

REVIEW

Integrating functional traits into trophic rewilding science

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Abstract

1. Trophic rewilding is gaining rapid momentum as a means of restoration across the world. Advances in research are elucidating the wide-ranging effects of trophic rewilding and megafauna re-establishment on ecosystem properties and processes including resilience, nutrient cycling, carbon sequestration, productivity and plant richness.
2. A substantial gap remains in trophic rewilding research on how rewilding affects the frequency and expression of plant functional traits, a key hypothesised avenue by which megafauna can affect biodiversity and ecosystem processes. Yet, there is extensive literature examining the effects of mammal herbivory and exclusion on plant traits from which we may infer potential effects of megafauna reintroductions.
3. Here, we synthesise the literature to show the multifaceted ways that plant functional composition responds to mammalian herbivory and explore how these responses are modulated by the density and identity of herbivores as well as resource availability, ecosystem productivity and historical contingency. We further explore these interactions in a quantitative analysis on European plant species. In addition, we link these broad patterns between mammal herbivory and traits to literature on plant invasions to predict how trophic rewilding may be able to reduce invasive plant dominance, as ecosystems around the world are transitioning towards novel states, occupied by a mix of native and introduced species.
4. Expanding current research on herbivore effects (and their implications for trophic rewilding) beyond plant species richness and towards measurable functional traits can help assess and quantify processes that were not previously possible. Trait approaches can help to test mechanistic hypotheses on the top-down impacts of large herbivores on plant communities to reveal links between trophic rewilding and ecosystem processes and properties.
5. *Synthesis.* Given the rapid, much-needed expansion of restoration and rewilding activities across the world, trait-based ecology offers a pathway to generalisable predictions of the ecosystem impacts of rewilding, particularly in the context of both the unique landscape processes associated with rewilding (e.g.

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landscape scale spatiotemporal variability, dispersal) and of widely emerging novel ecosystems.

KEYWORDS

functional traits, grazing, herbivory, invasion ecology, large mammals, novel ecosystems, plant-herbivore interactions, trophic rewilding

1 | INTRODUCTION

Restoration and rewilding are an increasingly popular means to increase the biodiversity and function of degraded ecosystems (Carver et al., 2021; Gann et al., 2019). However, most current terrestrial restoration activities do not fully restore biodiversity to reference levels over timescales commonly captured by direct observation (Atkinson et al., 2022; Crouzeilles et al., 2016; Jones et al., 2018). Furthermore, given that abiotic and biotic drivers of global change are reaching historically unprecedented levels, attaining such reference targets is increasingly unfeasible (Kerr et al., 2023; Williams et al., 2021). Compounding these issues, there is growing demand for restoration and rewilding activities across the world and commitments to do so from industry and government, presenting a new set of logistical and financial opportunities and challenges. While passive restoration approaches may offer landscape-scale and cost-effective restoration of many degraded areas (Huang et al., 2019; Prach & del Moral, 2015), these are most effective in less degraded ecosystems (Reid et al., 2018). Simultaneously, trophic rewilding has emerged as a restoration approach over the past two decades (Guyton et al., 2020; Schmitz et al., 2023; Svenning et al., 2016, 2024; Sweeney et al., 2019). This approach broadly aims to 'restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems' and often involves the reintegration of extant large herbivores and carnivores as they disproportionately affect ecosystem processes (Svenning et al., 2016). Following initial (re-) introduction, a hands-off management approach that achieves reduced human agency is strived for.

As a conservation and restoration tool, trophic rewilding has shown utility from relatively 'intact' areas and nature reserves to more degraded and marginal areas with disrupted dispersal networks and areas with an overabundance of introduced or native species (Bonavent et al., 2023; Dvorský et al., 2022; Guyton et al., 2020; Sweeney et al., 2019; Vidal et al., 2013). Nonetheless, we still lack the capacity to predict the outcomes of trophic rewilding across environmental and ecological conditions, including novel ecosystems (Brudvig & Catano, 2021). Predicting ecological dynamics in novel ecosystems, that is, self-sustaining systems without historical precedent in environmental conditions or biotic composition that cannot be reverted to the historic state (Hobbs et al., 2006), will be key to future restoration efforts as novel ecosystems are spreading rapidly (Hobbs et al., 2009). Finding new ways to better predict the outcomes of restoration and rewilding activities over the longer term will aid in planning and prioritisation.

Public and scientific interest in trophic rewilding is increasing. However, there remains a need for greater mechanistic understanding of the effects of megafauna restoration on biodiversity and ecosystem processes across environments (Forbes et al., 2019), differing ecosystem starting points (Schweiger et al., 2019), at large spatial scales (but for examples of larger scale studies, see Gordon et al., 2023; Guyton et al., 2020; Tanentzap et al., 2023) and in terms of differing faunal composition (e.g. with or without megaherbivores or large carnivores; Trepel et al., 2024). Here, we explore the idea that the application of trait-based approaches to understanding the consequences of the reinstatement of trophic complexity has the potential to fill this gap, complementing emerging evidence that a trait focus can improve our understanding of plant community responses to trophic rewilding (Pringle et al., 2023; Trepel et al., 2024). A complimentary recent meta-analysis highlights that utilising animal functional traits can improve the prediction of herbivore effects on vegetation compared to using nativeness (Lundgren et al., 2024). While trophic rewilding and the restoration of large mammal communities involve a range of processes and associated effects, here, we largely focus on herbivory. Expanding current research on the effects of herbivore reintroduction beyond plant species richness and towards functional traits can help to understand the effects of trophic rewilding on environments (and processes therein) that have not yet been widely investigated (Forbes et al., 2019; Laughlin, 2023a), and act as a means to test mechanistic hypotheses on the top-down impacts of large herbivores on plant communities in contexts relevant for trophic rewilding. 'Functional traits' are defined as morpho-physio-phenological characteristics which impact fitness indirectly via their effects on growth, reproduction and survival, which then in turn may enable the prediction of ecosystem function (Lavorel & Garnier, 2002; Violle et al., 2007). Explicit linkages between rewilding and the functional trait distributions in plant communities remain rare (though see Potter et al., 2022).

In this review, we broadly explore this gap and review existing literature on the effects of herbivory, particularly of megafauna (i.e. animals ≥ 45 kg body mass; Moleón et al., 2020), on plant traits. We highlight that trait-based approaches may enable a more generalisable link to the ecosystem function of the resident plant communities, and hence many other taxa, at rewilding sites and beyond. Furthermore, traits provide a way to create generalisable indices that are not confounded by taxonomy and can be applied across different ecosystems, which we see as particular utility amidst the global emergence of novel ecosystems (Hobbs et al., 2006; Radeloff et al., 2015) caused by anthropogenic global change. We conduct a

case study utilising two new continental-scale databases of species' grazing and productivity requirements in the European flora (Midolo et al., 2023; Tichý et al., 2023) to explore generality in trait herbivory patterns. We then link these ideas with invasion biology to generate a set of hypotheses for how trophic rewilding could be used to restore ecological links and processes to increase community functional diversity in part by reducing the overabundance of plant species with certain trait combinations.

2 | STRATEGIES FOR COPING WITH MAMMALIAN HERBIVORY

Plants have evolved alongside herbivory pressure, including from mammalian megafauna, for the last 50 million years (Butler et al., 2010; Huang et al., 2023; Sanisidro et al., 2023) and therefore have directly and indirectly developed a wide diversity of traits to avoid, resist and tolerate being eaten (Charles-Dominique et al., 2016; Dantas & Pausas, 2020; Dawkins et al., 1979). Here, we use the definitions of these strategies sensu Archibald et al. (2019), where before defoliation, plants exist along an avoidance-attractance spectrum (i.e. palatability); during defoliation, they may resist consumption by possessing physical or chemical traits that enable them to protect tissues from being eaten; and lastly plants may tolerate herbivory by surviving an event through compensating overall fitness impacts through compensatory growth or reproduction.

Recent palaeoecological studies provide quantitative evidence of megafauna-plant trait relationships over very long timescales, showing that Quaternary extinctions of megafauna in southeastern Australia are associated with decreases in large-seeded and -fruited species (Adeleye et al., 2023). By evolving seeds and fruits consumed by megafauna, many plants can gain a dispersal benefit in the presence of large herbivores (Guimarães Júnior et al., 2008; Pires et al., 2018) given their particularly high impact on dispersal capacity of plant propagules (Fricke, Ordonez, et al., 2022). Indeed, the role of megafauna in seed dispersal has been elucidated (Fricke, Ordonez, et al., 2022; Vellend et al., 2003; Vidal et al., 2013; Wunderle, 1997), including in species with fruits not directly targeted by megafauna (Janzen, 1984).

Spines, thorns and prickles on leaves or stems or whole-plant traits such as particular canopy architectures can help to resist herbivory from mammals. Evidence shows that spinescence relates to the Eocene expansion of herbivorous mammals and increases in regional aridity in central Tibet (Zhang et al., 2022), and similar patterns are reflected across the continents through the Cenozoic (Gélin et al., 2023). Moreover, plants may redirect resources below ground to ensure persistence during grazing from above (Dalglish & Hartnett, 2006; Qian et al., 2017). Conversely, simply growing tall can be an effective means to escape the reach of herbivores and avoid herbivory altogether (Staver & Bond, 2014). Furthermore, low-growing grasses can tolerate herbivory by growing fast enough (or resist herbivory by growing very close to the ground), and this compensatory growth is a common strategy to cope with grazing in open

ecosystems (McNaughton, 1979) and can outpace herbivory with sufficient resources (Borer et al., 2020). In a large quantitative synthesis of the literature, Díaz et al. (2007) show that grazing consistently reduces the abundance of taller growing species. Timmermann et al. (2015) show a consistent pattern across Danish semi-natural ecosystems that have undergone reductions in grazing, with taller species 'winning' over time. However, the capacity of plant communities to tolerate and regenerate from grazing such as in grazing lawns depends on rainfall, site productivity, herbivore densities and both herbivore and plant community composition (Hempson et al., 2015; McNaughton, 1986; Roberts et al., 2011). Plant communities in higher productivity systems should more viably be able to pursue a tolerance strategy of compensatory growth compared to less productive areas where the negative effects of the loss of leaves and tissues are stronger resulting in a prevalence avoidance and resistance strategies.

Certain 'fast' or 'acquisitive' leaf economic trait values (Reich, 2014), such as low leaf dry matter content (LDMC) and high leaf nutrient content, are positively associated with plant palatability (avoidance-attractance spectrum; Archibald et al., 2019; Agrawal & Kotanen, 2003; Moles et al., 2013; Westoby et al., 2002). Some of these traits are also indicative of a species growth rate and so may be related to an individual plants ability to tolerate herbivores via compensatory growth. In general, smaller leaves may allow plants to avoid herbivory during the vulnerable stage of leaf expansion (Moles & Westoby, 2000), though more empirical evidence is needed. Likely, such a pattern would be dependent on herbivore assemblage characteristics (size, feeding mode) and coordination with other plant defences. Defence against herbivory is indirectly a part of the spectrum of leaf lifespan (Westoby et al., 2002) and specific leaf area (SLA; or its inverse, leaf mass per unit area), where lower SLA leaves may deter herbivores. However, this effect may also depend on herbivore type, for example, being shown to vary between deer and sheep, with a stronger selectivity for higher SLA species by deer (Lloyd et al., 2010). In addition, some plants, particularly grasses, may silicify to reduce herbivory (Cooke et al., 2016; de Tombeur et al., 2023).

Empirical studies of large herbivore exclusion or manipulation show some consistent responses in community-weighted mean (CWM) traits to grazing, though sometimes not in the direction expected given the predicted relationship between palatability and leaf economic traits. For instance, Török et al. (2018) show that CWM SLA increased with grazing intensity across four different grassland types, contrary to the expectation that species with higher SLA leaves should be less able to deter herbivory. Equally, Niu et al. (2016) document increases in CWM leaf nutrient content (C, N and P), SLA and decreased LDMC in response to grazing, showing a selection pattern for species with faster growth and regrowth in these systems. Jiang et al. (2023) show that grazing can increase CWM 'conservative' traits (i.e. increased CWM LDMC, leaf C:N ratio, lower SLA and leaf foliar nutrients) and van der Plas et al. (2016) show via factorial exclusion of difference herbivore size classes that smaller ungulates quickly shifted communities towards dominance

of low SLA and low nutritional value via selective grazing of more palatable species. In the same work, large grazers had a similar but more delayed impact on trait values, indicating a different dynamic of herbivore impacts on traits in the community depending on the herbivore functional traits (van der Plas et al., 2016). It should be noted that CWM traits are not the most robust means of modelling community change, being prone to type I error (Miller et al., 2019), with new methods emerging that help to reduce these potential errors (Maitner et al., 2023).

These contrasting results are not necessarily inconsistent with each other and may be indicative of the differences in non-selective herbivores consuming both 'fast' and 'slow' species resulting in a decreased relative abundance of slow species versus more selective herbivores reducing the abundance of more palatable species. Divergent results may also occur for a variety of other reasons. For instance, the initial composition of the plant community and the temporal extent of the study could have strong effects on community trait responses to trophic rewilding (e.g. Schweiger et al., 2019), or larger herbivores may favour specific functional types (Bråthen et al., 2021). Additionally, longer or shorter grazing histories may alter a regional species pool (Schweiger et al., 2019). There is broad evidence of defence traits coupled with leaf economic traits (Armani et al., 2020). First, lower SLA species have a general purpose defence via an increase in toughness, which can broadly limit herbivory (Hanley et al., 2007; Onoda et al., 2011; Westoby et al., 2002). Second, producing defensive compounds and structures has a higher opportunity cost in shorter lived species (Bryant et al., 1983), and this has been theorised and shown empirically as the resource availability hypothesis (Coley et al., 1985; Endara & Coley, 2011). While palatability has been associated with leaf economic spectrum (Westoby et al., 2002), recent work shows that leaf calcium and magnesium concentrations (a second axis of leaf chemistry rarely considered) are better predictors of overall digestibility (Mládková et al., 2018). These traits, while largely unexplored (Těšitel et al., 2021), may be an important characteristic of determining the effects of herbivores on plant communities. Indeed, trophic rewilding may itself change nutrient transport (Doughty et al., 2016), resulting in zoogeographical effects on plant nutrient composition (Le Roux et al., 2020; Sitters et al., 2017). Interestingly, the effects of mammal herbivory on nutrient cycling may be best explained by the traits of the plant community (du Toit & Olff, 2014).

As mentioned above, spinescence is strongly linked to resisting mammal herbivory and is employed in many different shapes and sizes. However, the degree of expression such physical defence ('resistance') traits (e.g. spine length, prickle density) can be highly plastic and therefore more indicative of herbivore pressure faced by an individual rather than indicative of a species constitutive adaptation to herbivore defence (Göldel et al., 2016; Mithöfer & Boland, 2012; Pérez-Harguindeguy et al., 2013; Wigley et al., 2020). However, not all species respond to herbivore pressure by altering the expression of spinescence. In some species, spinescence is entirely constitutive (e.g. many members of the Cactaceae—though this may be in part to their role in thermoregulation as well as defence), and

many species have simply not evolved spines. In multiple syntheses of herbivory defences, Moles et al. (Moles, Bonser, et al., 2011; Moles, Wallis, et al., 2011) show very limited support for latitudinal gradients in herbivory resistance-related traits, suggesting that this may be indicative of the greater cost of leaf loss in less productive environments (or, that these traits are more strongly driven by abiotic conditions; Janzen, 1974). Song et al. (2020) also show a unimodal relationship between the proportion of spinescent species with elevation in southwestern China. The same work shows a near identical relationship between mid-elevations and herbivorous mammal richness, and therefore, they find a strong linear relationship between herbivorous mammals and spinescence proportion across life forms (excluding annual herbs; Song et al., 2020). Such a relationship may be due to the filtering of physically defended species by herbivorous mammals, or co-evolution as in Africa (Charles-Dominique et al., 2016). In a spine removal experiment, Cooper and Ginnett (1998) show that spinescence also reduces small climbing mammal herbivory. Dantas and Pausas (2020) found that defence traits, including spinescence, are more common in Afrotropical savanna floras compared with neotropical savanna or compared to forest species from either continent (which the authors accredit to contemporary patterns of megafauna). However, in a follow-up study, the same authors also show a legacy of extinct megafauna on wood density, leaf size and spinescence in the neotropics (Dantas & Pausas, 2022). Ford et al. (2014) display the importance of large carnivores in structuring herbivore–plant trait relationships, where reduced impala abundance promotes less herbivory-resistant species of *Vachellia*. Other physical defences to resist herbivory include the development of a cage structured and divaricate growth forms to, for example, defend trees at vulnerable stages (Charles-Dominique et al., 2017; Churski et al., 2022).

Continental-scale analyses of plant defence syndromes have not found globally consistent and distinct syndromes of response to herbivory (Moles et al., 2013). However, regional and within-clade, genus and species studies have found distinct multivariate syndromes with a range of commonalities. Barton et al. (2019) show trait syndromes in woody plants shift during leaf development from chemically defended and fast-growing traits towards more physical defences at later stages of ontogeny. Kempel et al. (2011) show a trade-off between constitutive and induced resistance (measured as damage on undamaged vs. damaged leaves) across a range of species that more competitive species had lower constitutive but higher induced resistance. Gorné and Díaz (2022) show that grass species display more acquisitive trait combinations ('fast' species) following ungulate grazing in a combined field and common garden experiment. In the same study, woody legumes show the opposite intraspecific trait responses, becoming more conservative in leaf traits (Gorné & Díaz, 2022). Interestingly, in a meta-analysis spanning different types of herbivory and plant species, Carmona et al. (2011) found that variation in life-history traits (growth rate, flowering time) and morphological traits (size, branching, physical defences) explained susceptibility to herbivory in many more cases than secondary metabolites. Advances in functional traits with the metabolome have

utility in advancing our understanding of the roles of different metabolites in herbivore adaptation (Walker et al., 2022). The potential clustering of trait responses to large mammal herbivory by different life forms has not been widely investigated but forms an important part of the clustering of trait syndromes. Wigley et al. (2020) provide a handbook for a range of disturbance-related traits, including herbivory, that are stratified across broad life form categories. So, while plants have a myriad of strategies for avoiding, resisting and tolerating herbivory, broad trade-offs and syndromes have yet to be identified. Clear patterns have been described at regional scales or within certain life forms, but mechanistic understanding and predictive capacity lag.

3 | CASE STUDY OF EUROPEAN PLANT SPECIES

Broad patterns in species responses to herbivores can be challenging to quantify across large scales. We used a new database characterising disturbance indicators (specifically we used grazing tolerance) at the species level of the European flora (Midolo et al., 2023) in combination with plant traits from TRY (Kattge et al., 2020; Supporting Information) and ecosystem productivity values (Ellenberg N) from a related data set (Tichý et al., 2023) to conduct a simple broad-scale test of how a few key functional traits relate to a species grazing tolerance (maximum height, LDMC, SLA and leaf nitrogen content). We focused on these traits due to their relevance to growth and life history, as well as their general wide availability. This data set includes both woody and herbaceous species, so does not fully explore the traits unique to herbaceous species (Klimešová et al., 2016). For full details of methods relating to calculating this grazing pressure variable, see Midolo et al. (2023). In brief, for each species, an average 'grazing pressure' is calculated using comprehensive expert

elicitation to estimate the mean fraction of above-ground biomass removed by grazing for the habitat in which the species is typically found, where 0 corresponds to an ungrazed habitat and 1 means that all the vegetation is removed by grazing at least once a year (Midolo et al., 2023). We fit mixed models in R version 4.3.1 (using the 'lme4' package; Bates et al., 2015) of the relationship between each trait and the grazing tolerance value, with nested random effects for family and genus. Therefore, we describe the strength of the relationship using the marginal R^2 (Nakagawa & Schielzeth, 2013).

We found all four tested traits were significantly correlated with a species' grazing pressure, though much of the variance in the data remained unexplained. Maximum height was negatively related to grazing pressure (though very weakly so, $R^2 = < 0.01$; Figure 1). However, we found significant trends away from 'fast' species, towards 'slow' species across the other three traits (decreasing SLA, and leaf nitrogen content and increasing LDMC with increasing grazing pressure; Figure 1). We found that species found in high productivity ecosystems were taller growing than those found in low productivity systems under low to moderate grazing pressure, but this difference was negligible at higher grazing pressure (Figure 2a). Interestingly, when we included an interaction term for Ellenberg N, we found a weaker relationship between SLA and grazing preference in low-productivity ecosystems (low Ellenberg N), potentially reflecting limited suitability of 'fast' strategies (attractor, high tolerance) under higher abiotic constraints (Figure 2b). We found a similar pattern in maximum height with taller species under higher nutrients at low grazing pressure, but no differentiation in species heights at high grazing pressure. In doing so, we illustrate a general tendency for growth-related herbivore tolerance across a wide range of species. These trait values (higher SLA, high leaf N) are traits associated with invasive plants (Ordóñez & Olff, 2013) and early successional species (Lasky et al., 2014), suggesting that heavy grazing might suppress invasive and early successional plants. There are many more

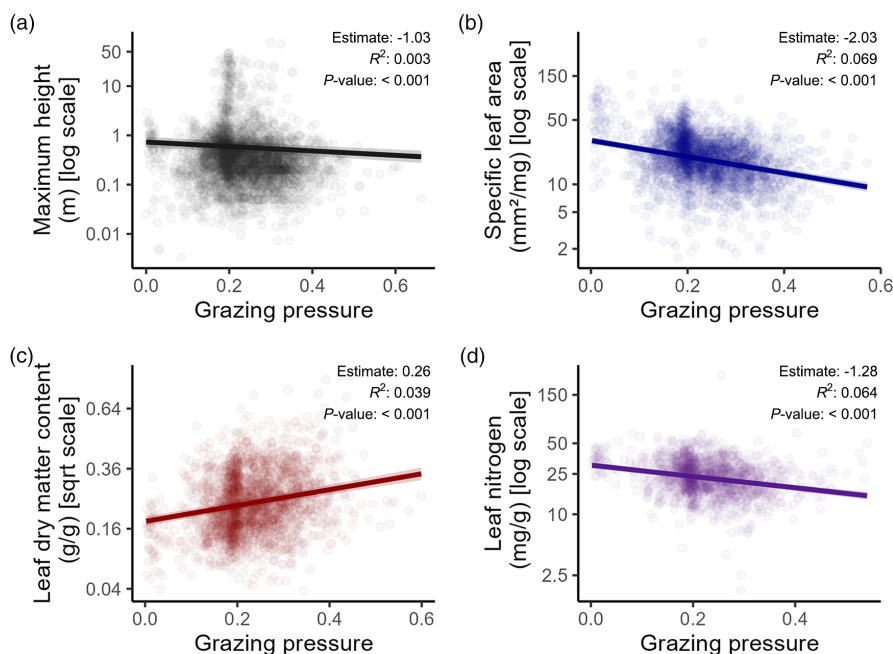
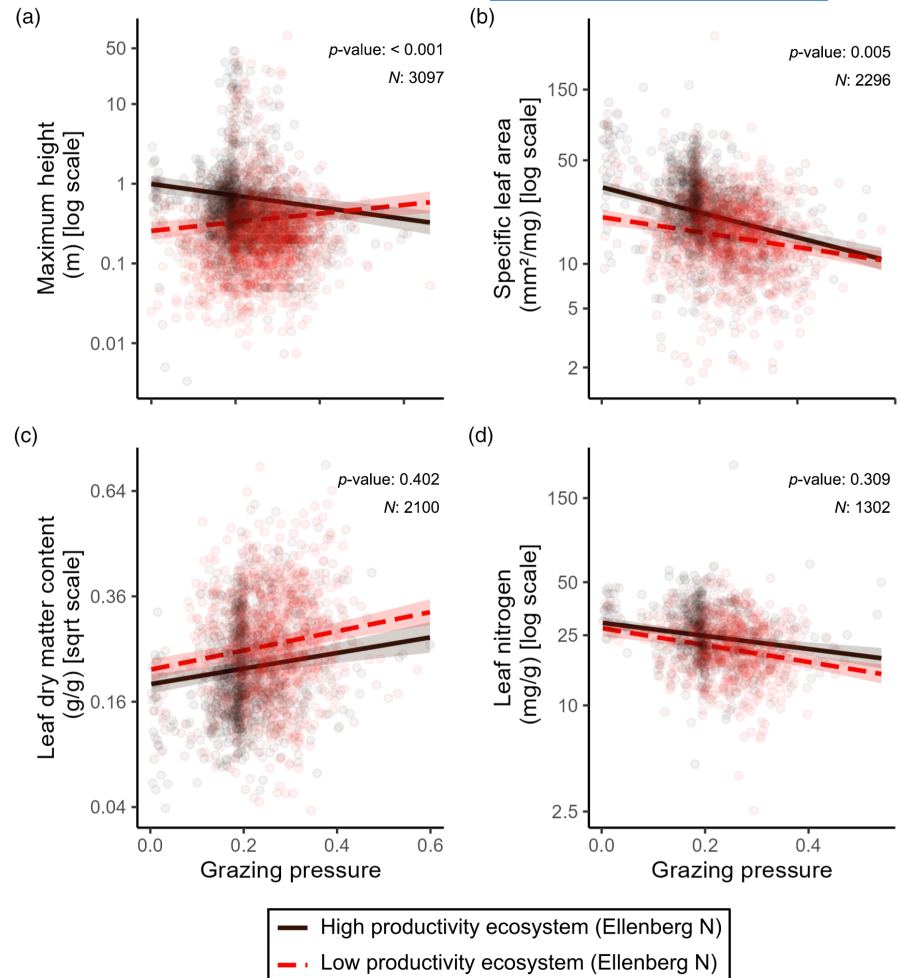


FIGURE 1 Relationship between species' grazing pressure tolerance and four plant functional traits ((a) species maximum height, (b) specific leaf area, (c) leaf dry matter content, and (d) leaf nitrogen content). Each dot represents a species. Sample sizes vary between traits: maximum height ($N=3628$), SLA ($N=2748$), leaf dry matter content ($N=2490$) and leaf nitrogen ($N=1597$). Models were fitted with family and genus as random effects, so the R^2 in each panel reflects the variance explained by grazing pressure only (marginal R^2 ; Nakagawa & Schielzeth, 2013).

FIGURE 2 Interactive relationship between each species' average habitat productivity (measured as Ellenberg's N; Tichý et al., 2023) and average grazing pressure with four plant functional traits ((a) species maximum height, (b) specific leaf area, (c) leaf dry matter content, and (d) leaf nitrogen content). The solid black line is +1 SD, and the dashed red line is -1 SD. The shaded envelopes are 95% confidence intervals. Sample sizes vary for each model, see *N* on each panel.



traits and many possible relationships between them with herbivore assemblages, and we have outlined general expectations of herbivore strategies in Table 1 based on the unified framework of Archibald et al. (2019) and a select range of common scenarios of mammalian herbivory.




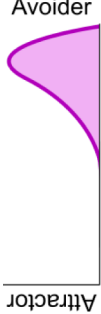

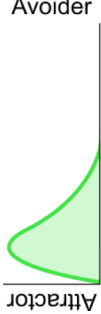






4 | ANTHROPOGENIC COMPLEXITIES IN PLANT TRAIT RESPONSES TO TROPHIC REWILDING

Looking at anthropogenically altered ecosystems can further complicate community-level patterns in large herbivore effects on traits for a range of reasons including disruptions to predator-prey dynamics (Prowse et al., 2014), non-analogue herbivores (Chynoweth et al., 2013) and changes in site productivity via nutrient additions (Borer et al., 2020; Segar et al., 2022). For example, livestock at stocking rates much higher than natural densities (Fløjgaard et al., 2022) or high (selective) mesoherbivore densities in simplified faunal assemblages or islands (Chollet et al., 2016) can have negative effects on diversity (Coggan et al., 2018). Recent longer term studies have improved our understanding of temporal diversity dynamics, providing important insights into the understanding of local species

extirpations and the effect of dominance shifts on species richness (Koerner et al., 2018; Wilfahrt et al., 2021). Understanding the relative influence of such complexities and how different parameters result in more positive, neutral or negative responses of diversity (including trait-based functional diversity) is a major outstanding challenge.

To meet global restoration targets large-scale actions will be needed, which undoubtedly will need to incorporate multiple approaches (e.g. trophic rewilding, alongside planting and natural recovery). While not explored in depth in this review, the implications of better understanding plant trait relationships with large herbivores will also aid in the design and implementation of plant-focused restoration projects as it has for other disturbances and ecosystem services (Laughlin, 2023a). Insights from applying a traits perspective to rewilding studies could also inform projects focused seeding and planting where herbivore pressure is a key bottleneck to survival and growth (Xu et al., 2023). Tools for designing species mixes for restoration based on their traits exist and are beginning to be used in an experimental setting (Andres et al., 2023; Ladouceur et al., 2022; Laughlin et al., 2018). However, to date, this has largely been focused on selecting species that are adapted to abiotic disturbances such as drought or fire (Laughlin et al., 2017), to maximise pollinator provisioning (M'Gonigle et al., 2017) and to increase resilience to invasion

TABLE 1 Hypothesised responses of plant trait strategies at the community/landscape scale under three common scenarios of megafauna herbivory regimes (Bakker et al., 2016): no or low mesoherbivore density, high mesoherbivore density, and a rewilding scenario with high trophic complexity that includes a mix of meso- and megaherbivores and large carnivores. Categories for different plant strategies (attractance–avoidance, resistance and tolerance) are based on Archibald et al. (2019).

Scenario	Description	Image	Greater diversity of herbivory modes and increased heterogeneity in herbivory
Before defoliation	Attractance–Avoidance spectrum traits (leaf size, leaf moisture, leaf and root nutrients ^a , leaf silica content, lifespan, chemical defence, specific leaf area/root length ^a)		
During defoliation	Resistance traits (prostrate growth, bud bank, below-ground storage, spinescence, divaricate growth)		
After defoliation	Tolerator traits (long flowering period, seed dormancy, increased leaf and root nutrients ^a , high specific leaf area/root length ^a , mycorrhizal associations)		
			
			
			
			
			
			

^aWe consider traits that are related to a species growth rate as well as palatability to be both related to a species avoidance–attractance (via palatability) and a species ability to tolerate herbivory via compensatory growth.

by weeds (Yannelli et al., 2018). However, herbivores can considerably reduce the establishment of plants in restoration projects (Xu et al., 2023). Therefore, while we focus here on how traits will help us predict and understand the ecosystem effects of large mammal reintroductions for rewilding, insights may also inform the design of species mixtures for seeding and planting activities where herbivory provides a strong bottleneck on establishment.

Intraspecific variability and plasticity in herbivory-related plant traits may modulate plant responses to trophic rewilding and may be shaped by anthropogenic impacts on the ecosystem. Trait filtering and resulting rapid evolution could mean that populations of plant species that have had natural grazers removed for a longer or shorter period may be less tolerant of reintroduced herbivores in the case of trophic rewilding, that is, an ecological memory effect (Schweiger et al., 2019). In line with the interspecific trait relationships described earlier, Jessen et al. (2020) show that grazing exclosures result in increased intra-specific plant height, decreased SLA and decreased C:N ratios. Notably, fertilisation decreased the trait differences between grazed and ungrazed plots, indicating either that increased nutrient availability due to herbivore presence may drive some of these observed changes or that fertilised communities 'cope' better with herbivory. Grazing has been shown in other systems to result in reduced intra-specific SLA and increased intra-specific leaf area (Streit et al., 2022), though not always (Zheng et al., 2022). Grazing is known to induce plant defences in the form of increased spines and reduced leaves in *Ilex europaeus* (Obeso, 1997). Burns (2014) shows how structural defences vertically decrease in plants that can grow tall enough to escape browsing height. *Salix phylicifolia* has been shown to exhibit intra-individual variation in chemical defence traits, allocating less leaf phenolics and less nitrogen to new growth on browsed twigs compared with unbrowsed twigs, creating a positive feedback loop of browsed twigs being repeatedly browsed and higher nitrogen and higher phenolics being avoided (Stolter, 2008). Therefore, dietary niche separation (via plant traits) may not just occur at the species level and instead can occur among different parts of the same plant or across ontogeny.

Importantly, there may be shorter term legacies of reduced herbivory to plant populations that shape how a given plant species respond to trophic rewilding. In one such example, Young et al. (2021) show that 'naïve' plant populations are affected differently by elephant herbivory when comparing fenced populations (25 years) of *Vachellia drepanolobium* (syn. *Acacia drepanolobium*) with unfenced populations that were continually exposed to native herbivory, with higher damage to naïve mature trees. Populations that have been naïve of large herbivores for a long period—which is the case in many situations where trophic rewilding is being suggested and prioritised—may be less equipped to defend themselves compared to the same species in places constantly exposed to large herbivores. In the same species, induced defences (in the forms of spines) have been shown to be much faster to adapt to damage (~2 months) compared with the speed at which they are lost (~5 years; Young & Okello, 1998;). In contrast, in the herbaceous clonal species *Trifolium repens*, time to allocate towards defence can be in the order

of 2–3 days (Gómez et al., 2010). Baseline monitoring of plant defences and community composition before rewilding will allow much greater elucidation of the potential role of such naivety in plant species responses to trophic rewilding.

The time since animal reintroduction (as well as how long those animals have been absent; Schweiger et al., 2019) may also shape divergent and variable responses of community trait profiles to trophic rewilding. Therefore, long-term study of rewilding sites will be crucial for building the full picture of ecosystem effects of large mammal reintroductions. Existing longer term studies of large mammalian herbivores provide some part of this picture. Laliberté and Tylianakis (2012) show that, after 27 years of manipulation, increased sheep grazing intensity increases functional diversity of the plant community. However, the effects of diversity were moderated by resource availability such that above-ground net primary productivity was negatively related to functional diversity under low resources, and positively related under high resources. Recent palaeo-scale studies in Australia and South America have begun to build a very long-term functional perspective of the effects of large mammal extinctions (Adeleye et al., 2023; Dantas & Pausas, 2022), themselves also linked to human impacts (e.g. Lemoine et al., 2023).

5 | HERBIVORE-PLANT TRAIT INTERACTIONS

A search for a unidirectional linear, or monotonic response of particular plant traits to large herbivores is unrealistic, and handling the multidimensionality of trait trade-offs will be key in understanding plant trait responses to rewilding with large herbivores (Laughlin, 2023b). This is largely because there are many ways for a plant species to coexist alongside herbivory (as well as many types of herbivory). The unified framework suggested by Archibald et al. (2019) for herbivory and traits (and fire) summarises how wide-ranging traits can aid a plant before, during and after an herbivory event. As highlighted earlier, strategies broadly fall into the categories of 'avoiding', 'resisting' or 'tolerating' being eaten (Archibald et al., 2019). Increases in 'fast' traits (i.e. traits associated with faster rates of ecosystem processes; Reich, 2014) in a community may be indicative of increases in species capable of sufficient compensatory growth as a resistance mechanism (herbivory 'tolerator') in response to herbivory. In contrast, the reverse is indicative of the dominance of herbivory 'avoiders' via decreases in palatability and 'resistors' with physical and chemical defences against herbivory. However, as highlighted above, it could also be a result of the selectivity of the herbivore community. Given larger animals' ability to forage on lower quality food (Hopcraft et al., 2012; Jarman, 1974; Potter & Pringle, 2023) as well as the physiological constraints of a larger bite size, large herbivores have been hypothesised to have relatively lower selectivity compared with smaller herbivores. Augustine and McNaughton (1998), while not explicitly considering plant functional traits, predict that under limited herbivore *selectivity*, tolerant strategies will prevail, but that the highest levels of grazing could make a

community more at risk of invasion by unpalatable species. Under higher herbivore selectivity, they predict that herbivory would reduce productivity, implying a more avoidance and resistance-dominated community (Churski et al., 2022; Kuijper et al., 2010). The authors also note that many studies show that selective herbivory leads to the dominance of unpalatable and chemically defended plant species (also seen in simplified megafauna assemblages such as deer overabundance; Wiegmann & Waller, 2006), but show how high levels of nutrient inputs (or recycling) can increase the tolerance capacity of a community. These patterns may be understood through coexistence theory (Chesson, 2000), which predicts that density-dependent predation (unselective feeding) will promote species coexistence (increased functional diversity), while predation independent of density (selective feeding) will lead to the extinction of the predated species. Interestingly, more 'intact' herbivore communities with large and megaherbivores, which are the target of trophic rewilding, are characterised by lower selectivity (Schowanek et al., 2021). Despite these wide-ranging relationships from positive to negative (or no effect at all; Lebbink et al., 2023), we see incorporating herbivore traits, densities and site conditions as an important way of resolving these idiosyncrasies.

While in some cases the identity of large herbivores does not appear important in explaining their effects on ecosystems (Veblen et al., 2016), this is often not true (e.g. Fensham & Skull, 1999; Lundgren et al., 2024; Price et al., 2022; Wells et al., 2022). For example, meso- and megaherbivores can have distinctly different effects on plant communities (Trepel et al., 2024). Body size, shoulder height and gape size have all been shown to affect feeding preferences in terrestrial animals (Moran & Catterall, 2010; Potter et al., 2022). Using a series of nested exclosures that prevented hare (*Lepus saxatilis*), impala (*Aepyceros melampus*) and larger grazers, zebra (*Equus quagga*) and white rhinoceros (*Ceratotherium simum*) from an African savanna, van der Plas et al. (2016) found that absolute vegetation height was reduced indiscriminately, and this relationship was explained by overall grazing pressure rather than the body size of the grazing community (van der Plas et al., 2016). However, CWM values of plant species heights did not reflect this change, indicating that the changes to the composition were not driving this effect. In the same study, the authors note that mesoherbivores shifted communities towards dominance by species with low SLA and leaf nutrition, but that in the longer term larger grazers had stronger effects on the same traits (van der Plas et al., 2016). Surprisingly however, the largest species in the experiment, white rhinoceros, did not have detectable effects on vegetation structure or composition over the study period, contrasting general findings for this species (Waldram et al., 2008). Considering the type, intensity, of herbivory provides important nuance on the potential overall effect and spatiotemporal heterogeneity in the effects of trophic rewilding on ecosystem function.

We predict that greater functional diversity in a herbivore community should result in greater functional diversity of plant communities since functionally dissimilar herbivores select for different foods and have different feeding modes, intake rates, home ranges

and non-trophic impacts (e.g. wallows, digging, carrion, redistribution of nutrients, decreased light interception; Table 1; Potter et al., 2022). For example, shifts in the body size distribution of herbivores could have positive effects on plant functional diversity and a strong filter on plant traits due to the shift away from more selective browsers towards mixed feeders or grazers (Clauss et al., 2013). Daskin et al. (2023) show grazing associated with fungi farming *Macrotermes* mounds by *Tragelaphus* spp. (spiral-horned antelopes) declined with body size and was more seasonally variable—an indication of lower diet quality and lower overall selectiveness in forage quality of larger antelope. Jarman (1974) shows a similar relationship across African antelopes, where smaller antelope species are more selective of higher quality forage (also see Hopcraft et al., 2012; Potter et al., 2022). Trophic rewilding also involving large predators will also indirectly affect plant functional diversity by changing the size and functional composition of the herbivore community. For example, predation may reduce the abundance of smaller mammals, but studies from areas with herbivore assemblages including 500+ kg species show that the reduction of smaller mammal abundance can be offset by increases in large herbivore biomass (Beschta et al., 2020; Le Roux et al., 2019). Predation may also result in spatially more heterogeneous herbivore impacts, where herbivore pressure is concentrated in smaller areas or at certain times of year to minimise predation risk. Large predators are therefore also hypothesised to result in functionally more diverse plant communities at the landscape scale. Megaherbivores, however, can homogenise this landscape of fear (Le Roux et al., 2018), given they are highly resistant to predation as adults (Pringle, 2018). Incorporating the functional composition of herbivore communities could be a key way to better predict large herbivore effects on plant traits, the functional composition of plant communities and the ecosystem properties and processes that emerge from that.

6 | TROPHIC REWILDING TO REDUCE ALIEN PLANT OVERDOMINANCE

The hypothesised links between large herbivores and the functional composition of plant communities open the door to considering how large herbivores would affect novel plant communities. Overall, the search for the traits of a 'model weed' has been limited given the complexity of abiotic and biotic conditions globally (Gioria et al., 2023; Moles et al., 2008). Nonetheless, there is broadly a tendency for invasive species to be characterised by fast growth rates and high reproductive output (Delmas et al., 2011; Mathakutha et al., 2019; Van Kleunen et al., 2010), both of which are 'tolerator' strategies for coping with herbivory (Table 1). Comparisons between native plants with introduced species support this notion showing a tendency for introduced species to have functional traits associated with fast growth and generation times including high SLA, high leaf N, small maximum height and small diaspores (Fristoe et al., 2021; Ordóñez et al., 2010). Among introduced species, at a local scale, SLA has also been shown to be higher in

invasive species compared with their naturalised but not overabundant congeners in Australia (Gallagher et al., 2015). Muñoz-Vallés and Cambrollé (2015) highlight that divergent strategies associated with maximising the space occupied (e.g. larger size vs. lateral spread rates, creeping vs. compact growth) were both associated with invasiveness, and it was a high affinity for either trait state that predicted invasion success. Native species can also behave in similar ways to invaders based on possessing particularly similarly competitive trait combinations (Muñoz-Vallés & Cambrollé, 2015, also resulting in negative effects on biodiversity (Czarniecka-Wiera et al., 2019). Harder to measure traits, for example, direct measurements of photosynthetic rates or resource use efficiency, also can explain invasion potential (Funk & Vitousek, 2007; Myers & Anderson, 2003). However as elsewhere in plant functional ecology, these traits are often overlooked in favour of simpler traits that are easier to measure (Laughlin, 2023c).

Climatic niches occupied by introduced species may diverge from those in their home ranges (shown in Australia by Gallagher et al., 2010), suggesting that invasive species may not always behave comparably in response to herbivores inside versus outside their natural range. Indeed, fast growth adaptations alone do not explain invasiveness, and the enemy release hypothesis has strong support for explaining the success of species in novel ranges whereby lower levels of herbivory and pathogen attack increase a species fitness in their new range (Keane & Crawley, 2002; Xirocostas et al., 2023). This increased fitness is explained by plants being able to allocate greater resources to growth and reproduction instead of a defence against enemies (Herms & Mattson, 1992), as well as the fact that they are simply not losing as many resources to consumption. This means that invasive species undergoing enemy release should be under selective pressure to lose herbivory and stress-tolerant traits (Díaz et al., 2015; Herms & Mattson, 1992).

Shifts to local environmental context can restructure community assembly to favour invasive species (Moles et al., 2008). This is supported by the notion that invasive species removal does not always have obvious benefits to native plants (Adams et al., 2020; Collings et al., 2023), as native species may be excluded due to the state shift which allowed new species to invade the habitat to begin with (Moles et al., 2008). Widespread trophic simplification and downsizing (Smith et al., 2018) can be considered one part of this altered ecological context, alongside climate change and increased nutrient inputs (Fowler et al., 2013). We therefore see trophic rewilding as conceptually moving a part of the altered ecological context 'back' towards the evolutionary range of conditions. Or, in the case of novel ecosystems and novel large mammals, broadly introducing processes that reduce dominance and promote diversity (Cuevas et al., 2020; Durigan et al., 2022). A plant traits perspective can enable the prediction of when large herbivore restoration (under trophic rewilding) would be most likely to reduce alien plant dominance (e.g. Mungi et al., 2023). As highlighted above, in many cases, the same traits that make invasive plants successful colonisers can also make them more vulnerable to herbivory (e.g. Scurr et al., 2008). In ecosystems

where alien or native palatable species dominate, high rates of herbivory can potentially create opportunities for less palatable species to establish by reducing dominance (Koerner et al., 2018; Mungi et al., 2023; Pringle et al., 2023). This idea is supported by recent empirical studies from Africa, India and Europe (Fűrész et al., 2023; Guyton et al., 2020; Mungi et al., 2023).

7 | CONCLUSION

We have summarised many of the ways in which commonly measured functional traits can structure the ability of plants to avoid, resist or tolerate herbivory, with implications for better predicting trophic rewilding outcomes. Leaves with higher moisture, lower density and more nutrients are generally preferred by herbivores, and leaves with higher magnesium and calcium can indicate overall digestibility. Physical defences such as spinescence and cagey architectures can help plants to protect valuable and vulnerable parts of the plants including leaves with high relative 'cost' and reproductive structures; however, the complexities of chemical defence mean that broad patterns in chemical defence remain elusive. These relationships between plant traits and herbivory are likely further modulated by productivity and rainfall (Carmona et al., 2012; Pérez-Camacho et al., 2012), the local and regional species pool (Liu et al., 2015), zoo-geochemical feedbacks (Doughty et al., 2016; Le Roux et al., 2020; Schmitz et al., 2018), abiotic heterogeneity (Freeman et al., 2022) and the initial state of vegetation. Despite globally variable patterns, regional patterns in herbivory-shaped systems and plant defence have been identified (Augustine & McNaughton, 1998; Coley et al., 1985; Endara & Coley, 2011).

To contribute substantially towards overcoming the anthropogenic biodiversity and climate change crises, restoration actions need to be scalable to large areas and effective in the long term (Malhi et al., 2022), also under emerging novel biosphere conditions (Svenning et al., 2024). Approaches to restoration will benefit from being integrative and encompassing, spanning dimensions such as planting and seeding, natural recovery and reintegration of appropriate disturbance regimes (e.g. through trophic rewilding and restored fire regimes). Surprisingly few studies have addressed the direct link between trophic complexity (or animal traits) and measures of plant diversity, especially of functional traits and functional diversity.

While trophic rewilding is not a silver bullet to halt biodiversity declines in isolation from other measures (notably area-based conservation and climate change mitigation), we have hypothesised some ways in which it is likely to have positive effects on community functional diversity and ecosystem function. A functional trait perspective will allow the assessment of the suitability of existing states of vegetation to the reintroduction of mammalian herbivory, as a strong theoretical basis continues to build (e.g. Archibald et al., 2019). For example, trophic rewilding should result in higher functional diversity of 'host' plant communities via decreased dominance and increased dispersal and heterogeneity of vegetation structure and

abiotic conditions (Le Roux et al., 2018; Tanentzap et al., 2023; Trepel et al., 2024). Large bulk-feeding herbivores should reduce the dominance of acquisitive species and increase light availability, promoting diversity (Koerner et al., 2018; Mortensen et al., 2018)—though this may be dampened in cases of very inflated nutrient levels (e.g. Campana et al., 2022). Furthermore, trophic rewilding should reduce non-native plant overdominance where invaders are characterised by a combination of palatable and acquisitive traits (as they often are; Ordonez et al., 2010; Svenning et al., 2024). Lastly, artificially overabundant herbivores (as in many livestock systems) and impoverished herbivore communities (e.g. dominated by deer; translating to higher herbivore selectivity) may result in reduction of positive or outright negative effects on plant diversity at the local scale (Trepel et al., 2024), due to their strong selective pressure on avoidant, resistant and tolerant trait combinations.

Given the rapid, much-needed expansion of restoration and rewilding activities across the world and in the context of rising ecological novelty worldwide (Svenning et al., 2024), we see trait-based approaches—to both the plant and animal components of the ecosystem—to be an important tool for predicting impacts on plant communities to assist the design, implementation and monitoring of trophic rewilding efforts to promote resilient and diverse ecosystems.

AUTHOR CONTRIBUTIONS

Joe Atkinson, Robert Buitenwerf and Jens-Christian Svenning led conceptualisation with input from all authors. Joe Atkinson led data analysis and writing of the manuscript with input from all authors.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

This paper reviews existing literature. All codes to reproduce the analysis are available at <https://osf.io/tcbkh/> (Atkinson et al., 2024). All data sets used in the analysis are publicly available and have been published elsewhere.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. List of sources for trait data.

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