

REVIEW

Global patterns in seed germination after ingestion by mammals

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ABSTRACT

1. Mammals play an important role in seed germination through the ingestion of fruits and seeds. Since seed germination is a basic step in seedling recruitment, understanding how mammals affect germination improves our understanding of the effect of loss of mammal populations on the dynamics of plant communities.
2. We used meta-analytical methods to describe global patterns in the effect of seed ingestion by mammals on seed germination success and rate. We collected data from 154 studies that included 115 mammal species and 448 plant species.
3. Our results showed a positive cumulative effect of mammals on seed germination. However, this effect differed between mammalian orders; thus, some groups such as elephants, primates, and new world marsupials emerged as important enhancers of seed germination. Also, the effect varied depending on the plant family and the bioregion. Increased seed germination after ingestion was positively related to fast germination.
4. This meta-analysis, the first to synthesise and compare most of the information presently available on how mammals affect seed germination after ingestion, shows a global positive effect of mammals as enhancers of seed germination. However, behind that positive effect lies a diversity of neutral, negative, and positive effects of different magnitudes, which may have multifactorial explanations. We hope that the patterns presented here open up new questions and help guide future research efforts.

INTRODUCTION

Seed germination, defined as the uptake of water and the elongation of the embryo axis (i.e., the radicle; Bewley 1997), is an obligatory step in seedling recruitment; therefore, it is a crucial determinant of posterior events such as seedling survival and seedling growth (Eriksson & Ehrlén 2008). The patterns of success and failure of germination of seeds have effects at the community level, determining to some extent the composition, spatial arrangement, and dynamics of plant communities (Jiménez-Alfaro et al. 2016).

Diverse internal factors (e.g., seed dormancy and morphology) and external factors (e.g., resource availability and interspecific interactions) determine seed germination (Hubbell et al. 2001, Iacona et al. 2010, Willis et al. 2014). Among those factors, the effects on germination caused by the ingestion of fruits and seeds by vertebrates have received extensive experimental attention (Samuels & Levey 2005). Through ingestion, vertebrates remove the fleshy pulp around seeds, which is full of components that prevent germination (disinhibition effect); ingestion may also change the structure of the seed coat

(scarification effect; Traveset et al. 2007). The effect of seed ingestion by vertebrates on seeds is generally dualistic: some of the ingested seeds can be negatively affected, while others can be positively affected (Genrich et al. 2017). For example, many seeds are damaged through interaction with hard structures of the gastrointestinal tract (GT; e.g., teeth and beaks) or by gastric acids (Traveset et al. 2008), while many other seeds are defecated while still viable, and germinate even faster and at higher rates than non-ingested seeds (Benítez-Malvido et al. 2014).

Among vertebrates, mammals are a diverse and abundant group of fruit and seed consumers that, over millions of years, have influenced the dynamics of seed germination in the ecosystems where they occur (Fleming & Kress 2011). Currently, 25% of all mammal species are threatened with extinction (Critically Endangered, Endangered, or Vulnerable; IUCN 2019), especially large and medium-sized frugivorous species such as primates, elephants (Elephantidae), ungulates, and carnivores (Bowyer et al. 2019, Ripple et al. 2019). Since many seeds depend on these mammals not only for dispersal but also for possible disinhibition and scarification (Traveset & Verdú 2002), the extinction of local populations of mammals may negatively affect dynamics of seed germination and seedling establishment (Nunez-Iturri et al. 2008, Brodie et al. 2009).

Many published studies have analysed the effects of seed ingestion by mammals on the success and rate of germination using similar methods, which allows the accumulation of these resulting effects through quantitative synthesis as an approach to explore patterns in a comparative manner at a global scale. A first effort was made by Traveset and Verdú (2002), who found that bats increase seed germination more than non-flying mammals, but they did not analyse the effects at the order or family level. More recently, Fuzessy et al. (2016) synthesised the effects of Neotropical primates, finding differences in how feeding guilds affect seed germination success and rate. Finally, Saldaña-Vázquez et al. (2019) synthesised the effects from bats, finding no overall effect on seed germination. However, the authors did find significant effects on the analysis at the genus level.

No study has synthesised the available evidence for mammals from all over the world at the same time, and this prevents comparisons at different taxonomic levels and bioregions. For the first time, we use meta-analytical methods to synthesise all the available studies of how mammals affect seed germination through GT scarification. We predicted that data synthesis would expose patterns at different taxonomic levels for both mammals and plants, thus increasing understanding of the functions of mammals and the potential consequences of defaunation. Specifically, we asked: (1) what is the global effect that

mammals have on the seeds they ingest? (2) Do orders and families of mammals have similar effects? (3) Is the effect of seed ingestion the same for different plant families? (4) Is the effect of mammals the same throughout the world? (5) In addition to affecting germination success, does ingestion by mammals also affect the rate of germination? (6) Do exotic and native mammals differ in their effects? We expect the patterns of seed germination presented here to open a new series of questions and guide future research efforts.

METHODS

Definitions

Seed germination (SG) was defined as the proportion of seeds that germinate in a seed lot, considering germination as the protrusion of the radicle (in Petri dishes or similar germination methods) or as the protrusion above the ground of the hypocotyl (in sowing methods) – this is also called ‘visible germination’, because initial stages of seed germination occur at biochemical level (Bewley 1997). Seed viability (SV) was defined as the proportion of seeds in a seed lot stained as viable after an embryonic respiration test with tetrazolium chloride (França-Neto & Krzyzanowski 2019). Mean germination time (MGT) was defined as the mean number of days from the beginning of the germination test until seed germination occurs in a seed lot (Ranal & de Santana 2006). First germination day (FGD) was defined as the number of days needed for the first seed to germinate in a seed lot (Heer et al. 2010).

Search strategy and study selection

The criteria established for an article to be included in this meta-analysis were as follows: (1) SG, SV, MGT, and/or FGD were quantified, both for a group of ingested seeds (treatment) and for a group of non-ingested seeds (control); (2) the number of seeds in both groups was reported; and (3) seed germination parameters were quantified for seeds ingested by a mammal. Studies reporting on more than one species were only included if the parameters for each species were not combined.

We gathered the studies from the Web of Science (May 2018) using an advanced search filter created for this study that contained keywords related to seed germination and mammals (Appendix S1). After selecting the studies that met the inclusion criteria, the references of those studies were read and other studies meeting the inclusion criteria were also selected. This process was done with all selected studies until no more studies meeting the inclusion criteria were found. Finally, we did a new search in Google Scholar database (June 2018) using keywords related to seed

germination and mammals. Again, the references of all selected studies were read.

Database

The database (Appendix S2) contained 22 variables: mammal species, mammal origin (i.e., exotic or native), mammal order, mammal family, plant species, plant origin, plant family, effect type, treatment mean, control mean, number of seeds in the treatment, number of seeds in the control, number of ingested seeds germinated, number of ingested seeds ungerminated, number of germinated seeds not ingested, number of ungerminated seeds not ingested, place of germination, country, bioregion, latitude, longitude, and source. For bioregions, we used Wallace's classical zoogeographic regions (Wallace 1876), with the updated delimitations based on mammals given by Krefl and Jetz (2010). The taxonomy of mammals follows the Mammal Taxonomy Database of the American Society of Mammalogists (Burgin et al. 2018) and plant taxonomy used follows Plants of the World Online, of the Royal Botanic Gardens (<http://www.plantsoftheworldonline.org/>). When numerical data in a study were reported in figures, these were extracted using the software WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer>).

Data analyses

To estimate the effect of ingestion by mammals on SG and SV, we used the natural log of the odd ratio (lnOR), as $\ln\text{OR} = \ln[(I_{\text{pos}}/I_{\text{neg}})/(C_{\text{pos}}/C_{\text{neg}})]$ where I_{pos} is the number of ingested germinated seeds, I_{neg} is the number of ingested ungerminated seeds, C_{pos} is the number of germinated seeds not ingested, and C_{neg} is the number of ungerminated seeds that were not ingested. To avoid failed calculations when the number of seeds was zero, we used the Haldane–Anscombe correction (Anscombe 1956, Haldane 1956), which adds 0.5 to all four values of the lnOR. We used effect sizes (lnOR) to calculate the cumulative effect sizes by categories (mammal orders, mammal families, and plant families). Effect sizes were also arranged in different datasets in order to calculate cumulative effects of mammalian orders by plant families and bioregions. Lastly, SG effect sizes of mammals ingesting both native and exotic seeds were accumulated in order to analyse differences related to plant origin; the same analysis was performed for native seeds ingested by native and exotic mammals.

Since heterogeneity among studies was expected (and, indeed, confirmed by Cochran's Q and I-square; see Appendix S3) because of different methods used for germination tests and the number and diversity of species included, we used a random-effects model with the

DerSimonian–Laird weighting method (DerSimonian & Laird 2015) to calculate the cumulative effect sizes (lnOR₊₊). For each effect size, we calculated the lower and upper 95% confidence intervals (CI), which were used to estimate the precision of the effect size. When the CIs did not overlap zero, we considered the effect size to be statistically significant. We performed the analyses with the software OpenMEE (Wallace et al. 2017).

Mammal ingestion effects on MGT and FGD were calculated using the natural log of the response ratio (lnRR) as follows: $\ln\bar{X}_I - \ln\bar{X}_C$, where \bar{X}_I is the mean value of ingested seeds and \bar{X}_C is the mean of non-ingested seeds (Borenstein et al. 2009). The standard deviation values were not available in 55% of MGT and 85% FGD effect sizes, so we could not use routine cumulative methods; therefore, we used a non-parametric Kruskal–Wallis test in order to test for differences in lnRR of MGT and FGD by mammal orders, followed by Tukey's HSD post hoc test to compare all pairs. To test for relationships between SG and seed germination velocity effects (MGT and FGD), we calculated the Pearson correlation coefficient. We performed the calculation of lnRR on an Excel spreadsheet, and we calculated the nonparametric Kruskal–Wallis test, the post hoc test, and correlations with the statistical software R, through R commander package (Fox 2005).

RESULTS

The search resulted in 154 studies (Appendix S4) from 48 countries in all six bioregions (Fig. 1). From those studies, we gathered 1116 effect sizes (SG = 850, SV = 38, MGT = 172, FGD = 56) from 448 plant species of 104 families and 115 mammal species of 12 orders.

Seed germination after ingestion by mammalian orders

The overall effect of ingestion by mammals on seed germination was positive and significant (lnOR₊₊=0.230; CI = 0.139, 0.321). Five orders of mammals (Fig. 2) tended to increase the germination of ingested seeds, but only the Proboscidea, Primates, and Didelphimorphia had a significant effect. Only one effect size was available for Microbiotheria, which also tended to increase the germination of seeds. The other six orders tended to decrease seed germination (Fig. 2), but only diprotodonts and rodents decreased it significantly after ingestion (Appendix S3).

Seed germination and viability after ingestion by mammalian families

Effects on seed germination of ingestion by members of 30 mammal families were available, with 11 families significantly affecting the germination of seeds positively and five families

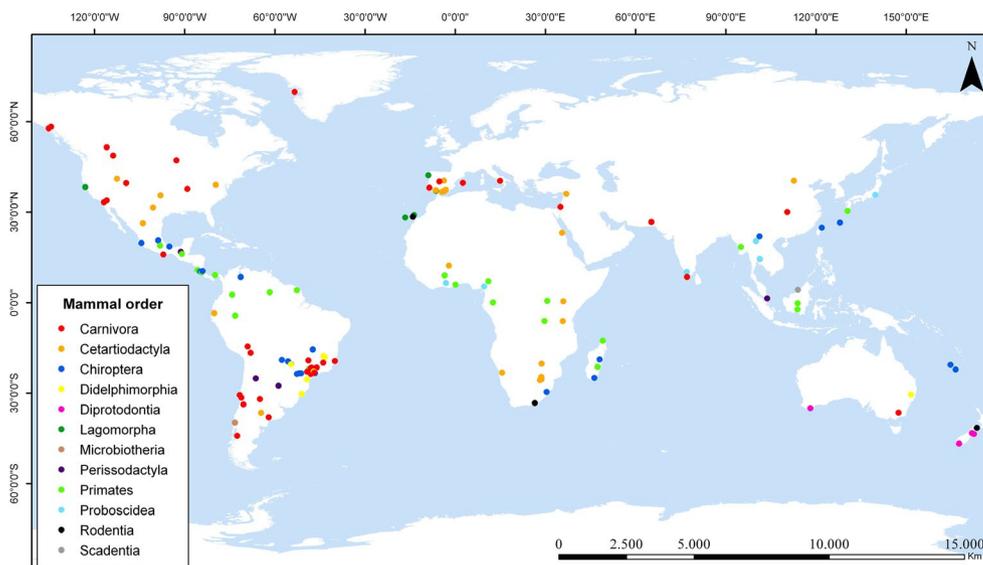


Fig. 1. Global distribution of studies of seed germination after ingestion by mammals included in this meta-analysis. [Colour figure can be viewed at wileyonlinelibrary.com]

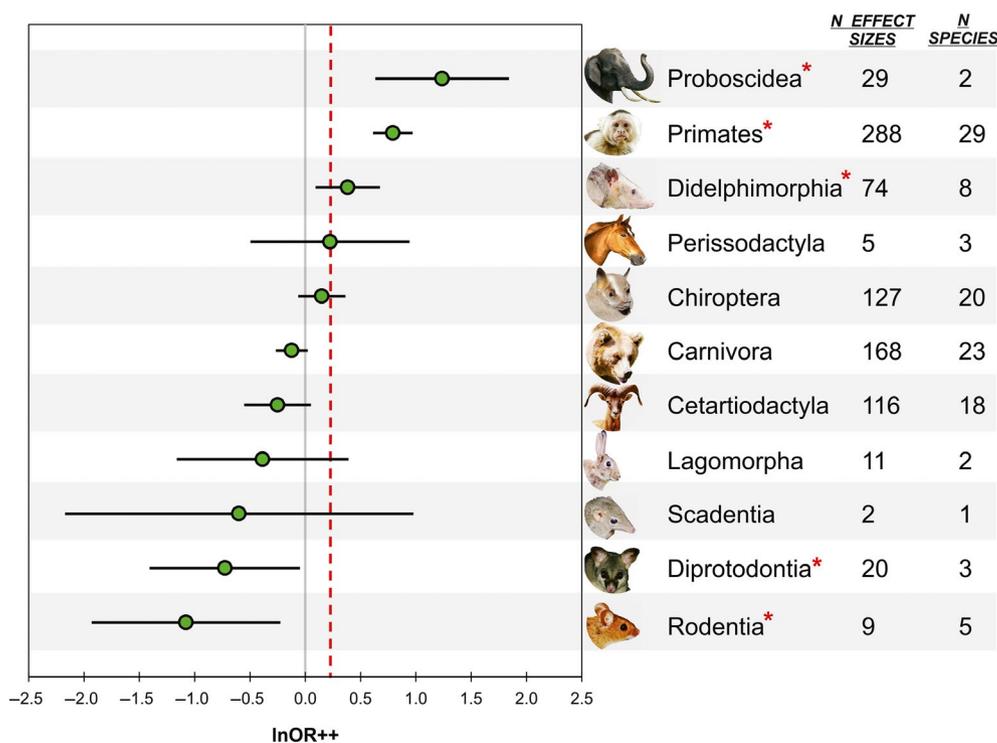


Fig. 2. Effect on seed germination of ingestion by mammals in different orders (lnOR++, calculated through the accumulation of lnOR, which represents the ratio between germinated and ungerminated seeds both for ingested and not ingested seeds). Cumulative effect sizes (dots) are reported with their 95% confidence intervals (horizontal lines). Effects are significant if the confidence intervals do not overlap zero, which is indicated by an asterisk. Dotted line indicates overall cumulative effect for mammals. [Colour figure can be viewed at wileyonlinelibrary.com]

affecting it negatively (Appendix S3). Families of Australian marsupials Macropodidae and Potoroidae showed the highest effects; however, they were calculated based only on one effect size. After Australian marsupials, primate families except

Cebidae (Fig. 3a), as well as Elephantidae, were the families that most increased germination.

The two bat families included in the analysis, Phyllostomidae and Pteropodidae, had a similar non-significant cumulative

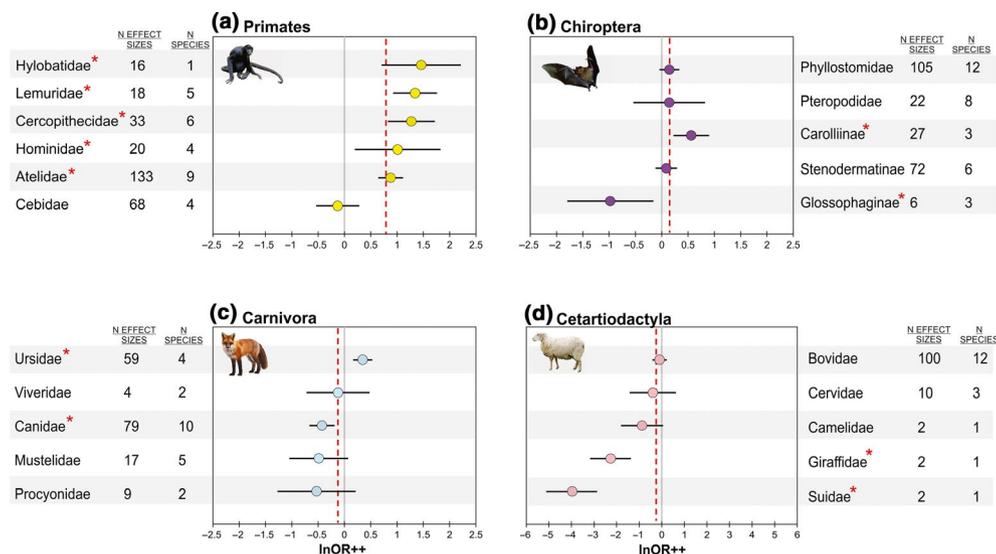


Fig. 3. Effect on seed germination of ingestion by mammals in different families ($\ln\text{OR}_{++}$, calculated through the accumulation of $\ln\text{OR}$, which represents the ratio between germinated and ungerminated seeds both for ingested and not ingested seeds). Cumulative effect sizes (dots) are reported with their 95% confidence intervals (horizontal lines). Effects are significant if the confidence intervals do not overlap zero, which is indicated by an asterisk. Dotted lines indicate overall cumulative effect for each family. [Colour figure can be viewed at wileyonlinelibrary.com]

effect (Fig. 3b), but analysis of subfamilies of Phyllostomidae showed that frugivorous bats of the Carollinae increased the seed germination significantly by ingesting seeds, while nectarivorous bats of Glossophaginae decreased it.

Among carnivores (Fig. 3c), only bears (Ursidae) had a positive effect on seed germination. The other four families of carnivores included in the analysis tended to decrease the germination of seeds after ingestion, particularly Canidae, which showed a significant effect. All families in Cetartiodactyla tended to decrease seed germination, but only Giraffidae and Suidae had a significant effect (Fig. 3d).

Effect sizes in seed viability were only available for five mammalian orders. Effect tendencies were similar to seed germination effects, with significant negative effects for the orders Rodentia (only *Atlantoxerus getulus* x *Rubia fruticosa*; $\ln\text{OR} = -2.995$; $\text{CI} = -3.963, -2.017$), Cetartiodactyla ($n = 16$; $\ln\text{OR}_{++} = -1.491$; $\text{CI} = -2.079, -0.901$), Lagomorpha ($n = 8$; $\ln\text{OR}_{++} = -1.142$; $\text{CI} = -2.120, -0.161$), and Carnivora ($n = 12$; $\ln\text{OR}_{++} = -0.778$; $\text{CI} = -1.187, -0.368$). In Diprotodontia (only *Trichosurus vulpecula* x *Crataegus monogyna*), there was a positive effect, but it was not significant ($\ln\text{OR} = 0.006$; $\text{CI} = -1.624, 1.640$).

Seed germination by plant families

Effects from 103 plant families were available (Appendix S3). Seeds from 61 families tended to increase their germination after mammalian ingestion, and 21 were

significantly affected. Another 41 families tended to decrease seed germination after mammalian ingestion, with 21 families significantly affected. Only seeds from family Anisophylleaceae (*Poga oleosa*) showed an $\ln\text{OR} = 0$, when ingested by *Loxodonta cyclotis* (Elephantidae); however, this was calculated based only on one effect size. Families with cumulative effects with more than ten individual effect sizes are illustrated in Fig. 4.

Seed germination by plant families and mammalian orders

In order to analyse the effect of particular mammalian orders on individual plant families, only families with more than ten effect sizes and more than one mammalian order were selected (Fig. 5). Primates were the group that most increased germination in five plant families, and Cetartiodactyla and Carnivora were the orders that most decreased germination in three families. Some orders that showed an overall non-significant effect on seed germination (Fig. 2) showed significant differences when analysed by plant families; Carnivora decreased seed germination in Annonaceae and Myrtaceae, but increased it in Lauraceae; Cetartiodactyla decreased germination of Cactaceae and Fabaceae; Lagomorpha decreased germination of Rubiaceae and Ericaceae; and Chiroptera increased seed germination in Piperaceae.

When analysed by families of plants, some mammalian orders with particular tendencies on overall effects (Fig. 2) sharply changed their tendencies (Fig. 5). Primates tended to decrease seed germination in Rubiaceae, Myrtaceae, and

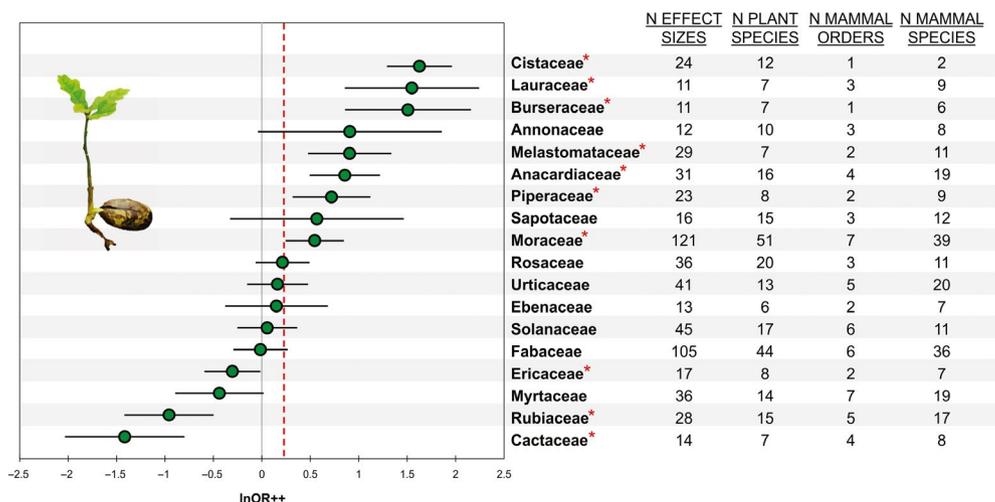


Fig. 4. Effect on seed germination of ingestion by mammals on seeds of plants in different families (lnOR++, calculated through the accumulation of lnOR, which represents the ratio between germinated and ungerminated seeds both for ingested and not ingested seeds). Cumulative effect sizes (dots) are reported with their 95% confidence intervals (horizontal lines). Effects are significant if the confidence intervals do not overlap zero, which is indicated by an asterisk. Dotted line indicates overall cumulative effect on plants. [Colour figure can be viewed at wileyonlinelibrary.com]

Solanaceae. Didelphimorphia significantly decreased seed germination of plants from the families Rubiaceae, Urticaceae, and Cactaceae and tended to decrease non-significantly seed germination in Myrtaceae, Solanaceae, and Piperaceae. Order Carnivora tended to increase seed germination in Moraceae, Solanaceae, and Anacardiaceae. Lagomorpha tended to increase germination in the family Anacardiaceae, and Diprotodontia increased it in the family Solanaceae.

Seed germination after ingestion by mammals in bioregions

Mammal orders had different effects on seeds in each bioregion (Fig. 6). The African bioregion showed the highest overall positive cumulative effect of mammals on seed germination, followed by Palaearctic and Neotropics. The Australian bioregion showed the lowest overall negative cumulative effect, followed very closely by the Nearctic. The Oriental region showed a non-significant overall cumulative effect. Some orders such as Cetartiodactyla and Carnivora changed from positive effects to negative effects or vice versa in different bioregions. Most orders in the Australian and Nearctic bioregions showed negative effects, while in other bioregions, such as the Neotropics, most orders in the analysis showed positive effects.

Germination of native and exotic seeds after ingestion by native and exotic mammal species

The cumulative effects of native mammals on seed germination after ingestion were similar for both native and

exotic seeds. However, ingestion by some mammal species had greater effects on the germination of native seeds than on exotic seeds, and for other species, the opposite was true (Fig. 7a). Evidence from exotic mammals (Fig. 7b) showed that they significantly decreased germination in exotic seeds more than in native seeds.

Seed species ingested by both exotic and native mammals showed a similar tendency in the effects on their germination, either decrease or increase (Fig. 7c). Only germination of seeds of *Myrtus communis* was decreased by exotic mammals and increased by native mammals. When effects were accumulated, seeds showed a significantly greater decrease in germination when consumed by exotic mammals than when consumed by native mammals.

Seed germination time

Mammalian orders had significantly different effects on mean seed germination time, with Proboscidea showing the shortest times and Lagomorpha the longest times (Fig. 8a). Effects on first germination day were also different among mammal orders, but the difference was not statistically significant (Fig. 8b). Both mean germination time and first germination day were negatively related to seed germination (Fig. 8c, d), indicating that a high likelihood of germination is associated with fast germination.

DISCUSSION

This is the first study synthesising and comparing all the available evidence on how ingestion by mammals affects seed germination among taxa and bioregions. Results

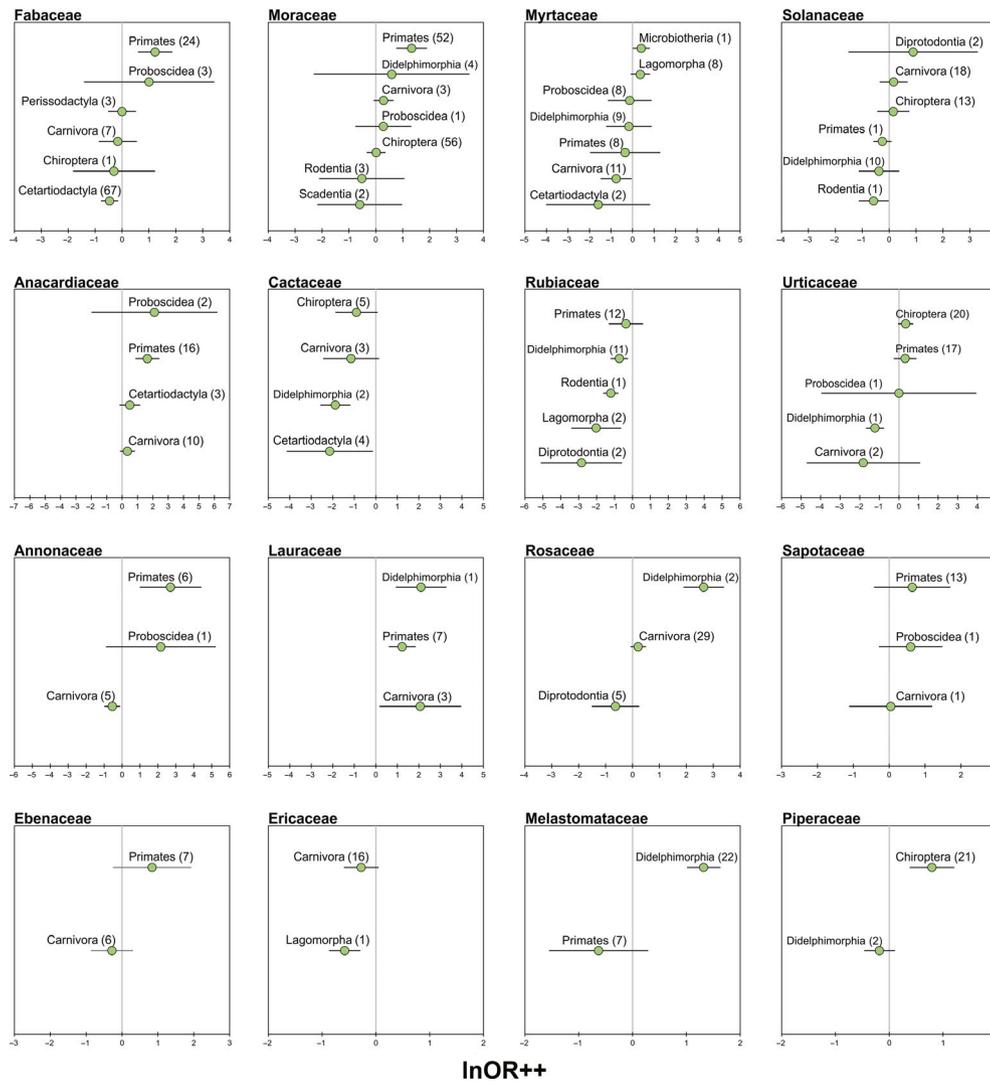


Fig. 5. Effect on seed germination of ingestion by mammals in different orders on seeds of plants in different families (InOR++, calculated through the accumulation of InOR, which represents the ratio between germinated and ungerminated seeds both for ingested and not ingested seeds). Cumulative effect sizes (dots) are reported with their 95% confidence intervals (horizontal lines). Effects are significant if the confidence intervals do not overlap zero. Numbers in parentheses indicate the number of effect sizes. [Colour figure can be viewed at wileyonlinelibrary.com]

confirm that ingestion by mammals, in general terms, results in enhanced seed germination, but that this effect cannot be extrapolated to all orders. Ingestion by elephants, primates, and new world marsupials increases seed germination the most. In addition, the effects of some orders cannot be extrapolated to all bioregions or to lower taxonomic levels such as families or subfamilies. The available evidence shows that exotic mammals do not favour the germination of exotic seeds more than native mammals, and that native seeds increased their germination much more when they were ingested by native mammals than by exotic ones. Lastly, we demonstrated that an increase in germination success is related to an increase in germination velocity.

The positive cumulative effect that mammals have on seed germination supports the view that mammals are an important group of plant mutualists in terrestrial ecosystems (Fleming & Sosa 1994), at least as increasers of seed germination. However, not all mammal species have the same effect. The meta-analysis by Traveset and Verdú (2002) finds a differential effect between flying and non-flying mammals: both had a significant positive effect, but flying mammals mostly increased seed germination. That pattern contrasts with our results; we found that bats tended to increase seed germination, but not significantly, as found by Saldaña-Vázquez et al. (2019), and that non-flying mammals had both negative and positive effects. These contrasting results are probably due to the low

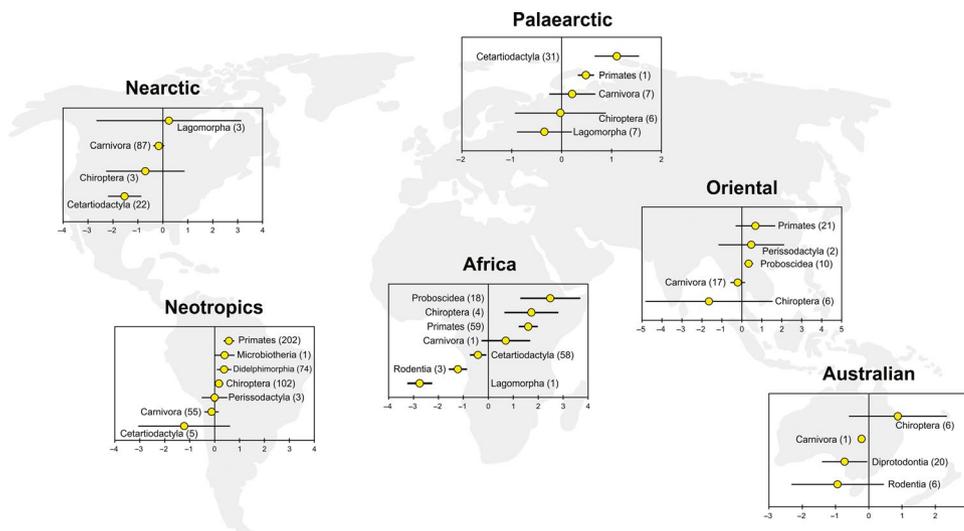


Fig. 6. Effect on seed germination of ingestion by mammals in different orders, in Wallace's six bioregions, modified by Kreft and Jetz (2010); x-axis: lnOR++, calculated through the accumulation of lnOR, which represents the ratio between germinated and ungerminated seeds both for ingested and not ingested seeds). Cumulative effect sizes (dots) are reported with their 95% confidence intervals (horizontal lines). Effects are significant if the confidence intervals do not overlap zero. Numbers in parentheses indicate the number of effect sizes. [Colour figure can be viewed at wileyonlinelibrary.com]

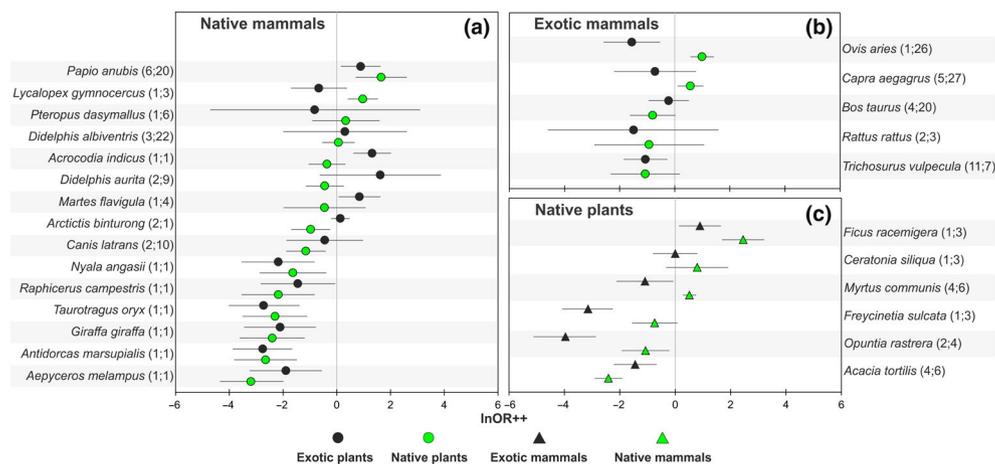


Fig. 7. Effect on seed germination of native (a) and exotic (b) mammals eating native and exotic seeds, and of native and exotic mammals eating native seeds (c) (lnOR++, calculated through the accumulation of lnOR, which represent the ratio between germinated and ungerminated seeds both for ingested and not ingested seeds). Cumulative effect sizes are reported with their 95% confidence intervals. Effects are significant if the confidence intervals do not overlap zero. Numbers in parentheses indicate the number of exotic and native effects accumulated, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

number of effects accumulated and the low diversity of species in Traveset and Verdú (2002). This also points out the temporary nature of patterns emerging from meta-analyses, which undoubtedly change as more evidence becomes available (Koricheva & Gurevitch 2013).

The conditions under which germination experiments have been performed may influence effect sizes (Robertson et al. 2006), contributing to their observed heterogeneity. An early meta-analysis found that effect sizes from glasshouse germination experiments were smaller than those from experiments in the laboratory or field (Traveset &

Verdú 2002). Recently, a meta-analysis of germination experiments of seeds ingested by primates found similar effect sizes among field, laboratory, and glasshouse experiments, except for the time of germination, which was significantly shorter in the field (Fuzessy et al. 2016). Although there were some small differences, effect sizes in our meta-analysis accumulated by mammal orders showed similar tendencies in their effects (see Appendix S3), suggesting that the conditions under which germination experiments were performed did not profoundly affect the results. In addition, these cumulative effect sizes were

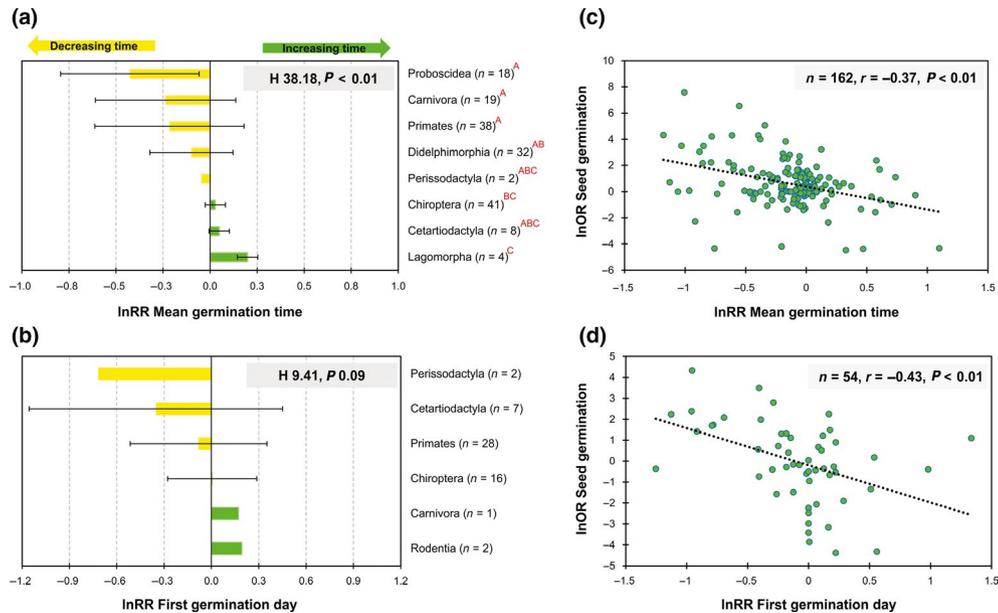


Fig. 8. Mean \pm SD of the InRR of mean germination time (a) and first germination day (b) of seeds ingested by mammals in different orders, and the negative correlations with seed germination (InOR, calculated from the ratio between germinated and ungerminated seeds both for ingested and not ingested seeds; c and d). In (a), different letters (superscripts) indicate significant differences between the orders as revealed by a Tukey's HSD post hoc test. [Colour figure can be viewed at wileyonlinelibrary.com]

significantly heterogeneous, suggesting that other factors influenced the effect, such as the species of plants and mammals involved.

When analysed at the family and subfamily levels, the patterns of seed germination remained similar to the patterns observed at the order level, suggesting that phylogenetic affiliation may be an important factor shaping the effect on seed germination. However, patterns in Cebidae (Primates), Ursidae (Carnivora), and Glossophaginae (Chiroptera) contrasted sharply with the pattern at the level of order, so in those taxa there could be clues about the characteristics that determine the effect of seed ingestion on seed germination. For instance, the cumulative effect of Cebidae was calculated on evidence from *Saguinus mystax*, *Leontocebus fuscicollis*, *Callithrix penicillata*, and *Cebus capucinus*, all of which are omnivorous primates that feed primarily on insects, exudates, and fruits (Porter 2001, Mckinney 2011, Vilela & Del-Claro 2011). This result is similar to a previous meta-analysis of Neotropical primates, which found that primates from the insectivore–frugivore feeding guild increased seed germination less than those from the frugivore and folivore–frugivore guilds (Fuzessy et al. 2016).

As in Cebidae, the evidence in Glossophaginae also suggested that diet type (and the related physiology and anatomy) is an important determinant of the effect on seed germination. The cumulative negative effects in this subfamily were calculated based on evidence from the

nectarivorous and pollinivorous bats *Glossophaga longirostris*, *Glossophaga commissarisi*, and *Leptonycteris yerbabuena*. In the study of *Leptonycteris yerbabuena*, the authors suggest that the decreased seed germination after ingestion was caused by the acids of the GT, which killed the plant embryos (Rojas-Martinez et al. 2015). However, reduction in germination after ingestion by nectarivorous bats could also occur for the opposite reason: these bats have simple GTs, and when they ingest fruits and seeds, their digestion is less efficient than in other bats (Kelm et al. 2008), probably reducing the scarification of seeds and perhaps generating the decreased pattern of seed germination that the authors observed.

As mentioned above, Ursidae significantly increased seed germination, contrasting with the other Carnivora families Viverridae, Canidae, Mustelidae, and Procyonidae. Most carnivores have shorter GTs than other terrestrial mammals (McGrosky et al. 2016), thus reducing the time of the GT–seed interaction, which in turn decreases scarification and seed germination. However, since in carnivores the GT length is positively related to body mass (McGrosky et al. 2016), it is not surprising that seeds consumed by big carnivores, such as bears that weigh hundreds of kilograms (Jones et al. 2009), experience enough scarification for seed germination to be enhanced.

When the effect of seed ingestion on seed germination was analysed by grouping seeds by plant families, diverse patterns emerged as follows: in some plant families,

germination was highly favoured by consumption by mammals, while in other families it was greatly reduced. Furthermore, most plant families were not equally affected by all mammal orders, and some plant families showed contrasting patterns of seed germination depending on the mammal taxon that consumed the seeds. This varied favouring of seed germination has been attributed to the co-evolution of some groups of frugivorous vertebrates with some groups of plants (Charles-Dominique 1986, Cypher & Cypher 1999); however, evidence supporting this hypothesis is still scarce (Traveset 1998, Saldaña-Vázquez et al. 2019). Whether the enhancement of seed germination after ingestion is the result of co-evolutionary processes or not will ultimately be determined by the interaction between the seed traits specific to the plant family and the traits of the GT of the mammal order.

Patterns of seed germination changed from one bioregion to another. Some mammals, such as elephants and primates, had positive effects on seed germination throughout the bioregions where they occur, whereas other mammals, such as bats and carnivores, had less consistent positive effects. These complex patterns are as expected, because plant and mammal species composition, and the pairs of interacting species, are not the same in each bioregion. Indeed, only three plant species and nine mammal species occurred in two or more bioregions. Even cosmopolitan mammals had different effects in each bioregion. For instance, goats feeding on seeds from Fabaceae trees had neutral effects on seed germination in the Nearctic (Kneuper et al. 2003) and the Neotropics (Ortega-Baes et al. 2002), while in Africa they had negative, positive, and neutral effects (Miller 1995, Tjelele et al. 2012, 2015).

Although it is generally believed that germination enhancement is beneficial for a plant, that is not always the case. As stated by Traveset (1998), whether the germination enhancement is beneficial and thus adaptive depends on the context in which germination occurs. Therefore, if an increase in the fitness of the plant is not evident, it is not possible to determine whether the increase in germination is advantageous. In addition to the increase in germination, we found a relationship between this increase and the increase in germination rate. Again, germinating faster does not necessarily represent a benefit for the plant (Leverett et al. 2018), since faster germination can place the seed, and the seedling, in an unfavourable situation both in terms of intra- or interspecific competition and in terms of environmental conditions (Orrock & Christopher 2010). Thus, the benefits of germinating and germinating faster depend on the context.

Despite greater success and velocity of germination in seeds that were ingested by mammals, non-ingested seeds from most plant species also germinated, suggesting that

passage through the mammalian GT is not necessary for germination to occur in many cases. However, the seeds of some plant species only germinated after they had passed through the GT of a mammal. Whether seeds depend on mammals for gut scarification or only for dispersal, the presence of mammals in ecosystems is vital for the life cycle success of many plant species (Fleming & Sosa 1994); for this reason, conservation concerns arise when mammalian groups that are good at enhancing seed germination face challenges. For example, in the order Primates, 60% of species are threatened with extinction and 70% have declining populations (Estrada et al. 2017). The loss of these mammals may negatively impact the recruitment of many plant species, altering in unpredictable ways the dynamics of plant communities.

Evidence suggests that some native mammals, such as *Didelphis aurita*, *Acrocodia indicus*, and *Martes flagivula*, favour the germination of some exotic plant species; however, most native mammals affected both native and exotic seeds in a similar way. Exotic mammals such as sheep and goats enhanced the germination of native seeds and reduced that of exotic plants. These exotic mammals may be candidates for ecological replacements to restore trophic interactions in ecosystems where native mammals have been annihilated (Svenning et al. 2016). However, we found that native mammals were better increasers of seed germination than exotic ones, suggesting that although rewilding processes can be carried out with exotic species, reintroducing native species probably maintains historic positive interactions that resulted from co-evolutionary processes.

Most studies of seed germination are based on visible germination, which is the elongation of the embryonic axis and the breaking of the seed coat. However, the initial steps of germination are not visible and occur at biochemical level (Bewley 1997). Analysis of the effect of seed ingestion on SV, quantified using biochemical analysis, agreed with the patterns that emerge from SG, and also suggested that low seed germination after ingestion by Rodentia, Cetartiodactyla, and Lagomorpha was caused by the death of the embryo and not by a lack of scarification. These three mammal orders have long GTs with large fermentation chambers (Hofmann 1989, Lovegrove 2010), which increases the time available for GT-seed interaction and the probability of negative change in the structure of the seed coat and killing of the embryo. This long GT-seed interaction time is reflected in longer gut retention times (Mancilla-Leyton et al. 2013, Tjelele et al. 2015) than in mammal orders without fermentation chambers (Duron et al. 2017).

The patterns found in this study generate many questions and will help to guide future research efforts. It would be very useful to understand the proximate

mechanisms behind the patterns of germination in seeds that have been ingested by mammals, particularly in relation to scarification and how it interacts with the morphology and physiology of seeds and GTs, and in relation to the ecological characteristics of the mammals with dietary specialisation. In order to understand the role of scarification, it would be valuable to use biochemical methods to determine, when germination does not occur, if this is caused by an excess of scarification and the death of the embryo, or by insufficient scarification. Finally, a deeper understanding of germination patterns will also require research to disentangle the roles of phylogeny and co-evolution between mammals and plants.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Advanced search filter used to gather the studies from Web of Science.

Appendix S2. Database containing all the values of the variables used in this meta-analysis.

Appendix S3. Effect sizes and heterogeneity by taxonomic groups and condition of germination.

Appendix S4. List of studies included in the meta-analysis.