Post-dispersal seed predation reflects tree species occurrence beyond local neighborhoods in a forest biodiversity experiment

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Abstract
Post-dispersal seed predation is a key mechanism underlying Janzen-Connell (JC) effects with seed predation expected to decline with increasing distance from conspecific trees. However, the spatial scale at which seed predators respond to the occurrence of their resource tree species remains poorly understood. In particular, mobile consumers may respond to resource distributions beyond the local neighborhood, potentially weakening distance-dependent patterns at the spatial scales commonly used to quantify biodiversity and neighborhood effects. Here, we tested whether tree species richness, vertebrate access, and conspecific tree occurrence at the plot and site level shaped post-dispersal seed predation in the BEF-China tree diversity experiment. We deployed paired open and vertebrate-exclusion seed cards tracking 41,580 seeds from seven tree species across 297 plots spanning monocultures to 16-species mixtures. Across the seven focal tree species, seed predation declined with increasing tree species richness, was consistently higher on open than on vertebrate-exclusion cards and differed strongly among seed identities. Contrary to the expectation of a local JC-type effect, seed predation did not differ between seeds of focal tree species present and absent from the focal plot, provided that the species belonged to the species pool of the respective site. In contrast, seeds of species absent from the site-level species pool experienced substantially lower predation. This pattern persisted across the tree species richness gradient. Our results provide little evidence that local conspecific occurrence drives post-dispersal seed predation at the scale of individual experimental plots. Thus, spatial patterns in seed predation consistent with processes underlying JC effects may emerge at scales larger than the local neighborhood, particularly when consumers are mobile. More generally, our findings highlight the importance of considering consumer mobility and spatial scale when interpreting seed predation effects on forest regeneration in biodiversity experiments.

Introduction
Forest biodiversity experiments have shown that tree species richness can alter herbivore damage, consumer diversity and multitrophic interactions (Schuldt et al. 2015, 2019; Fornoff et al. 2019; Albert et al. 2026). However, ecological interactions are commonly quantified at spatial scales defined by experimental plots, yet mobile consumers may perceive and respond to communities over much larger areas (Wiens 1989; Levin 1992; Nathan et al. 2008; Anttonen et al. 2023). Such scale mismatches

could obscure biodiversity effects when consumer behaviour relies on resources distributed beyond the focal plot. Post-dispersal seed predation could provide a critical test of this possibility precisely because agents of seed predation often exhibit mobility over greater distances while foraging than experiments at the plot level address. Especially as experimental forests mature, a key unresolved question is whether and how tree diversity also regulates consumer pressure during the reproductive stage. Post-dispersal seed predation is particularly relevant because it links tree diversity and community composition to the assembly of future seedling communities (Hulme 1998; Paine and Beck 2007). Yet we still lack a general framework for predicting how tree diversity regulates this demographic filter.

Post-dispersal seed predation is an early demographic filter that can strongly influence the transition from seed rain to seedling recruitment (Wang and Smith 2002; Bricker et al. 2010; Maron et al. 2019). Rodents, birds, and other vertebrate granivores may consume dispersed seeds directly, remove them to feeding sites, or transport and cache them elsewhere (Vander Wall et al. 2005). These predators are mobile, often consume seeds from multiple tree species and can integrate information about seed abundance and identity across entire foraging areas (Nathan et al. 2008; Lichti et al. 2017). Their choices therefore depend not only on seed identities, but also on the relative availability of focal seeds and alternative resources (Hulme and Hunt 1999; Ostoja et al. 2013). These responses generate contrasting predictions for diversity effects. Increasing tree richness may reduce predation on a focal species by lowering its relative abundance, diluting species-specific cues and embedding its seeds within a more diverse resource background (Root 1973; Barbosa et al. 2009; Jactel et al. 2021). Alternatively, diverse stands may provide more heterogeneous habitats and a broader or more continuous supply of resources, increasing the diversity and abundance of consumers (Stemmelen et al. 2022; Li et al. 2023). Post-dispersal seed predation is also a key mechanism underlying the density- and distance-dependent mortality predicted by the Janzen-Connell hypothesis (Janzen 1970; Connell 1971). Seeds close to conspecific adults, or occurring where conspecifics are locally abundant, are expected to experience greater consumer pressure, whereas spatial escape from conspecifics should reduce seed mortality. For mobile seed consumers, however, such spatial escape may depend on the scale over which consumers encounter and exploit seed resources. If their foraging ranges extend beyond individual tree neighborhoods or experimental plots, local conspecific occurrence may be less important than the occurrence of the same tree species across a broader spatial area. Shared predators may further connect tree species through predator satiation, distance-dependent consumption and apparent competition (Kelly and Sork 2002). Consequently, communities with equal richness may differ greatly in the resources they present to consumers. Existing BEF experiments have detected context-dependent effects of plant richness on seed predation (Pufal and Klein 2013; Dudenhöffer et al. 2016), but evidence from experimental forests remains scarce, and observational studies cannot readily separate diversity effects from habitat conditions, seed supply and tree species composition.

This scale dependence can be addressed by considering how the identity of dispersed seeds matches tree species occurrence at nested spatial scales (Schupp 1992). At the

plot scale, seeds can either match the local tree community, or represent species that are locally absent. Under a local Janzen-Connell expectation, seeds matching the focal plot should experience greater predation because nearby conspecific trees and their seed rain provide predictable resource cues for consumers (Janzen 1970; Connell 1971; Hulme and Hunt 1999). However, local absence may not necessarily imply spatial escape from mobile consumers whose foraging ranges can extend beyond individual tree neighborhoods or experimental plots (Nathan et al. 2008). Thus, a species may be absent from the focal plot but belong to the species pool of the respective site, or it may be absent from both the plot and the site-level species pool. Comparing these contexts allows local conspecific effects to be distinguished from broader-scale associations between seed consumers and tree species occurrence. We refer to this correspondence between the identity of dispersed seeds and tree species occurrence at different spatial scales as spatial matching. Tree species richness may further modify such spatial matching by changing the relative availability of focal and alternative resources within plots.

We tested these predictions in the BEF-China tree diversity experiment, where tree species richness and composition were experimentally manipulated across two sites with partly overlapping species pools. We deployed paired open and vertebrate-exclusion seed cards containing seeds of seven tree species across 297 plots ranging from monocultures to 16-species mixtures. Differences in species composition among plots and sites generated three nested resource contexts: species absent from both the focal plot and site-level species pool (−, −), species absent from the focal plot but belonging to the respective site-level species pool (−, +), and species present within both the plot and the site-level species pool (+, +). We addressed three questions: (1) Does post-dispersal seed predation decline with tree species richness, and does this tree species richness effect vary among tree species? (2) Does vertebrate access increase post-dispersal seed predation? (3) Is seed predation higher when the seed species matches the plot- or site-level tree community? We predicted that seed predation would decline with increasing tree species richness, that predation would be higher in open than in vertebrate-exclusion treatments, and that predation would increase with spatial matching, with the highest predation on seeds of species occurring within the focal plot. By linking experimental tree diversity to resource matching at nested spatial scales, our study extends the question of how tree diversity affects seed predation to consider the spatial scale at which consumers respond to the occurrence of their resources.

Methods

Study area

This study was conducted within the BEF-China platform (Bruelheide et al., 2014), located in Xingangshan, Jiangxi Province, southeastern China (29◦05’ – 29◦07’N, 117◦54’ – 117◦55’E). The region experiences an average annual temperature of 16.7 °C and an average annual precipitation of 1,821 mm (Yang et al., 2013). The platform consists of two study sites, established in 2009 (Site A) and 2010 (Site B), covering a total area of over 50 ha. In total, 566 plots (25.8 × 25.8 m) were randomly distributed across these two sites, with 271 plots in Site A and 295 plots in Site B. Each plot initially contained 400 trees planted on a 20 × 20 grid. Using a ‘broken-stick’ design, 40 native

deciduous and evergreen broad-leaved tree species were planted to create gradients of tree species richness ranging from 1 to 24 tree species on each site. Sites A and B were established from different but partially overlapping tree species pools, with eight species shared between sites. The core tree diversity experiment referred to here comprises 40 monocultures, 44 2-species mixtures, 28 4-species mixtures, 20 8-species mixtures, 16 16-species mixtures and 2 24-species mixtures totalling 150 plots per site.

Experimental design

We conducted a seed-card experiment in November 2025 during the forest seed rain to quantify post-dispersal seed predation in selected tree species representing a broad range of seed sizes, fruit types and phylogenetic lineages. The tree species were selected from the BEF-China species pool of 40 native deciduous and evergreen broad-leaved tree species and included *Koelreuteria bipinnata, Liquidambar formosana, Elaeocarpus chinensis, Machilus thunbergii, Cyclobalanopsis glauca, Lithocarpus glaber* and *Schima superba* (Table 1). Among these seven target tree species, two occurred exclusively at Site A, two occurred exclusively at Site B, and three at both sites. We conducted the seed card experiments across all 300 core plots, with 150 plots at each site. Because only a few 24-species plots were available on the BEF-China platform, we excluded these plots to avoid the excessive reuse of the same plot in studying multiple target tree species, resulting in 148 plots at Site A and 149 plots at Site B. The final number of plots used for the seed card experiment was 80, 88, 57, 40 and 32 at tree species richness levels of 1, 2, 4, 8 and 16, respectively. Based on our pretrial, we determined that the seed cards could be placed for a maximum of three days (approximately 72 hours) before risking the loss of all seeds. To minimize potential edge effects and (micro-)climatic interference, seed cards were simultaneously placed in the central area of each plot. Two seed cards were deployed in each plot, with a distance of 0.5 m between them. One card was enclosed within a vertebrate-exclusion cage, whereas the other was left uncovered as a control. The exclusion cages were constructed from wire mesh and measured 35 cm × 35 cm × 20 cm (length × width × height), with a mesh size of 1.5 cm. At the time of retrieval, each seed card was photographed, and the surrounding area was carefully inspected for seeds that had been removed from the card and been attacked. The recovered cards were then transported to the laboratory, where the seeds remaining on each card were classified as either healthy or attacked and counted separately for each target species. Seeds missing from the cards and not recovered in the immediate vicinity were also classified as attacked. Thus, our measure of post-dispersal seed predation included both directly observed seed attack and seed removal by consumers.

In addition, based on the occurrence of each focal species at the plot and site levels, we distinguished three spatial matching categories. The "−, −" category denotes species that were absent from both the focal plot and the species pool of the respective site. The "−, +" category comprised species that were absent from the focal plot but belonged to the species pool of the respective site. The "+, +" category comprised species occurring both in the focal plot and, by definition, in the respective site-level species pool. Because any species occurring within a plot necessarily belonged to the species pool of that site, the "+, −" combination was not possible.

TABLE 1 Characteristics of the 7 target tree species used in this study

Species	Family	Site	Fruit type	No. - - plots	No. - + plots	No. + + plots	Seed size (mm)	Seed mass (g)
Koelreuteria bipinnata	Sapindaceae	A	Capsules	149	134	14	6 × 5	0.10
Liquidambar formosana	Altingiaceae	A	Capsules	149	122	26	9 × 2	0.004
Elaeocarpus chinensis	Elaeocarpaceae	B	Fleshy	148	116	33	12 × 6	0.22
Machilus thunbergii	Lauraceae	B	Fleshy	148	115	34	11 × 10	0.03
Cyclobalanopsis glauca	Fagaceae	A/B	Nut	0	220	77	13 × 12	2.15
Lithocarpus glaber	Fagaceae	A/B	Nut	0	201	96	19 × 12	1.71
Schima superba	Theaceae	A/B	Capsules	0	222	75	9 × 5	0.005

Note: "−, −" indicates that the focal species is absent from both the plot and the species pool of the respective site. "−, +" indicates that the focal species is absent from the focal plot but belongs to the species pool of the respective site. "+, +" indicates that the focal species occurs within the focal plot and, by definition, belongs to the species pool of the respective site. Seed size was expressed as length × width, with data derived from the Flora of China. For species for which published seed size data were unavailable (*Elaeocarpus chinensis* and *Schima superba*), seed size was determined from measurements of 100 mature seeds. Seed mass was calculated as the average value of 100 mature seeds.

Seed card preparation

All seed cards (n = 594) were prepared in advance in the laboratory. Each seed card consisted of an A4-sized sheet of AA-240 dry abrasive paper, Li Fan contact adhesive, 70 seeds from seven target species, and fine sand. For each target species, 10 seeds were used and randomly placed on the adhesive-coated surface of the abrasive paper. The adhesive prevented accidental seed loss during transport and deployment while allowing seeds to be removed by seed consumers. Fine sand was then sprinkled over the remaining exposed adhesive to prevent the sticky surface from restricting the movement of seed predators, such as insects and rodents. After preparation, each seed card was placed individually in an envelope for transport and subsequently deployed in a designated plot. The cards were secured to the ground with drawing pins to minimize displacement or deformation caused by wind, rainfall, or disturbance by large wild animals.

Data analysis

All analyses were performed in R version 4.2.2 (R Core Team, 2022). The effect of tree species richness on post-dispersal seed predation was tested by fitting generalized linear mixed-effects models (GLMMs) using 'glmmTMB' (Brooks et al., 2017). For each focal tree species on each seed card, the response was specified as the number of attacked seeds relative to the number of healthy seeds and modelled using a beta-binomial error distribution with a logit link to account for overdispersion. Before model fitting, tree species richness was log2-transformed to linearize its relationships with the response variable. For visualization, predictor values on the x-axes were back-transformed and displayed on their original scales to improve interpretability. Model residuals were assessed using the DHARMa package (Hartig, 2020), and Wald χ^2 and p-values were obtained using the Anova function from package 'car' (Fox & Weisberg, 2019).

We fitted three complementary GLMMs to separate plot- and site-level associations between focal tree species occurrence and seed predation. In the first GLMM, we fitted the model using three species shared between Site A and Site B. Because these species belonged to the species pools of both sites, only two spatial matching contexts were possible: absence from the focal plot but membership in the respective site-level species pool (−, +) and occurrence within the focal plot (+, +). This model therefore tested whether plot-level conspecific occurrence affected seed predation when the focal species already belonged to the site. In the second GLMM, we fitted the model using four species restricted to the species pool of either Site A or Site B. Consequently, for each of these focal species, deployment at the site to whose species pool it did not belong represented the (−, −) context. At the site to whose species pool it belonged, the species was either absent from the focal plot (−, +) or occurred within the focal plot (+, +). This reciprocal design allowed us to contrast absence versus membership at the site-level (−, − vs −, +) and to test the additional effect of local conspecific occurrence within the plot (−, + vs +, +). The third GLMM included all seven species and was used to estimate the overall effects across species. In the first two models, tree species identity was included as a fixed effect, whereas in the overall model it was included as a random effect.

Across models, tree species richness, spatial matching context, vertebrate exclusion treatment and site were initially included as fixed effects together with their interactions with tree species richness. Plot was included as a random effect to account for the hierarchical sampling design. To optimize the model structure, we first sequentially removed non-significant interaction terms if their removal resulted in improved model performance (lower or equal AIC and improved fit statistics). The focal terms representing our hypotheses were retained throughout the model-selection procedure. Ultimately, the interactions between tree species richness and tree species (for the first two GLMMs), as well as between tree species richness and species occurrence status (all GLMMs), were retained.

To further evaluate differences in seed predation among species occurrence categories, post hoc comparisons were performed using estimated marginal means (EMMs) with the 'emmeans' package. Because spatial matching context was included in an interaction with tree species richness, comparisons were evaluated at the mean value of log2-transformed tree species richness. For the three species shared between sites, we compared the two possible contexts (−, + and +, +). For the four site-restricted species, all pairwise comparisons among the three contexts (−, −, −, + and +, +) were conducted with post-hoc Tukey tests to adjust for multiple comparisons. Estimated marginal means were back-transformed to the response scale and are presented as model-predicted seed predation rates with 95% confidence intervals.

Results

Species-specific responses of post-dispersal seed predation to tree species richness

Across all seven target species, post-dispersal seed predation decreased significantly with increasing tree species richness ($\chi^2 = 10.558$, $p = 0.001$; Fig. 3a, Table 2). When analysed separately, the relationship with tree species richness was not significant for

either the tree species belonging to the species pools of both sites (χ^2 = 1.751, p = 0.185; Fig. 1a, Table 2) or the four species restricted to the species pool of one of the two sites (χ^2 = 0.870, p = 0.350; Fig. 2a, Table 2). However, significant differences in seed predation were observed among tree species in both groups (shared species: χ^2 = 22.439, p < 0.001; site-restricted species: χ^2 = 70.769, p < 0.001). Despite these differences among species, there was no interaction between tree species richness and tree species, providing no evidence that the relationship between tree species richness and seed predation differed among species (Table 2).

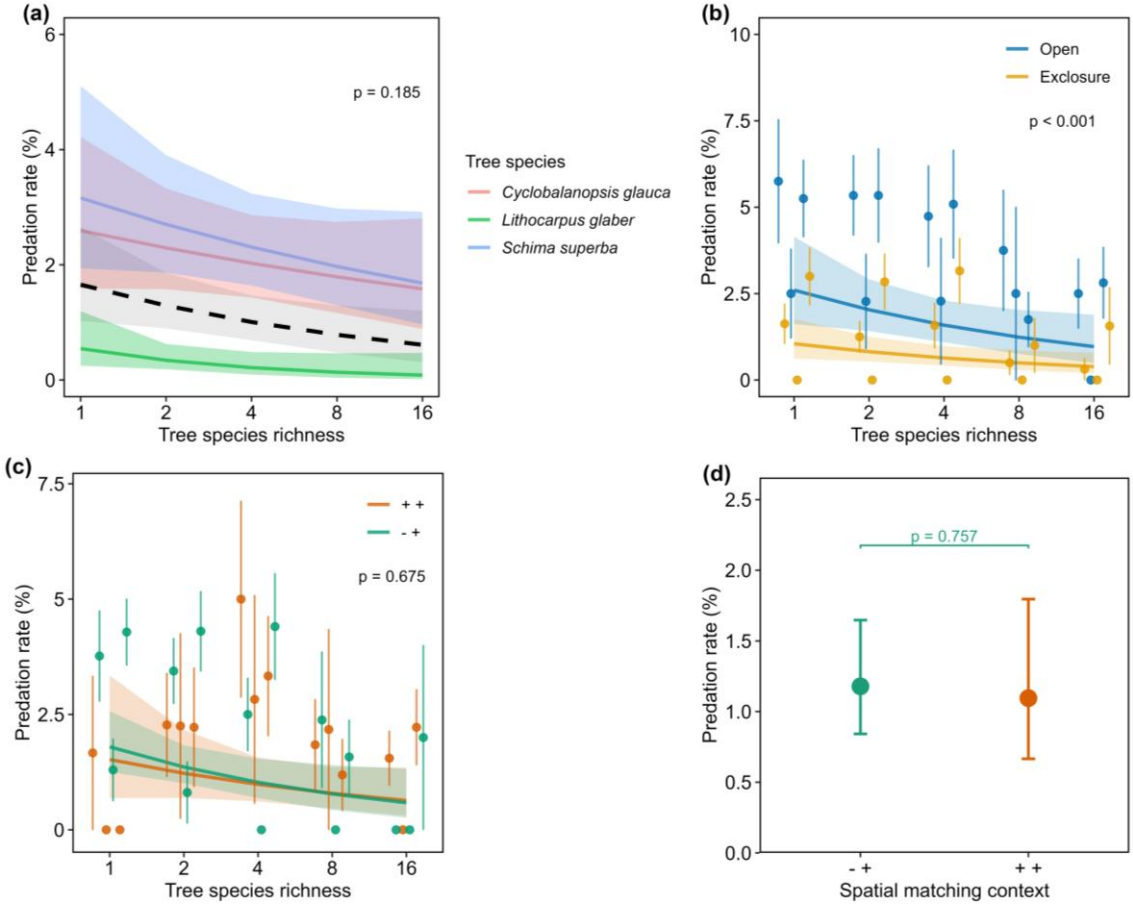

Figure. 1 Post-dispersal seed predation of the three focal tree species belonging to the species pool of both sites. (a) Model-predicted relationships between tree species richness and seed predation for *Cyclobalanopsis glauca, Lithocarpus glaber* and *Schima superba.* (b) Relationships between tree species richness and seed predation in the open and vertebrate exclosure treatments. (c) Relationships between tree species richness and seed predation for the two spatial contexts (−, +, and +, +). In panel (a), coloured lines show species-specific fitted relationships from the GLMM; the black line shows the overall fitted relationship, and shaded areas indicate 95% confidence intervals. In panels (b) and (c), points and error bars show the predicted mean predation rates and their 95% confidence intervals for each species, based on the GLMM. Panel (d) shows estimated marginal mean predation rates for the two spatial matching contexts (−, + and +, +), with points and error bars representing model-predicted means and 95% confidence intervals. P-values indicate the statistical significance of the predictor shown in the model.

Effects of vertebrate access

Vertebrate access consistently increased seed predation across the three modelled species groups and richness levels. Predation was significantly higher on open than on vertebrate-exclusion cards for species belonging to the species pools of both sites (χ^2 = 37.106, p < 0.001; Fig. 1b, Table 2), for species restricted to the species pool of one

site (χ^2 = 59.591, p < 0.001; Fig. 2b, Table 2) and across all seven focal tree species (χ^2 = 103.768, p < 0.001; Fig. 3, Table 2). Additionally, seed predation tended to decline with increasing tree species richness in both treatments, while the difference between the control and exclusion treatments generally persisted across the richness gradient.

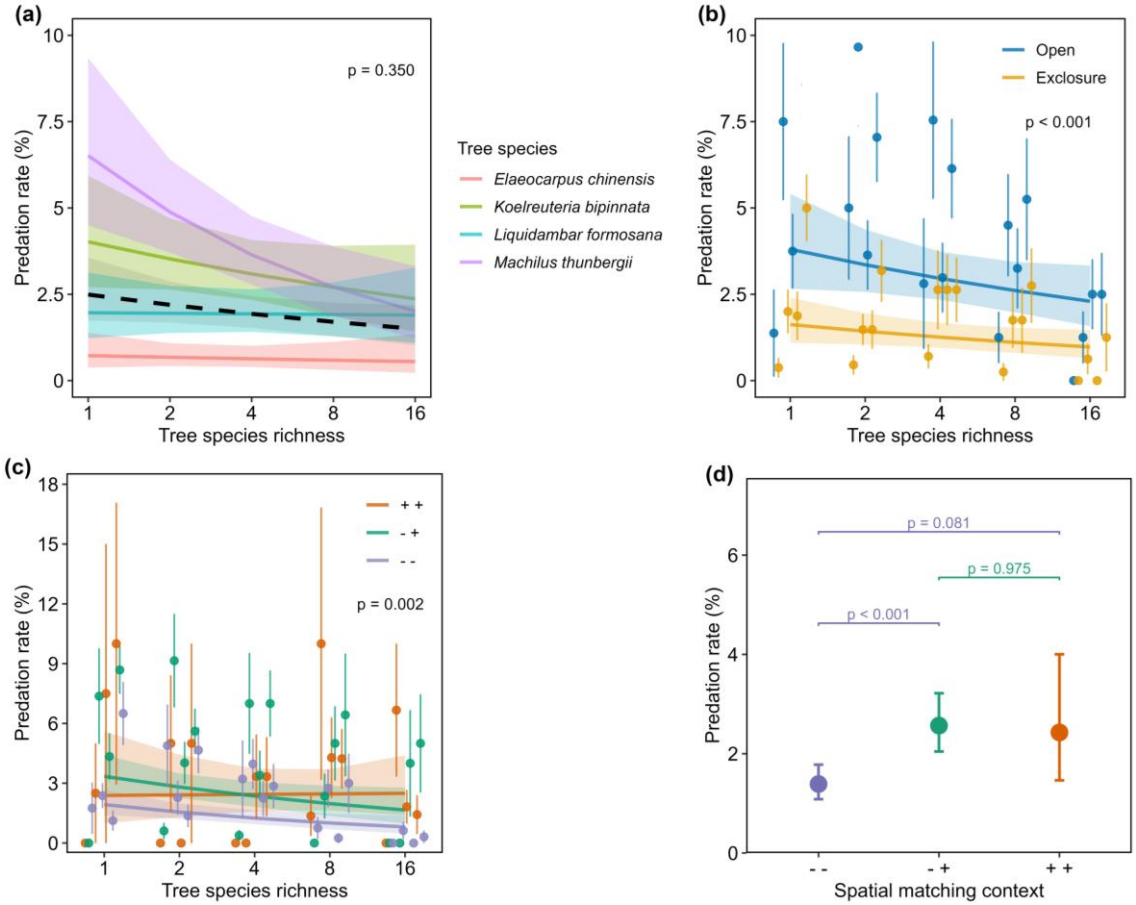

Figure. 2 Post-dispersal seed predation of the four focal tree species restricted to the species pool of one of the two sites. (a) Model-predicted relationships between tree species richness and seed predation for *Koelreuteria bipinnata, Liquidambar formosana, Elaeocarpus chinensis* and *Machilus thunbergii*. (b) Relationships between tree species richness and seed predation in the open and vertebrate exclosure treatments. (c) Relationships between tree species richness and seed predation for the three spatial matching contexts (−, −; −, +; and +, +). In panel (a), coloured lines show species-specific fitted relationships from the GLMM; the black line shows the overall fitted relationship, and shaded areas indicate 95% confidence intervals. In panels (b) and (c), points and error bars show the predicted mean predation rates and their 95% confidence intervals for each species. Panel (d) shows estimated marginal mean predation rates for the three spatial matching contexts (−, −; −, +; and +, +), with points and error bars representing model-predicted means and 95% confidence intervals. P-values indicate the statistical significance of the predictor shown in the model.

Effects of plot- and site-level species occurrence

Among the three species belonging to the species pools of both sites, seed predation did not differ significantly between species absent from the focal plot (−, +) and species occurring within the plot (+, +) (Fig. 1d). By contrast, spatial matching context significantly affected seed predation for the four site-restricted species (χ^2 = 12.356, p = 0.002; Fig. 2c) and across all seven focal species (χ^2 = 14.221, p = 0.001; Fig. 3c). In general, seed predation was lowest when the species was absent from both the focal plot and the species pool of the respective site (−, −), whereas predation was higher

for species belonging to the site-level species pool irrespective of whether they occurred in the focal plot (−, +; +, +). The interaction between species richness and spatial matching context was not significant in any of the three models (shared species: $\chi^2 = 0.139$, $p = 0.708$; site-restricted species: $\chi^2 = 1.845$, $p = 0.397$; all species: $\chi^2 = 3.173$, $p = 0.204$), showing that differences among spatial matching contexts did not vary significantly across the tree species richness gradient.

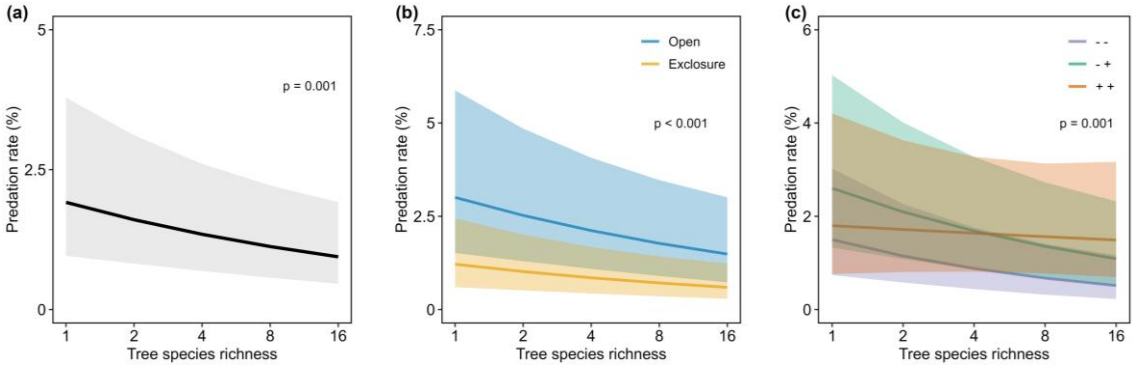

Figure. 3 Effects of tree species richness on post-dispersal seed predation across all seven focal tree species. (a) Overall model-predicted relationship between tree species richness and seed predation. (b) Model-predicted relationships between tree species richness and seed predation in the open and vertebrate exclosure treatments. (c) Model-predicted relationships between tree species richness and seed predation for the three spatial matching contexts (−, −; −, +; and +, +). Solid lines represent model-predicted means, and shaded areas indicate 95% confidence intervals. P-values indicate the statistical significance of the predictor shown in the model.

Table 2 ANOVA of fixed factors of the GLMMs

	GLMM-1 (3 species)			GLMM-2 (4 species)			GLMM-3 (all species)	
Fixed effects	df	χ^2	*p*	df	χ^2	*p*	df	χ^2	*p*
Tree species richness (TSR)	1	1.751	0.185	1	0.870	0.350	1	10.558	**0.001**
Tree species (TS)	2	22.439	**< 0.001**	3	70.769	**< 0.001**			
Species occurrence (SO)	1	0.174	0.675	2	12.356	**0.002**	2	14.221	**0.001**
TSR × TS	2	1.541	0.462	3	7.068	0.069			
TSR × SO	1	0.139	0.708	2	1.845	0.397	2	3.173	0.204
Site	1	6.414	**0.011**	1	2.772	0.095	1	5.088	**0.024**
Exclusion treatment	1	37.106	**< 0.001**	1	59.591	**< 0.001**	1	103.768	**< 0.001**

Note: For GLMM3, Tree species was considered random, thereby excluding main effect of and interaction effects with TSR. Statistically significant values are shown in boldface,

Discussion

Our results show that post-dispersal seed predation was mediated both tree species richness and the spatial match between seed identity and the occurrence of conspecific trees. Seed predation declined with tree species richness in the model combining all seven species, but this relationship was not detected when species shared between sites and species restricted to one site were analysed separately. Moreover, the effect of tree species richness on seed predation did not differ among seed species or occurrence categories in either analysis. By contrast, predation varied strongly among seed species, was consistently higher when vertebrates had access to

seeds, and showed a clear site-level home-away effect. Seeds belonging to the site-level species pool experienced similarly high predation irrespective of whether conspecific trees occurred within the focal plot, whereas predation was lowest for species absent from the experimental site. Together, these findings suggest that post-dispersal seed predation depends strongly on seed identity and vertebrate access, while the match between seed identity and conspecific tree occurrence operates at a spatial scale larger than the individual tree community represented by a plot.

We found a negative relationship between tree species richness and seed predation across all species. However, the absence of a significant richness effect within either of the two species groups – tree species occurring in both sites or those only occurring in one site – indicates that this relationship was comparatively weak. Increasing tree species richness seemed to have reduced the relative abundance and apparency of individual seed species, thereby diluting focal resources, as diverse stands may provide more heterogeneous habitats and a broader or more continuous resources for consumers. Recent studies have shown that consumer pressure can depend on interactions among resources and consumers, forest structure and spatial scale rather than on tree species richness alone (Anttonen et al. 2023; Guo et al. 2026). This interpretation is also supported by the strong differences among seed species and the absence of richness-by-species interactions, indicating that species differed primarily in their overall susceptibility to predation rather than in their species-specific response to species richness. Such differences are expected because seed size and other functional traits can strongly influence seed removal, handling and subsequent fate by various mammals (Dylewski et al. 2020; Wang 2020; Gu et al. 2025). In addition, the standardized seed-card design may have weakened the effect of plot species richness. Each card contained equal numbers of all seven species, creating a locally diverse and concentrated seed patch even in monocultures. This design was necessary to compare predation among species and plots under standardized conditions, but it may have partly weakened differences in local seed-resource composition associated with tree richness (Drescher and Nolan 2023). However, the significant decline across all species with tree species richness remains informative, although its magnitude may differ slightly from richness effects under natural seed deposition.

Vertebrate access produced the most consistent effect, with greater seed predation on open than on exclusion cards across all three GLMMs. This result identifies vertebrates as major consumers of post-dispersal seeds in the experiment, consistent with recent studies showing that vertebrate seed predators can strongly reduce seed availability and subsequent tree recruitment (Williams et al. 2021; Joyce et al. 2024; Wróbel et al. 2025). It also provides a plausible explanation for why tree communities influenced seed predation beyond the focal-plot scale. Vertebrate granivores can move across multiple plots, revisit profitable patches and respond to resources distributed across broader foraging areas (Lichti et al. 2017; Wootton et al. 2023). They may therefore integrate tree composition, seed identity, and seed production across larger spatial scales, obscuring effects at the plot scale. Empirical evidence further shows that small mammals can weaken the distance dependence of seed predation, suggesting that mobile consumers may extend natural-enemy effects beyond the immediate neighborhood of conspecific trees (Krishnan et al. 2022). However, some

seeds removed and not recovered may have been cached rather than consumed, meaning that our response represents removal from the original location rather than mortality in all cases. Nevertheless, the exclusion effect demonstrates that vertebrate behaviour strongly filters the seed pool available for subsequent recruitment.

Species occurrence status revealed a clearer spatial pattern in seed predation than local tree species richness. The significant effect of site in the model considering all seed species indicates that seed-predation pressure differed between the two experimental sites. However, accounting for site identity did not alter the effect of focal-species occurrence status, indicating that the lower predation of site-away species cannot be explained simply by overall differences in predation between the two sites. Seeds from species absent from both the focal plot and the site experienced the lowest predation, whereas site-home species experienced higher predation even when absent from the focal plot. This pattern supports a consumer home advantage operating beyond nearby conspecific individuals. The Janzen-Connell hypothesis predicts elevated enemy pressure near conspecific adults or in areas of high conspecific density (Janzen 1970; Connell 1971), although recent studies show that such effects vary substantially among species and life stages and are less consistent for seeds than for seedlings (Song et al. 2021). Our results suggest that, for vertebrate seed consumers, such effects may extend beyond the immediate neighborhood of conspecific adults and operate across multiple tree communities containing the focal tree species. The composition and the temporal dynamics of seed resources can generate strong indirect interactions among tree species sharing consumers (Yang et al. 2020; Mittelman et al. 2024). Repeated exposure to site-home seeds could therefore make consumers recognise them more readily, develop efficient strategies and associate them with profitable resource patches (Li et al. 2018; Yi et al. 2021; Zhao et al. 2025). Alternatively, the regular availability of these seeds may sustain higher consumer activity across the site (Prevedello et al. 2013; Liu et al. 2023). Under either mechanism, a seed does not need to occur close to a conspecific adult to experience higher consumer pressure; membership of the local site-level resource pool appears sufficient.

Importantly, the similar predation of plot-away/site-home and plot-home/site-home seeds implies that consumers connect discrete plots through their movements and prior experience. Once a species belonged to the site-level resource pool, an additional match at the plot scale did not increase consumer pressure. This site-level home advantage extends density- and distance-dependent enemy effects to the spatial scale of consumer foraging activities. Thus, the spatial scale of natural-enemy effects may depend not on plant distribution alone, but rather on the match between resource distribution and consumer mobility.

We expected increasing tree species richness would reduce post-dispersal seed predation through the dilution of the relative abundance of target species. However, differences in predation among species occurrence categories persisted across the richness gradient, suggesting that plot-level richness was not closely related to the process underlying the site-level home advantage. Seed availability depends on reproductive abundance and seed rain, neither of which necessarily changes monotonically with tree richness. In subtropical forests, interspecific synchrony in

seed production can modify rodent-mediated interactions among co-occurring tree species (Yang et al. 2020). However, the resource familiarity that consumers have developed across an entire site may remain influential even when a species is rare or absent from the focal plot. This could explain why differences among occurrence categories remained across the richness gradient.

This assumed consumer home advantage may influence forest community assembly. Preferential local removal of seeds belonging to the surrounding tree community could reduce the recruitment of locally established species and potentially increase opportunities for non-local or locally rare species. Such effects could contribute to forest compositional turnover and limit local dominance. However, whether these differences translate into seedling recruitment will also depend on seed dispersal, germination and subsequent herbivory or mortality. Our pattern provides a potential pathway through which consumer behaviour can influence forest compositional change. Overall, our results shift the interpretation of diversity effects from local species numbers towards spatial resource context. By showing how consumers respond to seed resource distributions across different scales, our study identifies consumer home advantage as a potential mechanism linking tree community composition to forest regeneration.

Data availability

The data will be made publicly available in an open data repository upon acceptance of the manuscript.

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Competing interests
The authors declare no competing interests.