing interest in the role of hippos on allochthonous nutrient transport, and their further effects on aquatic primary productivity and biodiversity. Schoelynck et al. (2019), for instance, demonstrated that hippos can significantly contribute to the global cycling of silicon by feeding on riverine

grasslands and defecating in water bodies, with potential cascading impacts on the silicon-limited estuarine diatoms. Recent studies have also linked African savanna elephants to changes in above- and below-ground carbon, paving the way to an exciting research avenue on megaherbivore impacts on global carbon cycling and carbon sequestration. Interestingly Sitters et al. (2020) and Wigley et al. (2020) found contrasting impacts of African savanna elephant on soil carbon in the same system, the former showing an increase and the latter a decrease in total organic carbon. In addition to investigating total organic carbon, future research should look at megaherbivore effects on the different soil carbon fractions (Lehmann and Kleber 2015) to better understand how they influence soil carbon stabilization processes and therefore carbon residence times. An exciting, although nearly untouched, area of research is the impact of megaherbivores on terrestrial and aquatic microorganisms. Our knowledge is limited to but a few studies that investigated for instance the impact of African savanna elephant dung on mycorrhizal colonization of plants (Paugy et al. 2004) and the impact of hippo dung on biofilm productivity and respiration (Subalusky et al. 2018).

Study limitations

We acknowledge that our focus on English language peer-reviewed journals may have limited our sample size. With this systematic review, however, we specifically aimed to assess the state of the empirical peer-reviewed literature and explicitly excluded non-peer-reviewed studies. To identify a possible language bias in our results, we did a posthoc assessment using Web of Science core collections database (15 October 2020), which revealed that the total number of studies on megaherbivores published in other major language peer-reviewed journals, that is, French, Spanish and Portuguese, was 342. In this assessment, we ran the search for the scientific names and the common names of the megaherbivore species in each language, excluding the term of effect, therefore making our estimate conservative. Using the 3% inclusion rate based on relevance and the 46% inclusion rate based on quality (the rates that we found for our original screening of articles in English), we estimated that we may have missed five type I and five type II studies published in French, Spanish or Portuguese language peer-reviewed journals that would qualify for inclusion in our analysis. This gives us confidence that our systematic review captured a representative sample of the current global scientific discourse (that is based on peer-reviewed empirical literature) on the extant megaherbivore effects on ecosystem and Earth system functioning.

The small number of qualifying studies that reported the impacts of a megaherbivore species on a particular response category (apart from African savanna elephant impact on some aspects of vegetation structure and biodiversity) prevented us from running a full quantitative meta-analysis. Instead, we synthesized the literature through a qualitative 'meta-analysis' using the vote-counting method. Although vote-counting is used widely in the field of applied ecology, it has been criticized for ignoring sample size and effect magnitude. Researchers

who use vote-counting often synthesize unweighted averages of effect sizes, when only study estimates but not variances are available (Stewart 2010). This can lead to bias, because it ignores the different volumes of information coming from studies of different size and quality (Stewart 2010). In contrast, we used vote-counting to qualitatively synthesize the impacts of the different megaherbivore species on a given response category (level 2). Instead of synthesizing unweighted effect sizes, we simply looked at the direction of the effect (increasing, decreasing, no effect). While this approach still ignores the size and quality of the study, it avoids the pitfall of using unweighted effect sizes. Despite these shortcomings, vote-counting allowed us to synthesize the overall impacts of the different megaherbivore species on a given response category, through identifying areas of agreement and dispute.

Concluding remarks

Our systematic review revealed that the empirical support for the thesis that extant megaherbivores (>1000 kg) shape ecosystem and Earth system functioning relies on very few, localized, studies and suffers from major taxonomic, thematic, geographic and environmental biases. This prevented us from running a strictly quantitative meta-analysis for any other species than the African savanna elephant. Therefore, we could not evaluate our follow-up hypotheses and thus it remains largely unclear whether 1) megaherbivores have disproportionately larger effects on Earth system functioning compared to their smaller counterparts, and how effects may vary among 2) species and 3) environmental gradients. Despite these shortcomings, our qualitative 'meta-analysis' revealed widely varying, context and species-dependent impacts of megaherbivores on the different response categories. Furthermore, interesting research avenues are gradually opening on the cascading effects of megaherbivores connecting different Earth system functions, and a few studies already report on megaherbivore effects on micro-organisms, nutrient transport and carbon cycling. Future research should, however, considerably increase the number of empirical studies on the ecological and Earth system effects of the different non-African savanna elephant megaherbivore species such as African rhino spp and hippo, and test the net effects of possible interactions among sympatric megaherbivore species. Furthermore, we must strategically expand the geographic distribution of studies across environmental gradients. Finally, we call for more, creative, studies that aim at differentiating megaherbivore effects from those of smaller large herbivores.

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