Functional traits—not nativeness—shape the effects of large mammalian herbivores on plant communities

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Abstract

Large mammalian herbivores (megafauna) have experienced extinctions and declines since prehistory. Introduced megafauna have partly counteracted these losses yet are thought to have unusually negative effects on plants compared with native megafauna. Using a meta-analysis of 3995 plot-scale plant abundance and diversity responses from 221 studies, we found no evidence that megafauna impacts were shaped by nativeness, "invasiveness," "feralness," coevolutionary history, or functional and phylogenetic novelty. Nor was there evidence that introduced megafauna facilitate introduced plants more than native megafauna. Instead, we found strong evidence that functional traits shaped megafauna impacts, with larger-bodied and bulk-feeding megafauna promoting plant diversity. Our work suggests that trait-based ecology provides better insight into interactions between megafauna and plants than do concepts of nativeness.

Large terrestrial mammalian herbivores (≥45 kg; henceforth "megafauna") have distinct effects on ecosystems by causing disturbance, consuming low-nutrient vegetation, and dispersing seeds and nutrients (*1*, *2*). These effects were ubiquitous for ~55 million years until the extinctions of the Late Pleistocene and Holocene (~130,000 to 7000 years before present) (*3*). More recently, humans have introduced numerous megafauna, which have partially counteracted these declines numerically (*4*) and functionally (*5*, *6*), and which contribute some lost ecological functions, such as increasing water availability through well digging and reducing wildfire (*7*, *8*).

However, introduced megafauna can also reduce native plant abundance and diversity and promote introduced plants (*9*). These effects are generally interpreted as evidence that the impacts of introduced megafauna are distinct from those of native megafauna (*10*). Accordingly, conservation policy has prioritized the eradication and culling of introduced megafauna, even though 50% of these species are threatened or extinct in their native ranges (*11*).

The notion that native and introduced species have distinct effects is most often justified by the functional postulate that long-term community-wide coevolutionary history shapes ecological interactions (*12*–*14*). Coevolution has been inferred at broad macroevolutionary scales [e.g., the evolution of grasses and grazers throughout the Cenozoic, or the evolution of plant defenses (*15*, *16*)] and plays a role in specialized interactions, as evidenced by the consequences of introduced pathogens (*17*). However, these observations have been extended to justify a broader biological reality to nativeness in which coevolution also shapes diffuse, generalist interactions with high taxonomic precision, such as between individual plant and megafauna species. Nativeness has thus become central to conservation policy (*18*); widespread notions of ecological "health" (*19*); and basic biodiversity data, which only count populations thought to be native (*20*).

However, critics have argued that coevolution is unlikely to shape generalist interactions in the same way it does specialized ones and that long-term community-wide coevolution is unmeasurable (*21*, *22*). Instead, critics have suggested that ecological factors, such as predation, the environment, and functional traits, may sufficiently explain the effects of both introduced and native organisms (*23*, *24*). If so, and if it were impossible to determine the nativeness of an organism from their actual effects, then nativeness would remain a description of dispersal history but would not be a meaningful way to understand ecological interactions (*23*).

We employed a meta-analytic dataset of 3995 responses from 221 studies to evaluate whether nativeness and/or ecological factors (Table 1) could explain the effects of wild herbivorous megafauna (≥45 kg) on plant abundance (N = 3221 responses) and plant diversity (N = 774) (*25*, *26*). Studies consisted of comparisons between adjacent areas with different densities of megafauna due to exclosures, management (e.g., hunting), or introduction or eradication disparities (e.g., neighboring islands with and without introduced megafauna). The final dataset had a global extent (albeit one biased toward North America, Europe, and Australia; fig. S1) and included 2908 plant responses (160 studies) to 110 native megafauna species and 1087 responses (62 studies) to 20 introduced megafauna species (*25*).

Table 1. The main hypotheses and results.
Contrary to our predictions, we found no evidence that megafauna nativeness, novelty, or coevolutionary history explained their effects on plant diversity or abundance. Instead, we found strong evidence that functional traits explain megafauna impacts on plants.

Hypothesis	**Result**
Introduced, "invasive," or feral megafauna have more negative effects on native plants than do other megafauna.	We found no evidence that introduced, "invasive," or feral megafauna have more negative effects on native plant abundance or diversity (Fig. 1 and tables S1 and S2).
Introduced megafauna have more negative effects on native plants than do native megafauna, especially on oceanic islands, which lack evolutionary exposure to mammalian megafauna.	We found no evidence that introduced megafauna have more negative effects on native plant abundance and diversity than do native megafauna—regardless of the evolutionary exposure of the landform (Fig. 2 and tables S1 and S2).
Introduced megafauna promote introduced plants more than native megafauna do, especially on oceanic islands.	We found no evidence that introduced megafauna promote introduced plant abundance or diversity more than native megafauna do (Fig. 2 and tables S1 and S2).
Coevolutionary history between megafauna and individual plants or native plant communities shapes the impacts of megafauna on plants.	We found no evidence that "coevolved" megafauna have different effects on native plant abundance or diversity than do evolutionarily novel megafauna (Fig. 3 and tables S1 and S2).
Phylogenetically and functionally novel introduced megafauna have more negative effects on plants.	We found no evidence that more phylogenetically or functionally novel megafauna have more negative effects on native plant abundance or diversity (Fig. 3 and tables S1 and S2).
The effects of megafauna on plants are shaped by environmental factors (net primary productivity, maximum annual temperature and precipitation, absolute latitude, human footprint index).	We found no evidence that environmental factors shape megafauna effects on plant diversity and abundance (tables S1 and S2).
The effects of megafauna on plant are shaped by megafauna functional traits (dietary selectivity, body mass, dietary preference, and fermentation type).	We found strong evidence that dietary selectivity, body mass, and dietary preference shape megafauna effects on plants (Fig. 4 and figs. S2, S3, and S6). We found no evidence that fermentation type (proportion of biomass with hindgut fermentation) shapes megafauna impacts on plants.
The effects of megafauna on plants are shaped by megafauna diversity (measured as species and functional group richness).	We found no evidence that megafauna species and functional group richness shapes their impacts on plants (fig. S9). However, we did find weak evidence that more diverse megafauna communities suppress introduced plant abundance.

No evidence for a biological reality to nativeness

Multilevel meta-analytic models found that native and introduced megafauna had similar effects (measured as Hedges' *g*) on native plant abundance and diversity (Fig. 1, A and B; planned contrast *P* value range = 0.25 to 0.94). Megafauna nativeness did not improve model quality relative to intercept-only null models [likelihood ratio test (LRT), *P* value range = 0.22 to 0.95]. These effects were consistent when only considering megafauna species studied in both their native and introduced ranges (fig. S2; contrast *P* values = 0.30 to 0.94, LRT *P* values = 0.75 to 0.97). See table S1 for model estimates and table S2 for model comparison and planned contrast test statistics.

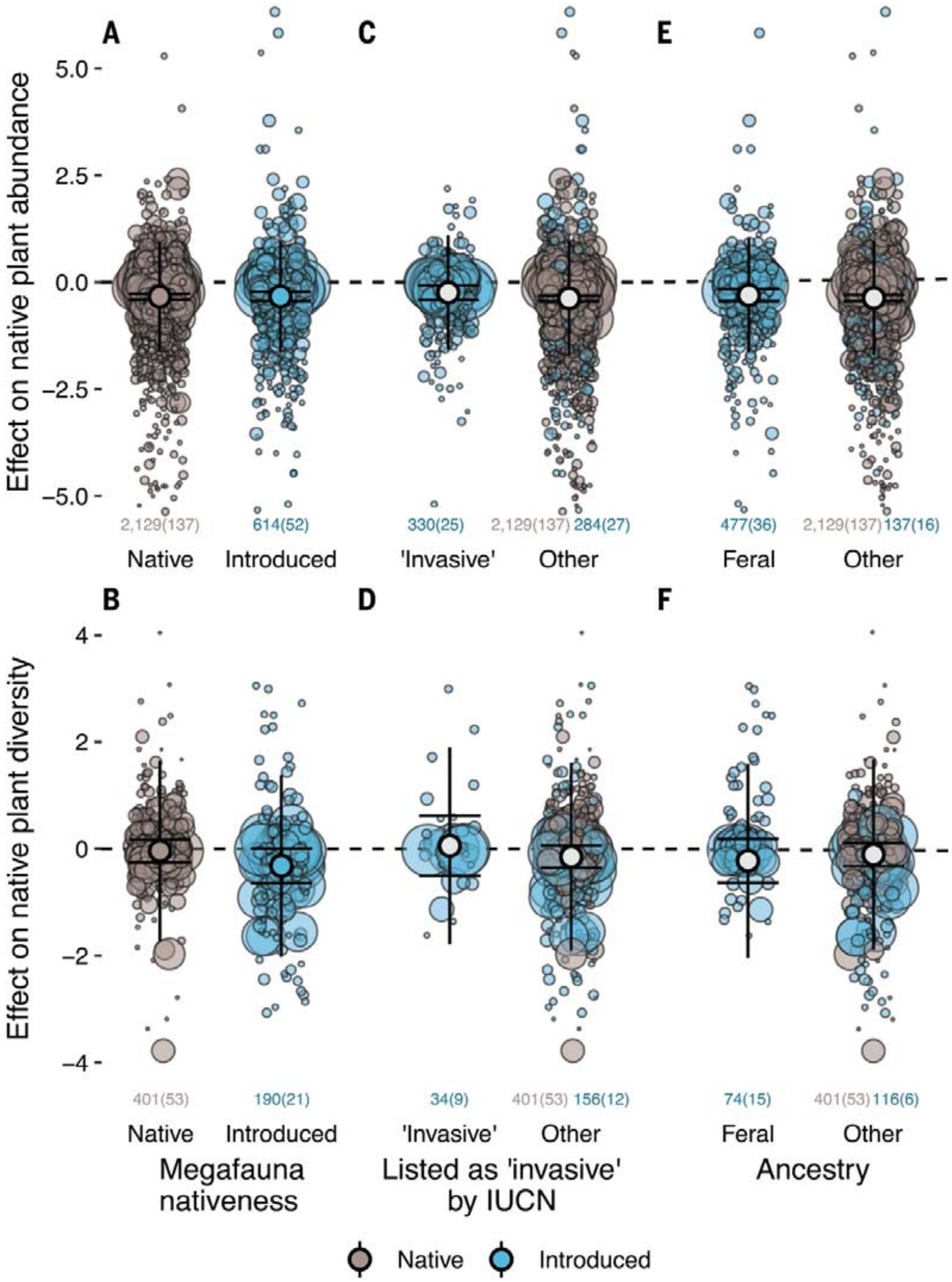

Fig. 1. Native, introduced, "invasive," and feral megafauna have similar effects on native plant abundance and diversity.

(**A** and **B**) There was no evidence that native (gray) and introduced (blue) megafauna had different effects on native plant abundance (A) or native plant diversity (B). (**C** and **D**) There was no evidence that introduced megafauna considered among the world's 100 "worst" invasive species (*27*) and feral megafauna (**E** and **F**) had different effects than other megafauna. The horizontal dashed lines indicate no effect on plant abundance or diversity. Points indicate individual responses, with size indicating the inverse of sampling variance, with larger points thus having greater influence on the model. Model estimates are shown with points, with 95% confidence intervals (horizontal error bars) and prediction intervals (vertical bars). Text annotations state the number of plant responses, with the number of studies in parentheses. IUCN, International Union for Conservation of Nature.

However, not all introduced megafauna are considered equally problematic. “Invasive” megafauna are thought to have uniquely detrimental effects on ecosystems (*27*), and some argue that feral megafauna (wild but descending from domestic populations) have distinct effects due to human selection on their ancestors (*28*). However, there was no evidence that the effects of “invasive” megafauna (n = 3 species) or of feral megafauna (n = 6) on native plant abundance and diversity were different from the effects of other megafauna (Fig. 1, C to F; invasive: contrast P values = 0.15 to 0.50; feral: contrast P values = 0.41 to 0.60). Neither of these factors improved model quality (LRT P values = 0.15 to 0.62).

Introduced megafauna are considered to have particularly distinctive effects on oceanic islands, whose biota did not evolve with mammalian megafauna (*29*). Likewise, it has been suggested that introduced megafauna may promote introduced plants more than native megafauna do, especially on oceanic islands, in a process called an “invasional meltdown” (*30*). We thus analyzed the effects of native and introduced megafauna on oceanic islands relative to continents and offshore islands, whose biota have been exposed to mammalian megafauna for millions of years. Because of limited sample size, we grouped plant abundance responses on continents and offshore islands (*26*).

On continents and offshore islands, native and introduced megafauna alike had similarly negative effects on native plant abundance (Fig. 2A; omnibus P values < 0.0001, contrast P value = 0.94) and neutral effects on introduced plant abundance (Fig. 2B; omnibus P values = 0.25, contrast P value = 0.35). There was no evidence that the effects of introduced megafauna on oceanic island native plant abundance were different from the effects of native megafauna on continents and offshore islands (Fig. 2A; contrast P value = 0.82), and there was no evidence that introduced megafauna on oceanic islands increased the abundance of introduced plants relative to native ones (Fig. 2, A and B; contrast P value = 1.0). The inclusion of megafauna nativeness or landform evolutionary history did not improve model quality relative to models containing only plant nativeness (LRT P values = 0.16 to 0.17).

There was also no evidence that native and introduced megafauna had different effects on native plant diversity on continents or offshore islands (Fig. 2C; contrast P values = 0.59 to 0.83). Nor was there evidence that introduced megafauna on oceanic islands had different effects than native megafauna on offshore islands or continents (Fig. 2C; contrast P values = 0.22 to 0.97). Introduced and native megafauna also had similar effects on introduced plant diversity (grouped across landforms because of insufficient sample size; Fig. 2D; contrast P value = 0.89). As with abundance, these effects tended to be more neutral than their effects on native diversity, but not significantly so (contrast P values = 0.08 to 0.81).
Instead, megafauna, both native and introduced (contrast P values = 0.69 to 0.79), tended to have more negative, albeit nonsignificant, effects on plant diversity on islands (both offshore and oceanic) relative to continents (Fig. 2C; Hedges’ g, [95% confidence intervals]: continents = 0.01, [−0.2, 0.2], islands = −0.53, [−1.0, −0.1], contrast P value = 0.06). The inclusion of megafauna nativeness or landform evolutionary history did not improve model quality (LRT P values = 0.38 to 0.63), but landform itself (island versus continent) did (LRT P values = 0.02).

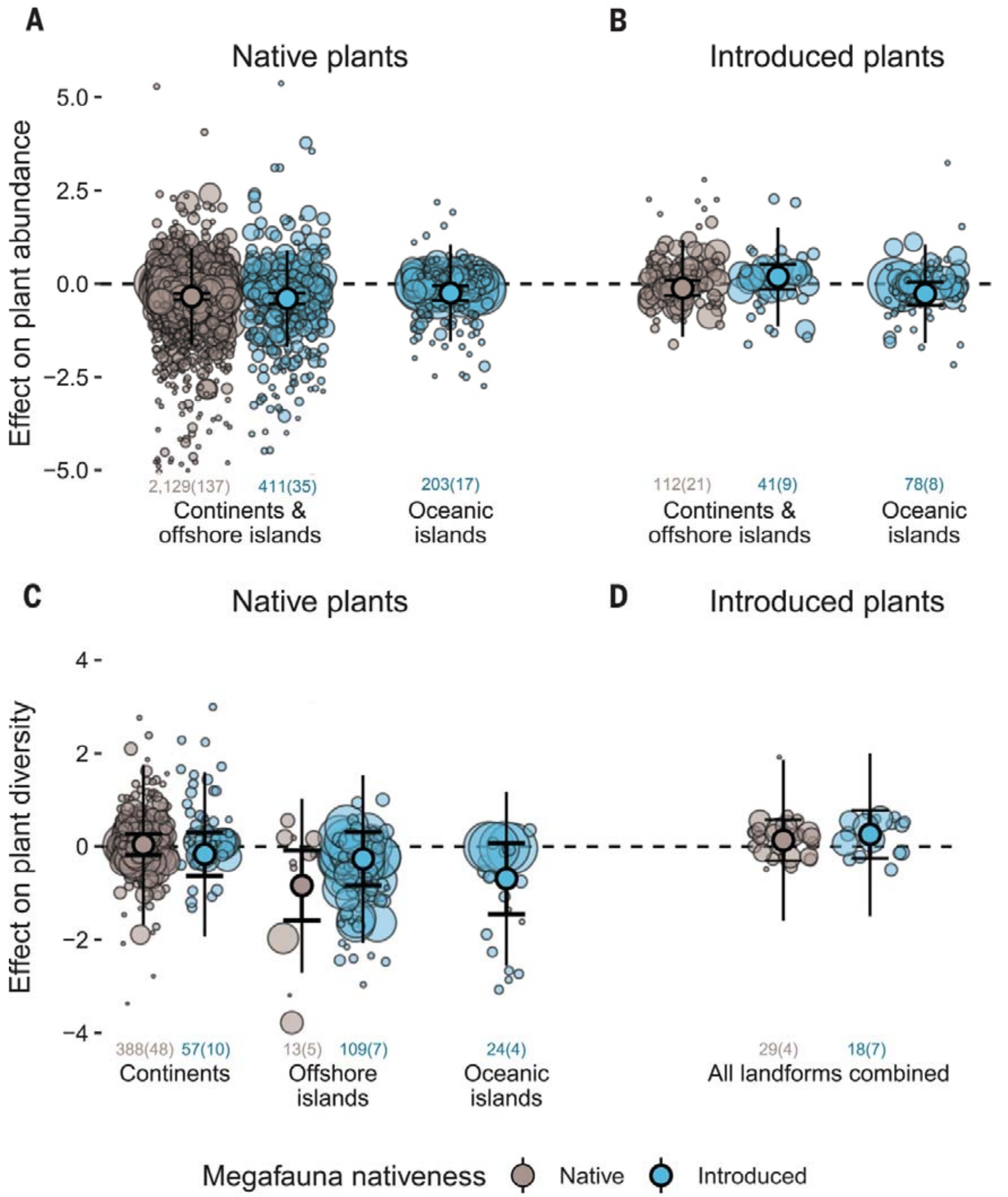

Fig. 2. Nativeness and landform evolutionary history do not influence megafauna impacts on plant abundance or diversity.

There was no evidence that native and introduced megafauna had different effects on (**A**) native or (**B**) introduced plant abundance, regardless of landform evolutionary exposure to mammalian herbivorous megafauna. Continents and offshore islands were grouped owing to insufficient sample size. (**C**) There was no evidence that native or introduced megafauna had different effects on native plant diversity on continents, offshore islands, and oceanic islands. Instead, there was strong evidence that megafauna, native and introduced, tend to suppress diversity on islands (both offshore and oceanic) relative to continents. (**D**) There was no evidence that introduced megafauna facilitate introduced plant diversity more than native megafauna do. Introduced plant diversity responses were analyzed across all landforms owing to insufficient sample size. All planned contrast tests between native and introduced megafauna were nonsignificant.

No evidence that coevolutionary history shapes megafauna impacts

Some introduced megafauna interact with plant species with which they have shared a native range and with which they have potentially coevolved (*13*). The effects of megafauna on these plants are expected to be distinct from the effects of megafauna on noncoevolved plants, such as herbivory-sensitive oceanic island endemics (*31*). To test this, we focused on species-level plant abundance responses (N = 1247) and compared the plant species distribution [from (*32*)] to reconstructed megafauna distributions in the absence of extinctions and range contractions and under modern climate (*26*, *33*). We found that megafauna had similar effects on plant species regardless of whether they shared a native range ("coevolved") or whether they only recently began interacting, following the introduction of either the megafauna or the plant species (Fig. 3A; contrast P value = 0.24).

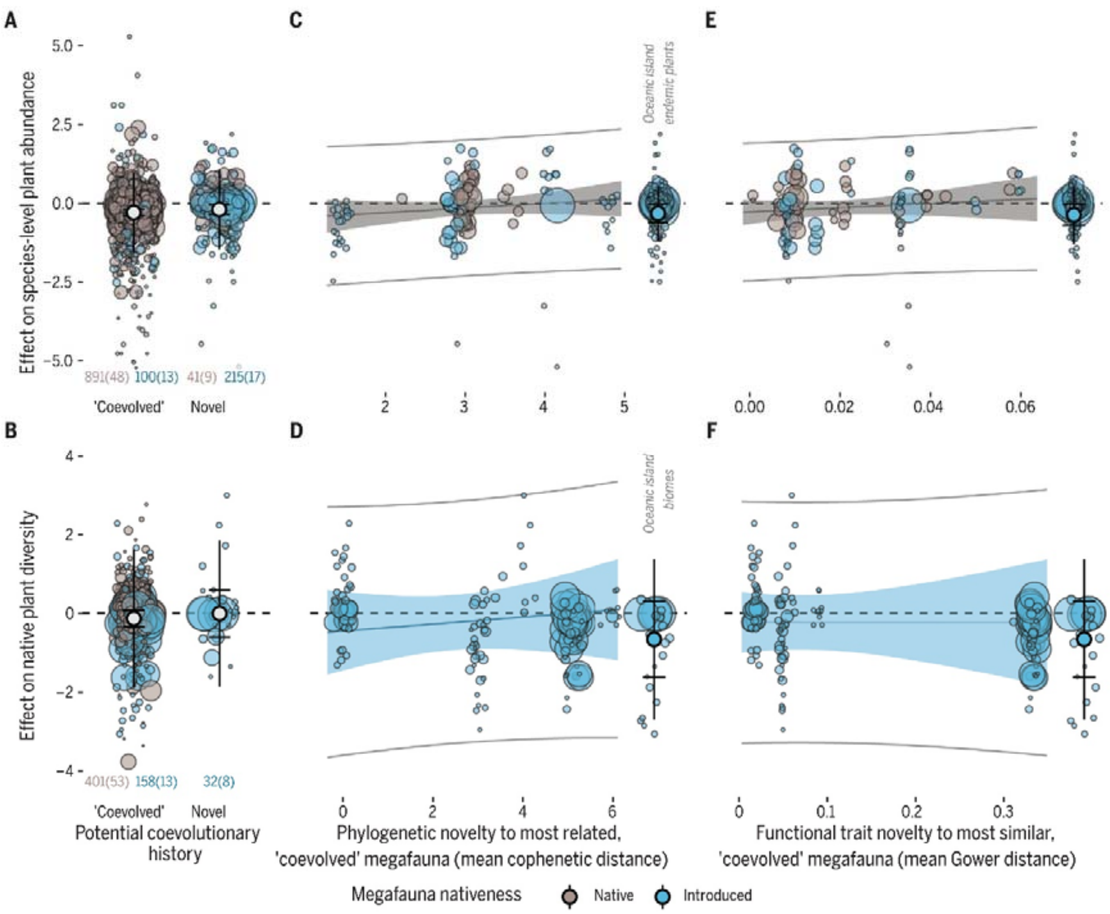

Fig. 3. Coevolutionary history and phylogenetic and functional novelty of introduced megafauna do not shape effects on native plant abundance or diversity.
(**A**) There was no evidence that megafauna impacts on species-level plant abundance were affected by whether the plant and megafauna species have shared a native range and have potentially coevolved ("Coevolved") relative to megafauna-plant species pairs whose native ranges do not overlap ("Novel"). Introduced plants are included in this analysis. (**B**) There was no evidence that megafauna impacts on local plant diversity were influenced by whether a megafauna shared potential coevolutionary history with the study area biome (e.g., introduced from a continent to an offshore island in the same biome, or introduced within the megafauna's prehistoric distribution). (**C** to **F**) There was no evidence that the phylogenetic or functional novelty of "novel" introduced megafauna relative to the most similar "coevolved" megafauna shaped their effects on native plant abundance [(C) and (E)] or native diversity [(D) and (F)]. Novelty was estimated as cophenetic distance and Gower distance, respectively. Oceanic island endemic plants and oceanic island biomes, which have no evolutionary

history with any mammalian megafauna, are indicated on the far right of (C) to (F). All novelty measures are community-wide averages, weighted by relative biomass per megafauna species. Model estimates for (C) to (F) are shown with solid lines, with 95% confidence intervals shown with shaded belts and prediction intervals shown with ribbons.

To explore effects on plant diversity, we tested whether biomes that share evolutionary history with the introduced megafauna (e.g., introduced horses *Equus caballus* in their prehistoric North American distribution) are differentially affected compared with biomes with novel megafauna species (e.g., introduced horses in Australia). To do so, we compared the introduced megafauna to prehistorically native megafauna in the study location's biome (using the same reconstructed megafauna distributions as above). Megafauna introduced from continents to adjacent offshore islands within the same biome were considered coevolved. We found no evidence that coevolved megafauna have different effects on native plant diversity than evolutionarily novel introduced megafauna (Fig. 3B; contrast P value = 0.70). Neither of these estimates of coevolutionary history improved model quality (LRT P values = 0.24 to 0.70; table S2).

Some, ourselves included (*5*), have suggested that introduced megafauna that are closely related or functionally similar to prehistoric native megafauna may have more positive effects on native plants than do more phylogenetically or functionally novel introduced megafauna. We tested this by calculating the phylogenetic and functional novelty between each introduced megafauna and the most similar prehistoric native species (*26*). Contrary to our predictions, we found no evidence that phylogenetic or functional novelty influenced the effects of megafauna on species-level plant abundance or on native plant diversity (Fig. 3, C and F; P values = 0.23 to 0.99). Neither of these factors improved model quality (LRT P values = 0.24 to 0.99).

Strong evidence that functional traits shape megafauna impacts

We then tested a suite of factors (n = 24) hypothesized to influence megafauna impacts. These factors may have obscured cryptic differences between native and introduced megafauna but may also provide ecological explanations for megafauna impacts. These included megafauna functional traits (body mass, dietary selectivity, fermentation type, dietary preference for grazing relative to browsing), environmental variables (maximum annual temperature and precipitation, absolute latitude, human footprint index, and net primary productivity), megafauna diversity (species and functional group richness), and methodological factors (duration of megafauna exclusion and measurement scale) (*26*). Megafauna functional traits were relativized by relative biomass per community (available for 78.4% of observations) (*26*).

For each variable, we used likelihood ratio tests to compare an intercept-only null model, a model containing the variable, and a model containing the variable as well as megafauna nativeness (see table S2). We then tested for significant differences between native and introduced megafauna while controlling for each variable (*26*).

Megafauna nativeness did not improve model quality for any model, which suggests that nativeness provides negligible information value (LRT P values = 0.10 to 0.97; table S2). Likewise, we found no significant difference between the effects of native and introduced megafauna when controlling for functional traits, environmental and methodological variables, or megafauna community richness (contrast P values = 0.09 to 1.0).

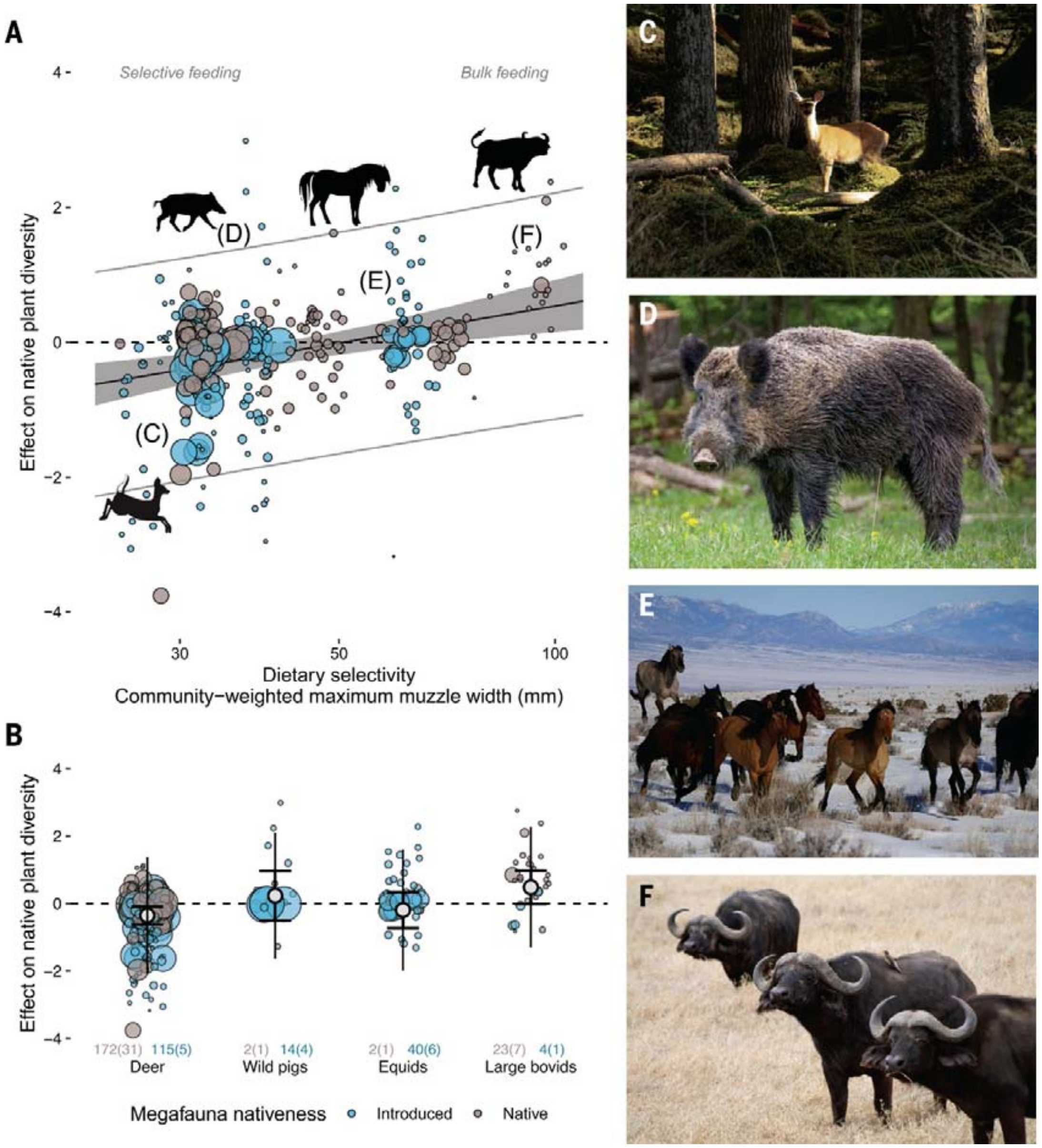

Fig. 4. Dietary selectivity influences megafauna impacts on plant diversity.
(**A**) There was strong evidence that megafauna communities dominated by bulk-feeding generalists increased local plant diversity. Dietary generalism was estimated with muzzle width of each megafauna community (maximum, weighted by relative biomass per species; see fig. S3 for mean muzzle width). Letters in the plot indicate the taxa highlighted in (C) to (F). [Icons: Gabriela Palomo-Munoz, Jan A. Venter, Herbert H. T. Prins, David A. Balfour, and Rob Slotow (vectorized by T. Michael Keesey)] (**B**) Effect sizes for select groups of representative taxa from communities where these species constitute >50% of total megafauna biomass. Deer include all Cervidae, and wild pigs include all Suidae (primarily introduced wild boar, *Sus scrofa*). Equids include all Equidae but primarily feral horses (*Equus ferus caballus*). Large, broad-muzzled bovids include the genera *Bison*, *Bos*, and *Syncerus.* (**C**) Native and introduced deer can reduce plant diversity by selectively browsing preferred plants (*49*, *50*). [Photo: Murray Foubister] (**D**) Pigs are distinct for belowground foraging and are dietary generalists, despite their relatively narrow muzzles (*51*). Feral pigs often increase plant diversity, at times doubling native plant diversity by suppressing competitive dominants (*52*). [Photo: Valentin Panzirsch] (**E**) Feral horses (*E. ferus caballus*) appear to have mixed effects on local plant diversity. (**F**) Bulk-grazers, like cape buffalo (*Syncerus caffer*) and bison (*Bison bison*), tend to increase plant diversity (*53*). Our results suggest that this is driven by their inability to selectively feed, forcing them to consume the most abundant (i.e., competitively dominant) plants. [Photo: Stig Nygaard]

Instead, we found strong evidence that dietary selectivity best explained the effects of megafauna on native plant diversity (slope = 0.26, *P* value = 0.0002, LRT *P* value = 0.002). Communities dominated by selective feeders tended to decrease diversity, whereas communities dominated by nonselective bulk feeders tended to increase diversity (Fig. 4 and fig. S3). Dietary selectivity was estimated with muzzle width, as larger-muzzled megafauna are limited in their ability to select preferred plants (*34*) and are therefore more likely to consume competitively dominant ones, thus freeing subdominant species from competition (*35*).

Larger-bodied megafauna communities also had more positive effects on native plant diversity (fig. S4; slope = 0.20, *P* value = 0.02, LRT *P* value = 0.03). This was not a function of megafauna biomass, which did not influence plant diversity (fig. S5, biomass/net primary productivity: slope = 0.10, *P* value = 0.21), supporting the observation that larger megafauna are not equivalent to a similar biomass of smaller megafauna (*2*).

Megafauna dietary preference for graminoids also influenced their effects on different plant growth forms (diversity LRT *P* value = 0.01; abundance LRT *P* value = 0.006; table S2), with a negative relationship on graminoid abundance and diversity (fig. S6; *P* values = 0.001 to 0.01); a positive relationship with forbs (*P* values = 0.02 to 0.03); but with nonsignificant effects on woody plants (*P* values = 0.09 to 0.54).

Megafauna impacts on plants were not shaped by any environmental variable (table S2) or any megafauna diversity measure (i.e., species or functional group richness; fig. S7). However, megafauna diversity had a significant negative interaction with introduced plant abundance (fig. S8; *P* value = 0.02), supporting that more diverse megafauna communities may suppress introduced plant dominance (*36*). While megafauna body mass and its interaction with plant nativeness also improved model quality, this relationship was nonsignificant (fig. S9; *P* value = 0.09).

Discussion

We found that theory developed in native systems explains patterns across native and novel ones (*37*), with nonselective and larger megafauna tending to have more positive effects on plant diversity. Many prehistoric assemblages were dominated by large-bodied bulk-feeding megafauna (*38*). Overexploitation, agriculture, and predator persecution has led to communities dominated by small, selective feeders (*39*). The restoration of predators and large megafauna, that is, trophic rewilding (*40*), would likely shift biomass back toward larger-bodied bulk feeders (*41*) with implications for plant diversity.

We found no evidence that nativeness shapes the effects of megafauna on plants. Our results are corroborated by other meta-analyses that have failed to find consistent differences between the effects of native and introduced organisms (*42*). While some introduced organisms, particularly specialists or predators on islands, may have distinct effects relative to native species, our results suggest that generalizing to megafauna is empirically unjustified and a conflation of history with ecology.

We note that our analyses did not consider subtleties in compositional change nor other aspects of ecosystem functioning [soil, arthropods, other vertebrates, etc., but see (*43*)]. Our results suggest that these factors will also be shaped by functional traits (fig. S6) as well as by contexts not captured in our analysis, such as predation (*44*). Thus, as with native megafauna, introduced megafauna may come into conflict with the conservation of other species. We suggest that ecological reasoning provides better insight into such conflicts than do notions of nativeness.

We evaluated megafauna impacts at the plot scale, a key scale for understanding local vegetation dynamics. However, negative effects on plant diversity at the plot scale can scale up to positive effects at landscape scales if megafauna use areas at different intensities, thereby increasing landscape heterogeneity [(*45*), but see fig. S10]. Moreover, care should be taken in inferring the effects of megafauna on plant populations themselves from plot-scale data. The effects of megafauna on herbivory-sensitive oceanic island endemics (*31*) will be masked at the plot scale if those plants are already locally extirpated. The persistence of these species will likely depend on the availability of refugia, as in native systems, where herbivory-sensitive plants are often restricted to inaccessible habitats [e.g., cliffs (*46*)].

Given their similar impacts, the same empirical claims used to argue for the eradication of introduced megafauna could be used for any megafauna, except for a key normative difference: native megafauna are considered to "belong," while introduced ones are not. As such, the effects of introduced megafauna can be described as "harmful," regardless of what those effects are [e.g., (*47*)]. The intrusion of normative values into science not only excludes those with different beliefs and reduces public trust in science (*48*) but can also hinder the conservation of wild and diverse ecosystems (*11*). We argue that the effects of introduced megafauna should be studied as any other wildlife would be studied, through the lens of functional ecology, with the normative dimensions of their "belonging" considered separately and with transparency.

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Competing interests: The authors declare that they have no competing interests.

Data and materials availability: All data and the core analysis scripts are provided in Dryad (*24*).

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