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REVIEWS AND SYNTHESES

Seed size predicts global effects of small mammal seed predation on plant recruitment

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Abstract

Recent studies demonstrate that by focusing on traits linked to fundamental plant life-history trade-offs, ecologists can begin to predict plant community structure at global scales. Yet, consumers can strongly affect plant communities, and means for linking consumer effects to key plant traits and community assembly processes are lacking. We conducted a global literature review and meta-analysis to evaluate whether seed size, a trait representing fundamental life-history trade-offs in plant offspring investment, could predict post-dispersal seed predator effects on seed removal and plant recruitment. Seed size predicted small mammal seed removal rates and their impacts on plant recruitment consistent with optimal foraging theory, with intermediate seed sizes most strongly impacted globally – for both native and exotic plants. However, differences in seed size distributions among ecosystems conditioned seed predation patterns, with relatively large-seeded species most strongly affected in grasslands (smallest seeds), and relatively small-seeded species most strongly affected in tropical forests (largest seeds). Such size-dependent seed predation has profound implications for coexistence among plants because it may enhance or weaken opposing life-history trade-offs in an ecosystem-specific manner. Our results suggest that seed size may serve as a key life-history trait that can integrate consumer effects to improve understandings of plant coexistence.

Keywords

Biotic resistance, community assembly theory, enemy release, functional traits, invasive plant, life-history trade-off, meta-analysis, plant recruitment, seed predation, seed size.

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INTRODUCTION

Most theoretical frameworks in ecology postulate that predicting the success of organisms within their environments requires understanding how species' traits interact with key environmental processes (Grime 1977; Tilman 1982; Keddy 1992; Chesson 2000). However, given the great diversity of phenotypes expressed across the breadth of species, incorporating the multitude of possible species' traits into a predictive framework becomes untenable. Recent global studies of plant traits demonstrate that by identifying key subsets of functional traits that critically link life-history trade-offs with species fitness, we can improve understandings and prediction of plant community structuring at global scales (Adler *et al.* 2014; Díaz *et al.* 2016; Kunstler *et al.* 2016). To date, this work has focused on identifying functional traits that can explain plant success in the context of plant–plant interactions. However, consumers can strongly influence plant communities via herbivory (McNaughton 1979; Olff & Ritchie 1998), seed predation (Brown & Heske 1990) and seed dispersal (Vander Wall 2010; Thomson *et al.* 2010). If consumers target key plant life-history traits linked to fitness, then integrating such consumer interactions into coexistence and community assembly theory could advance understandings of plant community structuring processes at global scales (Larios *et al.* 2017; Pearson *et al.* 2018).

Post-dispersal seed predation is a particularly strong consumer interaction capable of influencing plant populations, distributions and community structure (Harper 1977; Brown & Heske 1990; Orrock *et al.* 2003; Howe *et al.* 2006; MacDougall & Wilson 2007). Importantly, post-dispersal seed predation is closely linked to seed size, a key plant life-history trait. While several seed traits can influence foraging decisions, seed size affords an overriding trait allowing foragers to assess overall energetic benefits vs. handling costs of seeds (Wang *et al.* 2013; Lichti *et al.* 2017), with optimal foraging theory predicting that larger seed sizes will be favoured for higher energetic returns up to the point where larger size inhibits handling time (Pyke *et al.* 1977). Such size-dependent foraging links seed predation to plant seed-size fecundity trade-offs

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(Shmida & Ellner 1984; Tilman & Pacala 1993; Muller-Landau 2010; Paine *et al*. 2015) and long-term life-history trade-offs via trait syndromes (Adler *et al*. 2014). These plant seed-size trade-offs derive from energetic constraints on reproductive output that generate alternative life-history strategies wherein plant species either produce few large or many small seeds; with large-seeded species allocating resources toward fewer, better-provisioned seeds capable of establishing in a range of conditions; and small-seeded species maximising seed numbers over provisioning, thereby increasing chances that some seeds will reach favourable microsites (Turnbull *et al*. 1999; Moles & Westoby 2004; Muller-Landau 2010). Hence, size-dependent seed predation may influence plant coexistence by affecting fitness outcomes tied to these trade-offs. For example in grassland communities, targeted predation by rodents on large-seeded species can undermine the recruitment advantage of large- over small-seeded species (Maron *et al*. 2018), generating a stabilising effect on coexistence. If size-dependent seed predation patterns are universal, as predicted by optimal foraging theory (Pyke *et al*. 1977; Petchey *et al*. 2008), such predation could link consumers to key life-history traits driving plant community assembly globally. To date, no global reviews of seed predation (Hulme 1998; Moles *et al*. 2003; Chen & Moles 2015) have examined seed predator effects on plant recruitment.

A ubiquitous hurdle to understanding ecological phenomena at global scales is conditionality (Agrawal *et al*. 2007). Because many ecological processes vary with changing abiotic and biotic conditions, ecological context must be accounted for to understand community assembly processes within and across systems (Pearson *et al*. 2018). For seed predation, differences in seed size distributions and seed predator identity patterns among ecosystems are predicted to influence foraging patterns (Moles *et al*. 2007; Radtke 2011). Accounting for such conditionality could help explain contrasting patterns of seed predation documented in grasslands (e.g. Reader 1993; Maron *et al*. 2012) vs. forest ecosystems (e.g. Dirzo *et al*. 2007; Moyano *et al*. 2019). Another increasingly prevalent and novel source of conditionality arises from biological invasions shifting local floras toward exotic plants (Kuebbing *et al*. 2013). Elucidating how introduced plants interact with ecological filters like seed predation is essential to understanding invader success. A central debate in invasion ecology surrounds the question of whether species' origins (provenance) or species' traits better explain invasion outcomes (Davis *et al*. 2011; Simberloff 2011). Theoretically, functional traits that predict assembly outcomes within native communities should also predict the success of exotic species (Pearson *et al*. 2018). Accordingly, traits, not provenance *per se*, should predict invader interactions within the community, with the role of provenance conditionally explained by inherent species traits, as demonstrated by numerous seed predation studies (Pearson *et al*. 2011, 2014, 2018; Maron *et al*. 2012; Connolly *et al*. 2014). In contrast to this prediction, the only global study to consider provenance effects in consumer interactions found that native herbivores suppressed exotic but not native plant abundance while exotic herbivores did the opposite (Parker *et al*. 2006). However, because this study did not evaluate associated traits, the relative importance of provenance vs. traits remains unclear. Global studies that simultaneously evaluate the influence of species traits and provenance are needed to better test these ideas.

We conducted a literature review and meta-analysis to evaluate whether seed size might serve as a functional trait that can globally predict the effects of native post-dispersal seed predators on seed removal rates and plant recruitment. We further evaluated the extent to which ecosystem context (e.g. grassland, temperate forest, tropical forest) and provenance (native vs. exotic) might influence these patterns. Our review focused on small mammal, primarily rodent, seed predators for several reasons. First, initial broad literature searches indicated that this group was most studied, especially regarding experimental evaluations of seed predator impacts on plant recruitment, thereby providing a more expansive global data set. Second, other important seed predator guilds like ants, birds and larger mammals tend to vary more than small mammals in their importance as seed predators across ecosystems (e.g. Mares & Rosenzweig 1978; Haas & Heske 2005; Chen & Moles 2015; Petit *et al*. 2018). Third, by focusing on small mammals (up to 1 kg in size), our review emphasised prominent rodent families that are globally distributed, important seed predators, allowing us to control for variation in seed predator size and functional identity across systems.

METHODS

Overall approach

Our strategy for evaluating small mammal effects on seed removal and plant recruitment involved two complementary approaches, each with different strengths and weaknesses. First, we examined studies wherein researchers offered seeds in the field to quantify seed removal rates by post-dispersal seed predators. Second, we evaluated experiments wherein researchers sowed seeds in paired cages that allowed or precluded seed predator access in order to quantify post-dispersal seed predator effects on plant recruitment. Because seed-offering studies are simple to perform, they are widely employed, providing abundant data representing many plant species and a broad global distribution (Fig. 1). However, these studies are not conducive to meta-analysis because most only quantify seed removal rates, that is they generally lack a control and treatment design that quantifies experimental effects. Additionally, seed removal rates may not reflect predator effects on plant recruitment if plants are not seed-limited and/or if density-dependent or density-independent mortality factors over-ride seed predator effects on recruitment (Hulme 1998; Crawley 2000). Hence, seed sowing experiments are required to explicitly measure the effect of post-dispersal seed predators on plant recruitment. Such studies also conform to the experimental design required for meta-analyses. However, being logistically challenging, these studies are less common, generating less data on fewer species from fewer regions globally (Fig. 1). By examining both types of studies using relevant analytical approaches, we gained a more complete picture of small mammal seed predator effects on plants.

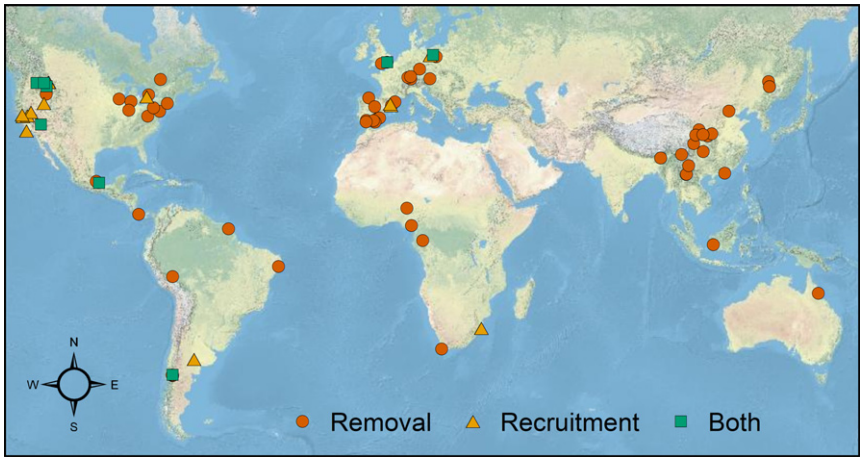

Figure 1 Locations of studies identified in a global literature review providing data for analysis of small mammal seed removal rates and/or small mammal effects on plant recruitment. Note that symbols for some studies are not visible due to overlap.

Literature review and data extraction

To obtain studies that quantified small mammal seed removal rates and/or experimentally evaluated the effects of seed removal on plant recruitment, we first considered data from the global literature review conducted by Moles *et al.* (2003). We then supplemented these studies with more recent work (published from January 2002 through November 2019) by searching the Web of Science Core Collection for peer-reviewed studies using the search term combination: ('seed remov*' OR 'seed predat*' OR 'seed offer*') AND ('small mammal*' OR 'rodent*' OR 'granivor*'). We also screened studies found through this search for relevant citations.

From this literature pool, we filtered studies based on the following criteria. All studies considered for our evaluation were conducted in natural systems, that is not urban or agricultural settings. In this definition, we included European grasslands, which are often sustained by mowing (Tälle *et al.* 2018), and North American old-field systems, which are seral stages of post-agricultural systems returning to their natural state. We focused on studies examining primarily seeds, not fruits, though studies incorporating seeds removed from fruits were included. Likewise, seeds attached to well-developed samara or samara-like dispersal structures (e.g. *Acer*, *Fraxinus*) were excluded, as these adaptations can affect total diaspore mass and shape in ways that alter seed handling and removal. Seed offerings above the ground surface were excluded. Because consumer origins could influence outcomes (Parker *et al.* 2006), we also excluded studies where small mammal seed predators could be identified as introduced (e.g. from some island systems), as these were too few to address consumer origins in analyses. In all cases, only studies that reported results by individual plant species could be included. Additionally, for seed removal studies, given that study-level variables such as study design, seed predator community and environmental context (e.g. background resource levels, competition, etc.) could have large effects on measured responses, we only included studies that provided data for > 1 plant species to control for such variation. We did not impose this restriction on plant recruitment studies given that such studies were limited in number, but exclusion of single-species studies did not alter meta-analysis results (Appendix S1).

Data from qualifying studies were extracted directly from the text or tables of publications, or from figures using Web Plot Digitizer Version 4.0 (https://automeris.io/WebPlotDigitizer/). For seed removal studies, we obtained data on the proportion of seeds removed per plant species during seed removal trials. In studies reporting multiple seed removal rates per species, we used the following rules to select one value (to overcome the complication of trying to account for non-independence among species x study replicates in models). When seed removal studies presented data for multiple trials or time points per species, we used data from the last or longest reported time interval with one exception: if the removal rate approached 100% for multiple plant species (potentially truncating responses), we used the middle trial or median time point. In studies presenting data for multiple sites or ecological contexts (e.g. variation by habitat, distance from habitat edge, or forest age), we randomly chose a single scenario. For studies of seed predator effects on plant recruitment, we extracted data on the mean number of seedlings or proportion of seedlings recruiting per species, associated measures of variation (SD or SE) and sample size for both small mammal exclusion (treatment) and small mammal access plots (control). In studies reporting small mammal effects multiple times per species, we selected one estimate (for reasons noted above) using the following criteria. For studies reporting effects over multiple years and/or ecological contexts, we selected the scenario with the highest overall recruitment in the control plots to maximise potential to detect seed predator effects. The exception to this rule was that in studies including both disturbed and undisturbed treatments, we used data only from disturbed treatments to exclude effects of plant competition, which can vary by seed size (e.g. Maron *et al.* 2012).

Geographic and habitat information was recorded for all studies. The latter was used to define the following ecosystem types: grasslands (including European grasslands and old-field systems as defined above), temperate forest, tropical forest and other (e.g. desert, shrublands, coastal dunes). Plant species provenance (i.e. native or exotic) was taken directly from the study when possible (most cases), and otherwise from the Plants of the World online database (Royal Botanic Gardens Kew 2020). Seed mass data for studies from Moles *et al.*'s (2003) global review were obtained from Appendix I in that

publication. For remaining studies, we gathered seed mass data directly from the source publication or a related publication when possible (85% of cases). If authors did not include seed mass, we obtained this information from the following published databases, prioritised in the order listed: Seed Information Database (Royal Botanic Gardens Kew 2019), LEDA for Northwest European flora (Kleyer *et al*. 2008) and Botanical Information and Ecology Network Database (Maitner *et al*. 2018). In cases where multiple seed masses were given per species in a database, we chose the record from the most proximate geographic region, when given, otherwise we chose the first record listed. Seed mass (+1) was natural log-transformed for analysis.

Seed removal analysis

We tested for variation in seed removal rates as a function of seed mass and other factors of interest using generalised linear mixed models (GLMMs) with a beta distribution and a restricted maximum-likelihood (REML) estimator, implemented via PROC GLIMMIX in SAS version 9.4 (SAS Institute 2016). The proportion of seeds removed was treated as the response variable after applying a small, linear transformation to eliminate zeroes and ones (Smithson & Verkuilen 2006). Study source was included as a random factor to control for the covariance of species responses originating from the same study (see above). Our base model tested for an overall effect of seed mass by including this term as a fixed factor. We also included a quadratic term for seed mass in the base model to allow for a nonlinear relationship apparent in scatterplots.

Two subsequent models were built from the base model to test for the influence of additional fixed factors on seed removal and the seed mass relationship (see Tables S1-S3 for model summaries). For the first such model, we added ecosystem type and its interaction with both seed mass terms to the base model. Data from the 'other' ecosystem category were omitted from this analysis given that they were derived from disparate systems with differing seed size distributions. In a second model that used the full seed removal data set, we added provenance and its interaction with the seed mass terms to the base model. To ensure that provenance tests were not confounded by the fact that most seed removal studies (95% of studies from Moles et al. [2003] and 74% of studies from our literature search) presented data for native species alone, we also repeated the analysis using only the subset of data that considered both native and exotic taxa within the same study (18% of all studies) to better isolate any potential differences. We did not test for effects of both provenance and ecosystem type in the same model because the complexity of such a model overreached the data available. In particular, exotic species were not represented in the tropical forest category. To help ensure that this imbalance in sample size by ecosystem type did not confound provenance tests, we repeated the latter analysis excluding data from tropical forests.

Plant recruitment meta-analysis

To conduct a meta-analysis of effects of small mammal exclusion on plant recruitment, we used multilevel random effects models with a REML estimator implemented via the rma.mv function in the metafor package (Viechtbauer 2010), R version 3.5.2 (R Core Team 2018). The response variable was the effect size metric, Hedges' g, which compared mean values between exclosures and controls, as calculated using the escalc function in the metafor package. Hedges g is a unit-free index that standardises the difference between experimental groups by accounting for the pooled sampling variance (Rosenberg *et al*. 2000). Zero g values signify no difference in plant recruitment between exclosure and control plots, while positive and negative g values indicate trends toward increased and decreased recruitment respectively. For the 5% of data points included in our meta-analysis that did not report variance metrics necessary for calculation of g, we employed linear regression models using data from studies with complete information to provide an estimate of variance (Lajeunesse 2013). This form of imputation is a reliable, yet simple approach for estimating missing values in a given data set (see McCary *et al*. 2016). As with the removal analysis, we included study source as a random factor in our meta-analysis to control for the covariance of responses originating from the same study (64% of studies included data for multiple species). First, we ran a model with no moderators to test whether effect sizes varied significantly among studies using the Q_t statistic. A significant Q_t based on a χ^2 distribution indicates that the variance among effect sizes is greater than that expected by sampling error alone. We next ran two models with moderators, that is fixed factors (see Table S4 for model summaries). As done in the seed removal analysis, the base meta-analysis model tested for an overall relationship between the response and seed mass. We again included a quadratic seed mass term in the base model to allow for a nonlinear relationship. In the second model, we examined whether patterns differed by species' provenance (native vs. exotic) by including this term and its interaction with the seed mass terms. The significance of moderators was assessed using the test statistic Q_m based on the χ^2 distribution. We could not consider the influence of ecosystem context on recruitment patterns given the paucity of data from most ecosystem types (see Results). Effect size means for native and exotic species, respectively, were calculated using the predict function in the metafor package, with seed mass set to the mean value across cases.

We checked our meta-analysis against the quality criteria established by Koricheva & Gurevitch (2014) for ecological studies. To meet these criteria, we tested for temporal changes in effect sizes potentially indicative of publication bias or changes in methodology etc. Although we found that effect sizes varied negatively with publication year ($Q_m = 4.1$, $P = 0.04$), this was driven by one early study with three data points; when this study was excluded, the relationship was no longer significant ($Q_m = 1.4$, $P = 0.24$). We also estimated the fail-safe number, or the number of studies that would have to be added to change the results of the meta-analysis (Rosenberg *et al*. 2000). This number was 10,944, indicating that the observed results are a reliable estimate of the true effect based on the criteria in Rosenberg (2005).

RESULTS

Literature review

The Moles *et al.* (2003) global literature review provided 13 studies that met our criteria for evaluating variation in seed removal rates by small mammals and our search generated an additional 58 studies (Appendix S2). These 71 studies provided 372 data points (n = 116 from Moles et al.) representing 297 plant species and 78 families. Native taxa comprised 316 data points representing 256 species and 72 families (from 68 studies), whereas exotics comprised 56 data points representing 44 species and 22 families (from 16 studies; note: 2 species are classified as native in some studies and exotics in others). In addition, the literature search produced 25 studies that met criteria for evaluating the effects of seed predators on plant recruitment, 8 of which also provided seed removal data (Appendix S2). These studies generated 115 data points for 87 species belonging to 29 families, with native taxa comprising 63 data points for 51 species and 25 families (from 17 studies), and exotics comprising 52 data points for 39 species and 14 families (from 13 studies; note: 3 species are classified as native in some studies and exotics in others). Seed removal studies were conducted primarily in North America, Asia and Europe (Fig. 1), with data points well-distributed among grasslands (23%), tropical forest (35%) and temperate forest (29%). Most plant recruitment studies were conducted in North America and Europe (Fig. 1), with data points primarily from grasslands (77%), followed by tropical forest (8%) and temperate forest (7%).

Seed removal

In evaluating variation in small mammal seed removal rates via GLMM analysis, the base model showed a positive relationship with seed mass ($F_{1,313}$ = 30.3, P < 0.0001) that reversed for seed sizes > 150 mg (equivalent to 5.0 on ln seed mass + 1 scale; Fig. 2), as indicated by the significant negative quadratic term ($F_{1,365}$ = 33.9, P < 0.0001). This unimodal seed mass pattern held when we accounted for ecosystem type in a separate model (Table S1). In this model, the relationship between seed removal and seed mass did not vary significantly with ecosystem type (seed mass x ecosystem: P = 0.29; seed mass^2 x ecosystem: P = 0.43), and the proportion of seeds removed did not differ among ecosystems (P = 0.49). However, given that seed mass varied significantly among ecosystem types ($F_{2,271}$ = 310.4, P < 0.0001), each ecosystem type generally represented a differing portion of the unimodal seed mass relationship describing seed removal (Figs 2 and 3). In grasslands, where seed sizes were smallest, seed removal rates increased with seed mass, while in tropical forests, where seed sizes were largest, seed removal rates decreased with seed mass. In temperate forests, with their intermediate seed sizes, seed removal patterns spanned the unimodal seed mass relationship.

In a separate model that accounted for species provenance in addition to seed mass, seed removal showed the same unimodal relationship with seed mass (Table S1). This relationship did not vary significantly with provenance (seed mass x provenance: P = 0.83; seed mass^2 x provenance: P = 0.96), and the proportion of seeds removed did not differ between native and exotic species (P = 0.53). Results were comparable when we repeated analyses using only the subset of data from studies that included both native and exotic plant species (Table S2), and from the three ecosystem types that included both native and exotic species (Table S3). Seed mass per species did not differ by provenance when we controlled for ecosystem type ($F_{1,184}$ < 0.1, P = 0.79).

Plant recruitment

Meta-analysis showed that small mammal seed predator exclusion significantly increased plant recruitment overall, with a large mean effect size (g = 0.9, 95%CI 0.66–1.11) and significant variability among cases (Q_t = 426.1, P < 0.0001). Similar to the pattern seen for seed removal, the base model showed that the seed predator exclusion effect varied positively with seed mass (Q_m = 38.0, P < 0.0001), with this relationship again reversing for larger seeded species (Fig. 4), as represented by a significant negative quadratic term (Q_m = 40.6, P < 0.0001). The unimodal seed mass pattern was comparable in a separate model that also accounted for species provenance (Table S4). In this model, the seed mass relationship did not vary significantly with provenance (seed mass x provenance: P = 0.41; seed mass^2 x provenance: P = 0.71). Although the small mammal exclusion effect was significantly larger for native relative to exotic species (P = 0.03), the difference was modest (Fig. 4).

DISCUSSION

Focusing on traits that reflect fundamental plant life-history trade-offs can help explain plant community structure at

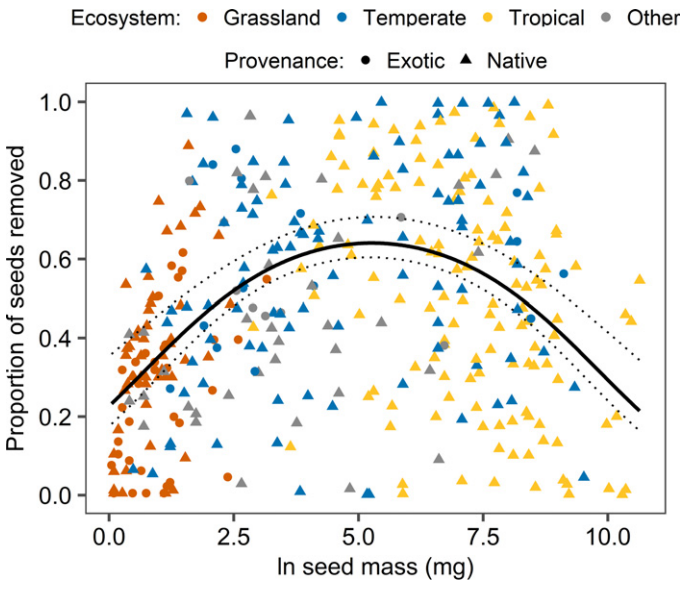

Figure 2 Overall relationship between small mammal seed removal rates and seed mass (ln [mg + 1]), as assessed using data from a global literature review, analysed via generalised linear mixed model analysis. Data points represent residual variance in seed removal values after accounting for the random effect of study predicted from the model. The solid line indicates the predicted seed mass relationship, which did not vary with ecosystem type or provenance (see text), and the dotted lines represent the 95% confidence interval.

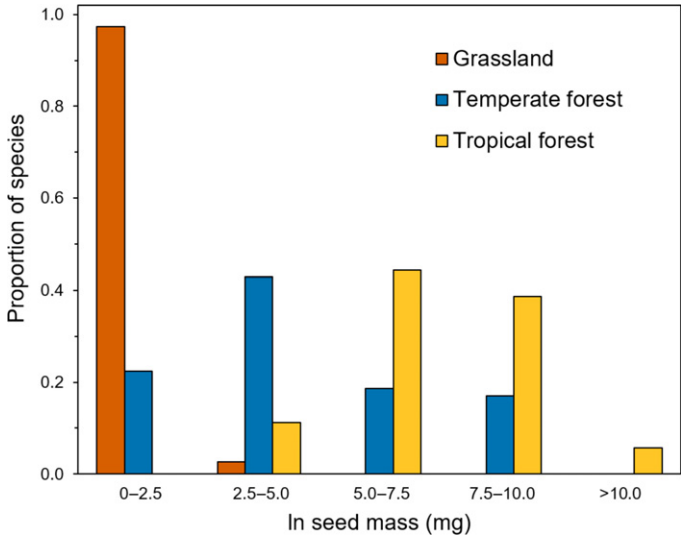

Figure 3 Seed size distribution for plant species included in analysis of small mammal seed removal rates by ecosystem type. Seed mass (ln [mg + 1]) was lowest in grasslands ($\bar{x}$ = 0.9 ± 0.2 mg, back-transformed: $\bar{x}$ = 1.5 ± 0.5 mg), followed by temperate forests ($\bar{x}$ = 4.4 ± 0.2 mg; back-transformed: $\bar{x}$ = 80.1 ± 17.0 mg), and tropical forests ($\bar{x}$ = 7.1 ± 0.2 mg; back-transformed: $\bar{x}$ = 1254.8 ± 195.2 mg).

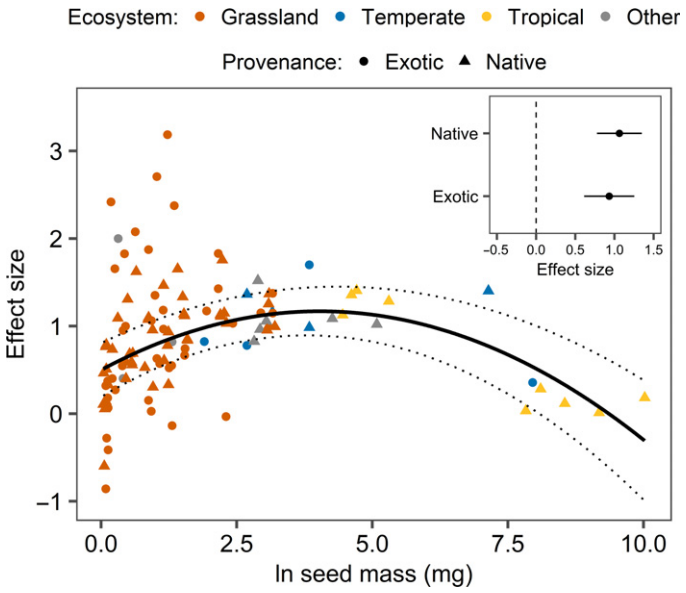

Figure 4 Overall relationship between effects of small mammal exclusion on plant recruitment and seed mass, as assessed using data from a global literature review, analysed via multilevel meta-analysis. Data points represent residual variance in effect sizes (Hedges *g*) after accounting for the random effect of study predicted from the model. The solid line indicates the predicted relationship, and the dotted lines represent the 95% confidence interval (indicative of a significant effect size when not overlapping zero). Provenance did not significantly affect the seed mass relationship, although effects on recruitment were modestly greater for native relative to exotic species (inset gives mean effect sizes and 95% confidence intervals).

global scales (Adler *et al.* 2014; Kunstler *et al.* 2016). However, consumers can strongly influence plant community structure (e.g. Louda 1982; Brown & Heske 1990; Olff & Ritchie 1998), and linkages between consumer effects and key plant life-history traits affecting assembly processes are poorly understood. In conducting a global literature review and meta-analysis of seed predation, we found that seed size, a trait representing fundamental life-history trade-offs in plant offspring investment, predicted small mammal seed removal rates and the effects of seed removal on plant recruitment for both native and exotic plants, with the greatest negative impacts on seeds of intermediate size at the global scale. Importantly, variation in seed size distributions among ecosystem types was linked to differences in seed predation patterns, with small mammals targeting relatively large-seeded species in small-seeded ecosystems and relatively small-seeded species in large-seeded ecosystems. Establishing the linkage between seed size and the effects of this ubiquitous seed predator guild on plant recruitment has important ramifications for plant coexistence and community assembly theory.

Early pioneers of plant–consumer interactions hypothesised that post-dispersal seed predation could strongly influence plant community structure (Janzen 1971; Hulme 1998). However, evaluating this hypothesis has been hindered by the fact that most seed predation studies quantify seed removal rates without evaluating how seed predation affects plant recruitment (see Larios *et al.* 2017, this study). Longer-term, larger-scale *in situ* experiments demonstrate that post-dispersal seed predation by small mammals can substantially influence plant community structure via size-dependent seed predation (Brown & Heske 1990; Howe & Brown 2001; Maron *et al.* 2012, 2018), but such studies are few and mostly restricted to grasslands and arid systems. Our meta-analysis of 25 seed sowing experiments shows for the first time that such size-dependent, post-dispersal seed predation by small mammals can strongly and directionally influence plant recruitment across ecosystems at global scales (Fig. 4). These findings also demonstrate the widespread importance of this consumer process and highlight the need to understand how seed predation may be linked to plant life-history trade-offs and plant coexistence.

Seed size is an important trait reflecting fundamental plant life-history trade-offs between high investment in fewer propagules better-endowed to overcome environmental challenges vs. low investment in many propagules that increases the likelihood that some individuals will reach favourable microsites (Turnbull *et al.* 1999; Moles & Westoby 2004; Muller-Landau 2010). Importantly, seed size is linked via trait syndromes to other life-history trade-offs that influence plant–plant and plant–environmental interactions at later life stages (Moles & Westoby 2006; Adler *et al.* 2014; Díaz *et al.* 2016; Maron *et al.* 2018). Hence, strong consumer effects on plant recruitment tied to seed size could profoundly influence plant coexistence. For example Chen & Valone (2017) found that, in the Chihuahua desert of the southwestern USA, where environmental variability favours small-seeded annuals, rodent seed predation focused on large-seeded species exacerbated discrepancies in the relative abundance of small- vs. large-seeded plants, generating a destabilising effect on coexistence. In contrast, in perennial grasslands of Montana, USA, where

large-seeded species recruit more strongly than small-seeded species when competing with established bunchgrasses, rodent preferences for large-seeded species undermined this recruitment advantage (Maron *et al.* 2018), generating a stabilising effect on coexistence. These studies demonstrate the potential importance of seed predators on plant coexistence, but they also suggest that such effects may be conditional.

Controlling for key sources of conditionality can be essential for deciphering ecological processes (Agrawal *et al.* 2007), particularly at global scales. System-specific differences in seed size distributions have been predicted to generate important differences in seed foraging patterns across ecosystems conditioned by forager responses to seed availability (Radtke 2011). Our results supported this prediction. Overall, we found a global pattern of size-dependent seed removal that was unimodal, with the highest seed removal rates occurring at about 5.0 mg seed mass on the log-transformed scale (equivalent to 150 mg on the raw data scale; Fig. 2). These patterns suggest that, given a full range of seed sizes, an optimum exists wherein small mammals select for larger seeds that offer higher foraging returns up to a point where larger seed sizes inhibit handling ability, consistent with predictions from optimal foraging theory (Pyke *et al.* 1977; Vickery 1984). However, as our data show, different ecosystems represent different portions of the global seed size distribution, with seed sizes increasing from grasslands to temperate and tropical forests (Fig. 3; see also Moles *et al.* 2007). Accordingly, we found that seed removal patterns shifted with ecosystem type in a predictable manner – small mammals selected for larger seeds in the small-seeded grasslands and for smaller seeds in large-seeded tropical forests, with intermediate patterns in temperate forests (Fig. 2). While studies of seed predator effects on seedling recruitment were too few to test for ecosystem differences, our meta-analysis generated a similar unimodal relationship, including the same representation of ecosystem types across the seed size gradient (Fig. 4). Collectively, these results indicate that 1) small mammal seed predators substantively impact plant recruitment globally, 2) these impacts are linked to size-dependent seed foraging behaviours as predicted by optimal foraging theory, 3) these foraging behaviours link seed predator impacts to key plant life-history trade-offs, with ramifications for plant coexistence and 4) the way in which these impacts may affect plant coexistence are conditioned by ecosystem type.

Seed predation may also vary as a function of seed predator identity and body size (Radtke 2011; Chen & Moles 2015). We attempted to control for these factors as much as possible in a global assessment by focusing on small mammal seed predators up to 1 kg in size. These criteria largely restricted the seed predator guild in our analyses to three families of rodents, Muridae, Cricetidae and Sciuridae, that exhibit global to near global distributions, and ecological equivalents that are more regionally distributed (e.g. Dasyuridae in Australia, Echimyidae in South America, Heteromyidae in North America; see Nowak 1991 for distribution records). Therefore, interpretation of our results is limited accordingly, and fully understanding how seed predation affects plant communities will require expanding information on other important seed predator taxa. Nonetheless, studies evaluating the relative importance of key post-dispersal seed predator guilds tend to show that rodents are dominant seed predators across systems, with other prominent guilds like ants being most important in desert and Mediterranean systems, and invertebrates, birds and larger mammals playing more variable roles (Brown *et al.* 1975; Mares & Rosenzweig 1978; Whelan *et al.* 1991; de Casenave *et al.* 1998; Hulme 1998; Kelt *et al.* 2004; Haas & Heske 2005; Carrillo-Gavilán *et al.* 2010, Kulkarni *et al.* 2015). Even so, these other seed predator taxa can be very influential, and size-dependent seed predation by ants and has been shown to affect plant coexistence (Petry *et al.* 2018). More studies are needed to evaluate the importance of other seed predator guilds, with an emphasis on quantifying their effects on plant recruitment.

The unimodal seed predation pattern that we observed contrasted with findings from Moles *et al.*'s (2003) global review of post-dispersal seed predation which identified a weak negative relationship between seed size and seed removal rates. There are several methodologically and ecologically relevant explanations for the difference between their findings and ours, but two are particularly salient. First, we tried to control for an important source of conditionality by focusing on studies where small mammals were identified as the primary seed predators, whereas their approach incorporated all types of seed predators. Second, our models allowed for nonlinearity in the response, whereas theirs did not. When we reanalysed the portion of our data set that overlapped with Moles et al. (filtered based on our criteria), we obtained parallel results to those seen with our full data set: a positive albeit marginally significant relationship between seed removal and seed size ($F_{1,77} = 2.9$, $P = 0.09$) that reversed in direction at large seed sizes ($F_{1,94} = 7.2$, $P = 0.009$). Notably, when we dropped the nonlinear term associated with the latter pattern, seed removal varied negatively with seed mass ($F_{1,111} = 14.4$, $P = 0.0002$), paralleling the weak negative relationship reported by Moles *et al.* (2003). Hence, the data sets appear to generate similar patterns, but inclusion of the nonlinear term allowed us to distinguish the unimodal pattern from an overall negative relationship, and controlling for seed predator identity likely reduced other sources of variation such as divergent effects of seed predator identity and body size on seed size preferences (Chen & Moles 2015).

Changes in plant community composition arising from biological invasions presents another source of conditionality which can both influence and be influenced by local filters like seed predation. Given the importance of seed predation as a biotic filter to plant recruitment, a relevant question is whether seed predator effects on plants are predicted by species origins (Parker *et al.* 2006; Davis *et al.* 2011; Simberloff 2011) or by inherent species traits in accordance with community assembly theory (Pearson *et al.* 2018). Overall, we found that the trait of seed size predicted seed removal rates and the effects of seed predation on plant recruitment, with little influence of provenance. In the meta-analysis, there was some evidence of slightly stronger suppression of native over exotic plant recruitment. Why this difference might exist was unclear from the factors we evaluated, but the effect was quite weak relative to seed size effects (Fig. 4). In contrast to our results, Parker *et al.*'s (2006) global review found that provenance

alone predicted herbivore effects on plant abundance, with native herbivores more strongly suppressing exotic vs. native plants. One possible explanation for these divergent results is that different processes may underlie generalist herbivore vs. granivore interactions with exotic plants. However, the relative importance of provenance vs. traits that might influence herbivory were not addressed in their study. Local-scale studies explicitly evaluating the roles of provenance vs. traits in the context of local community assembly rules have also demonstrated that seed size predicts recruitment success for native and most exotic plants similarly. Notably, these studies also show that deviations from the predicted pattern can identify important cases where novelty conferred by provenance may help explain invasion outcomes (Pearson *et al*. 2011, 2014, 2018). Understanding the relative importance of novelty linked to provenance vs. inherent species traits in determining invasion outcomes will require more studies that simultaneously address these factors.

In the first global review of seed predation to link small mammal foraging patterns to demonstrable effects of these seed predators on plant recruitment, we establish a critical link between consumers and seed size, a key plant trait linked to life-history trade-offs and long-term fitness. The unimodal relationship we observed between seed size and both seed removal and seed predator effects on plant recruitment was consistent with predictions from optimal foraging theory (Vickery 1984). This finding suggests an important role for optimal foraging theory in predicting the effects of small mammal seed predators, and possibly other seed predator guilds, on plant recruitment. Notably, because some seed predators also act as seed dispersers via seed caching behaviours (Vander Wall et al. 2005, Vander Wall 2010) and caching behaviours are similarly influenced by seed size (Wang *et al*. 2013; Lichti *et al*. 2017, Gomez et al. 2019), optimal foraging theory may also help predict seed predator effects on seed dispersal. The fact that small mammals selected seeds based on size, irrespective of origins, suggests that inherent species traits rather than novelty *per se* may best predict invader success, but more work is needed that explicitly addresses this question. Our finding that ecosystem-specific differences in seed size distributions can generate divergent patterns of seed predation has important implications for understanding the conditionality of seed predator effects on plant coexistence. Further elucidating the role of seed predation in plant community assembly will require a greater emphasis on seed sowing experiments that quantify the effects of small mammals and other seed predator guilds on plant recruitment. Collectively, our results suggest that size-dependent seed predation by small mammals is a global phenomenon with important ramifications for understanding plant coexistence and community assembly.

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AUTHORSHIP

LD and MB initiated the project and conducted the literature review. LD, MB, YO and DP developed the analysis and the conceptual framework. LD, YO and MB conducted the analysis. DP wrote the first draft and all authors contributed to writing.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tqjq2bvvk.

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SUPPORTING INFORMATION

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

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