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Research article

Intraspecific variation in seed size mediates rodent–seed interactions: combined patch-level trait distributions to individual seed selection

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Rodent–seed interactions are influenced strongly by seed traits. Seeds in natural systems rarely exist in isolation; they aggregate into spatially discrete patches with distinct trait distributions, where individual seed fate depends on both its own traits and those of its neighbors. While individual seed traits have been extensively studied, the role of patch-level trait distribution, particularly, relative variability (measured by the coefficient of variation, CV) and asymmetry in trait distribution (quantified by skewness) remains poorly understood. We conducted a controlled field experiment in a subtropical forest to examine how patch-level variation in seed size (quantified by CV and skewness) mediates seed predation and dispersal by rodents. Using two Fagaceae species (*Lithocarpus pachyphyllus* and *Lithocarpus hancei*), we established artificial seed patches ($n=41$ per species) with standardized density and mean seed size but varying CV (0 to 0.68) and skewness (−0.74 to 2.75). Our results revealed that higher CV increased predation probability in *L. pachyphyllus* but reduced dispersal distance, while skewness showed no significant effects. *Lithocarpus hancei* exhibited no patch-level responses to trait distributions. However, both species showed context-dependent individual seed selection: the magnitudes and even the signs of effect of individual seed size on rodent foraging preference differed among patches. These findings demonstrate that intraspecific seed size variation mediates rodent-plant interactions through both patch-level and individual-scale processes, creating spatial mosaics of selection that may maintain seed size polymorphism. Our study highlights the importance of considering higher-order trait distribution statistics in seed dispersal ecology and provides mechanistic insights into how spatial variation in seed traits structures ecological interactions and potentially maintains trait diversity in plant populations.

Keywords: Coefficient of variation, plant-animal interactions, seed dispersal, seed predation, seed size variation, skewness

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Introduction

Seed dispersal by rodents represents a critical ecological interaction that shapes plant population dynamics, forest regeneration and biodiversity patterns. As both seed predators and dispersers, rodents exert dual selective pressures on plant reproductive strategies, by consuming seeds to reduce recruitment while inadvertently enhancing seedling establishment through scatter-hoarding (Vander Wall 2001, Lichti et al. 2017). The outcome of this interaction hinges on rodent foraging decisions, which are influenced by seed traits such as size, nutrient content and defensive compounds (Vander Wall 2010, Jansen et al. 2012, Liu et al. 2023). Among these traits, seed size plays a pivotal role in mediating rodents foraging preference and subsequent seed fate. Larger seeds typically provide greater nutritional rewards, leading to higher removal rates, increased caching probability, and longer dispersal distances compared to smaller seeds (Wang and Chen 2009, Xiao et al. 2015, Liu et al. 2023). However, larger seeds usually require substantially longer handling times, which reduce foraging efficiency and increase predation risk, thereby creating an optimal threshold where medium-sized seeds offer the best tradeoff between energy returns and handling costs, accounting for rodents' preference for intermediate sizes (Wang et al. 2013).

Current studies on rodent-seed interactions have usually focused on individual seed traits; for example, rodents preferentially harvest small, nutrient-poor seeds for immediate consumption while caching larger ones as future reserves, and rodents prefer to disperse larger seeds farther than smaller ones (Vander Wall 2010, Wang and Ives 2017, Liu et al. 2023). However, seeds in natural systems rarely exist in isolation; they aggregate into spatially discrete patches with distinct trait distributions (Medrano and Herrera 2008, Shimada et al. 2015, Wang and Ives 2017). Each patch functions as a 'foraging arena' where rodents encounter multiple seeds simultaneously, necessitating decisions that balance energy gain and predation risk across heterogeneous resources (Stephens and Krebs 1986, Shafir 2000). Optimal foraging theory (OFT) posits that such decisions maximize net energy gain per unit time while minimizing predation risk and handling costs (Charnov 1976, Vickery 1984). Within seed patches, both seed abundance (density) and trait distributions (specifically seed size CV and skewness) critically shape rodent foraging strategies (Shimada et al. 2015, Xiao et al. 2015). These patch-level characteristics directly mediate seed fate by governing tradeoffs between immediate consumption and cached investment through energy-optimizing and risk-sensitive behaviors (Stephens and Krebs 1986, Shafir 2000).

Empirical studies have robustly demonstrated abundance-dependent effects in seed predation and dispersal systems. The predator satiation hypothesis posits that increased seed abundance enhances seed survival by reducing consumption rates as seed predators become satiated (Kelly and Sork 2002, Xiao et al. 2013). Conversely, the predator dispersal hypothesis suggests that greater seed abundance promotes animal-mediated seed dispersal, potentially increasing seed dispersal rates or distances (Vander Wall 2002, Xiao et al. 2013). However, the role of trait distribution parameters, particularly coefficient of variation (CV, measuring relative variability) and skewness (quantifying asymmetry in trait distribution), in modulating these outcomes remains virtually unexplored. This oversight is striking given that natural plants frequently exhibit non-normal seed size distributions – populations may be skewed toward smaller or larger seeds, or display high variability (Zhang and Wang 2024, Hu et al. 2025).

Such distributional patterns could profoundly influence rodent foraging efficiency and decision-making. Seed patches with high CV in seed size presents foragers with a mix of high-reward (large) and low-reward (small) items, potentially altering selective pressures through frequency-dependent decision-making (Horst and Venable 2018). More specifically, high CV patches may amplify size-dependent preferences: consumption rates of small seeds increase while dispersal rates of large seeds are enhanced. Skewness distributions may produce more complex effects. Right-skewed distributions (many small seeds with few large ones) typically promote consumption, while left-skewed patches (many large seeds with few small ones) generally increase caching rates and dispersal distances. This occurs because rodents preferentially consume small seeds while removing and caching larger ones, with larger seeds typically being dispersed further (Vander Wall 2010, Wang and Ives 2017). However, opposite patterns may also emerge. In right-skewed distributions where large seeds are rare, rodents may compensate by caching some small seeds for future use, thereby increasing the caching rate of small seeds. Conversely, in left-skewed patches containing abundant large seeds, rodents' caching requirements may be more readily satisfied, leading to immediate consumption of some large seeds, and consequently decreasing the overall caching rate of large seeds. Regarding dispersal distance, left-skewed patches containing abundant large seeds may exhibit reduced initial dispersal distances. This pattern aligns with the rapid-sequestering hypothesis, which posits that rodents initially cache seeds near source plants (i.e. at shorter distances) to maximize harvest efficiency during peak seed production, subsequently redistributing these cached seeds to greater distances to reduce cache density and minimize pilferage risk (Jenkins and Peters 1992).

Despite the potential importance of trait distribution effects, only one previous study by Shimada et al. (2015) has explicitly examined how patch-level variation in seed traits influences rodent foraging behavior. Working with *Quercus serrata* acorns, they found that patches with higher size CV and lower tannin skewness experienced greater seed removal rate. While groundbreaking, this study had several important limitations that constrain our broader understanding of trait distribution effects. First, this study conflated seed predation and dispersal by categorizing all removed seeds (whether eaten or cached) into a single metric, obscuring the opposing fitness consequences for plants. Seed consumption represents reproductive failure, while caching offers recruitment potential; aggregating these outcomes risks misinterpreting ecological and evolutionary dynamics (Vander Wall et al. 2005, Wang et al. 2013, Cui et al. 2023, Yu et al. 2025). Second, the study only examined removal probability without considering dispersal distance, another critical component of seed fate that directly affects seedling recruitment success. Third, and perhaps most importantly, the research did not investigate how trait distributions at the patch level might modify rodent selection pressures on individual seed traits – a key mechanism that could help explain the maintenance of seed size variation within plant populations.

To address these knowledge gaps, we conducted a comprehensive field experiment examining how intraspecific variation in seed size, quantified through both CV and skewness, influences multiple dimensions of seed fate in two sympatric *Lithocarpus* species (*L. pachyphyllus* and *L. hancei*) in a subtropical forest. Our experimental design specifically controlled for seed density and mean seed size across patches while systematically manipulating the CV and skewness of seed size distributions in artificial seed patches. This approach allowed us to isolate the effects of trait distribution patterns from other potentially confounding variables. We focused on two fundamental questions: 1) how do patch-level seed size distributions (CV and skewness) influence overall patterns of seed consumption and dispersal? And 2) how do these distributional characteristics affect the direction and strength of rodent size selection at the individual seed level? By examining both patch-level patterns and individual seed fates simultaneously, we provide a more complete understanding of how intraspecific trait variation mediates ecological interactions between plants and their rodent dispersers.

Material and methods

Study site

The study was conducted in the Ailao Mountains National Nature Reserve (24°32′N, 101°01′E), Yunnan Province, southwest China, within a subtropical montane moist evergreen broadleaf forest ecosystem. Located at approximately 2500 m a.s.l., our study site has a mean annual temperature of 11.3°C and receives 1930 mm of annual precipitation. The forest canopy is dominated by Fagaceae, Lauraceae, Theaceae and Magnoliaceae species (Wen et al. 2018). Local rodent species, including Chinese white-bellied rat *Niviventer confucianus*, Asian red-cheeked squirrel *Dremomys rufigenis*, Anderson's white-bellied rat *Niviventer andersoni*, and south China field mouse *Apodemus draco*, serve as key seed dispersers in this ecosystem, particularly for Fagaceae species (Xiao and Zhang 2012, Liu et al. 2023).

Seed collection

We studied two Fagaceae species (*Lithocarpus pachyphyllus* and *L. hancei*) that rely on rodent scatter-hoarding for seed dispersal (Lang and Wang 2016, Wang et al. 2025). Both target species coexist sympatrically in the study forest and exhibit synchronized seed maturation from August to November. In October 2023, we collected newly matured seeds from the study forest, implementing a two-step exclusion protocol to remove damaged or insect-infested individuals. First, we visually inspected all seeds and discarded those with visible holes, cracks, or other signs of physical damage. Second, we conducted float tests on the remaining seeds, discarding buoyant seeds as these were presumed to be empty (and thus nutritionally valueless). In total, we obtained 4245 *L. pachyphyllus* and 5000 *L. hancei* seeds, which were stored under controlled refrigeration at 4°C prior to field experiments.

Experimental design

All seeds were individually weighed (fresh mass). For *L. hancei* (n = 5000), mean seed size was 1.8 ± 1.0 g (mean ± SD; range: 0.2–5.0 g; CV = 0.5; skewness = 0.8). Through 1000 iterations of random sampling (without replacement), we generated 60-seed experimental patches, ultimately selecting 41 unique seed combinations that maximized CV (0–0.68) and skewness (−0.23–1.92) ranges while maintaining consistent mean mass (1.8 ± 0.2 g; Supporting information). Our preliminary data from 27 maternal *L. hancei* trees in natural populations showed seed size distributions with CV ranging 0.26–0.64 and skewness ranging −0.96–1.31, confirming the natural occurrence of such seed size polymorphism. *L. pachyphyllus* seeds (n = 4245; mean = 2.3 ± 0.6 g, range: 0.8–5.0 g; CV = 0.3; skewness = 1.2), underwent identical resampling, yielding 41 patches with CV (0–0.47) and skewness (−0.74–2.75) variation at controlled mean mass (2.3 ± 0.2 g; Supporting information).

Seed releasing experiments

In November 2023, we established 82 seed release points (41 per species) within the same forest where seed collection occurred. This experimental timing was deliberately scheduled for November, coinciding with the end of both species' natural fruiting period (August to November), to minimize potential interference from natural seed availability. These points were spaced 30 m apart, a distance exceeding the typical seed dispersal range (< 20 m) of local rodents (Chen et al. 2022, Liu et al. 2023). Each release point was randomly assigned to one of the 41 patches for each species, ensuring unbiased spatial distribution of patches.

All experimental seeds were individually weighed (± 0.01 g) and uniquely marked with a numbered plastic tag (2.5 × 0.7 cm) attached via a 15 cm stainless steel wire (0.2 mm diameter) after drilling a 0.5 mm hole at the seed base (pilot tests indicated that the drilled seeds exhibited normal germination), ensuring unique identification for each seed. This tagging method allowed rodents to disperse and cache seeds while retaining visible plastic tags on the soil surface. Previous studies have shown that such tags have negligible effects on seed removal or consumption probabilities by rodents (Zhang and Wang 2001, Xiao et al. 2006, Wang et al. 2012; but see Wróbel and Zwolak 2013). This method has been widely used in plant-rodent interaction studies using seeds ranging from 0.01 to 60 g (Jansen et al. 2004, Wróbel and Zwolak 2017, Chen et al. 2022, Wu et al. 2024). In our study, the mean seed mass of both species (~ 2 g), was an order of magnitude greater than the tag mass (0.25 g, representing ~ 12.5% of seed mass). We therefore conclude that the additional tag weight likely had minimal impact on seed fate in our experimental system. At each release point, 60 seeds from a single patch were arranged in a 50 cm diameter circle with tags oriented radially outward. A total of 2460 seeds were released per species (60 seeds × 41 release points).

Seed fate survey

Seed fates were checked during 13 survey intervals: days 1, 2, 3, 4, 6, 8, 12, 16, 20, 24, 28, 36 post-releases, followed by a final post-overwintering assessment in May 2024. For each survey, a systematic search was conducted within a 30 m radius of each release point, supplemented by haphazard searches beyond this area. While interim surveys tracked short-term dynamics of scatter-hoarded seeds (including cache pilferage and secondary dispersal), all statistical analyses focused on the final post-overwintering assessment which best captures the ultimate predation versus dispersal outcomes and the cumulative effects of CV and skewness on seed fate. Seed fates were categorized as ignored (seeds remaining intact at their original release points), consumed by rodents (seeds partially or fully consumed either at or away from their release points), successfully dispersed (seeds scatter-hoarded in soil or under litter) and missing (seeds that were not retrieved with unknown fate) (Wang and Chen 2009, Wang and Ives 2017, Liu et al. 2023). For all seeds retrieved outside their original release points, we measured the dispersal distances between retrieved locations and release points. Additionally, successfully dispersed seeds were continuously monitored across subsequent surveys.

Data analysis

For the first question, we implemented linear regression models to evaluate how within-patch CV and skewness influenced three key seed fate parameters at the patch level (considering each release point as an independent foraging patch): 1) proportion of seeds consumed, 2) proportion of seeds successfully dispersed, and 3) mean dispersal distance with species analyzed separately. Significant CV effects on both consumption probability and dispersal distance were detected for *L. pachyphyllus* but not *L. hancei*, prompting additional analyses with species × CV interaction terms. These revealed a marginal significant interaction effect on both dispersal distance ($\chi^2 = 3.36$, $p = 0.06$) and consumption probability ($\chi^2 = 3.21$, $p = 0.07$), indicating interspecific variation in CV-dependent selection.

To address the second question, we first performed integrated analyses combining all patches using mixed-effects modeling. We constructed: 1) generalized linear mixed models (GLMMs) with binomial error distributions to analyze consumed and dispersal probabilities, and 2) linear mixed models (LMMs) with Gaussian error distributions for dispersal distances (log-transformed). All full models incorporated individual seed size, CV, skewness, their two-way interactions, and the three-way interaction (seed size × CV × skewness) as fixed effects, with release point included as a random intercept. Prior to modeling, all variables were standardized (mean = 0, SD = 1) to ensure direct comparability of regression coefficients. When significant interaction effects involving seed size were identified, we conducted simple slopes analyses by assessing the seed size–fate relationship at minimum, median, and maximum CV/skewness values to examine context-dependent effects across the full trait distribution range.

To better visualize how size effects vary across the CV/skewness gradient, we assessed individual seed size effects separately for each patch using: 1) generalized linear models (GLMs) with binomial distributions to examine size-dependent probabilities of seed consumed and successful dispersal, and 2) linear regression models to evaluate size effects on dispersal distances (log-transformed). This preliminary analysis revealed inter-patch variation in the strength and direction of size-dependent selection.

All statistical analyses were conducted in R software ver. 4.3.1. For all linear models and linear mixed models, residual normality was verified using the Lilliefors test implemented in the 'nortest' package (Gross and Ligges 2015), with all models meeting normality assumptions (Lilliefors test $p > 0.05$).

Results

Overall pattern of seed predation and dispersal by rodents

At the end of the experiment, the 2460 *L. hancei* seeds showed the following fates, 355 (14.4%) remained ignored, 1861 (75.7%) were consumed by rodents (958 consumed in situ and 903 transported before consumption), and 42 (1.7%) were successfully dispersed, while 202 (8.2%) were missing. Of the 945 seeds that were transported away from their original release points (including both consumed and successfully dispersed seeds), the mean dispersal distance was 3.5 ± 3.4 m, with a maximum dispersal distance of 22.11 m. The 2460 *L. pachyphyllus* seeds exhibited 0% ignored, 1846 (75.0%) consumed (161 in situ and 1685 after transport), and 115 (4.7%) successfully dispersed and 499 (20.3%) were missing. The transported seeds (n = 1800) showed a mean dispersal distance of 4.7 ± 3.8 m, with an exceptional maximum distance of 46.88 m.

Effects of CV and skewness on seed fate at patch-level

In *L. pachyphyllus*, rodent consumption rates varied significantly among patches (range: 46.7%–90.0%). Patch-level analysis revealed a positive relationship between seed size CV and consumption probability ($t = 2.02$, $p = 0.05$; Fig. 1a), while skewness showed no significant effect ($t = 1.12$, $p = 0.27$; Fig. 1b). Dispersal rates similarly varied across patches (0%–11.7%), though neither CV nor skewness significantly influenced this parameter. Mean dispersal distances (3.06–7.45 m) demonstrated a negative correlation with CV ($t = -2.28$, $p = 0.03$; Fig. 1e) but not with skewness ($t = 1.46$,

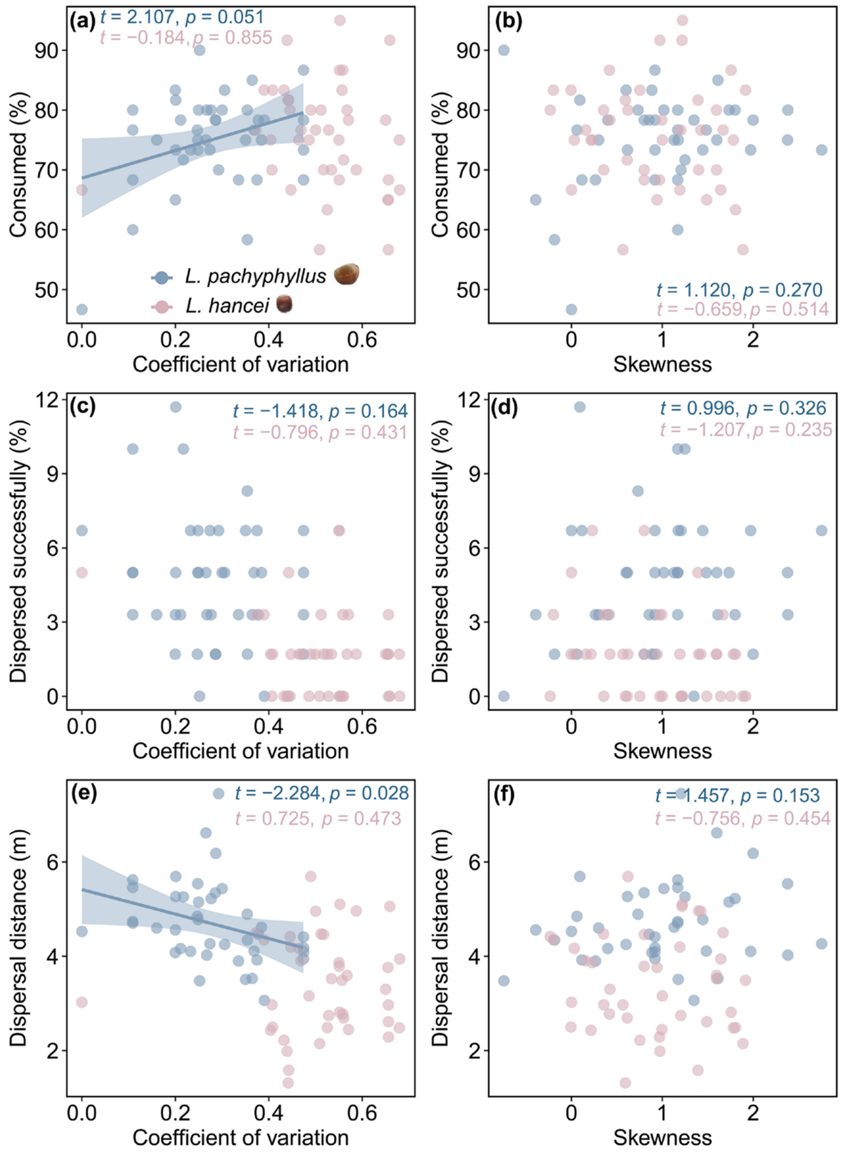

Figure 1. Effects of within-patch seed size variation (CV) and distribution skewness on seed fates in *L. pachyphyllus* (blue dots) and *L. hancei* (red dots): (a, b) proportion of seeds consumed per patch, (c, d) proportion of seeds successfully dispersed per patch, and (e, f) mean seed dispersal distance per patch. Shaded regions indicate 95% confidence intervals.

$p = 0.15$; Fig. 1f). Contrastingly, *L. hancei* showed no significant effects of either CV or skewness on consumption rates, dispersal success, or dispersal distance (all $p > 0.05$; Fig. 1, Supporting information).

Different individual seed size effects on seed fate among patches

The consolidated analysis of *L. pachyphyllus* revealed that larger seeds were less likely to be consumed ($z = -6.63$, $p < 0.001$) but were dispersed farther ($t = 5.30$, $p < 0.001$), with no size effect on dispersal probability ($z = -1.57$, $p = 0.12$; Supporting information). Patch-specific analyses showed heterogeneous patterns: eight patches mirrored the overall negative size-consumption relationship, while 33 patches showed no correlation (Fig. 2a). Dispersal distance patterns were similarly heterogeneous, with seven patches following the overall positive trend, one showing an inverse relationship, and 33 displaying no clear pattern (Fig. 2e). *L. hancei* exhibited an opposite overall pattern, with larger seeds being more frequently consumed ($z = 4.11$, $p < 0.001$; Supporting information). Patch-level variation was evident, with three patches showing positive, two negatives, and 36 no size–consumption relationships (Fig. 2b). Dispersal distance patterns were similarly heterogeneous to those of *L. pachyphyllus* (Fig. 2f).

The three-way interaction among seed size, CV, and skewness significantly influenced consumption probability in *L. hancei* ($z = -2.98$, $p = 0.003$) and dispersal distance in *L. pachyphyllus* ($t = -2.04$, $p = 0.04$; Supporting information). For *L. hancei*, the direction of individual seed size–consumption probability relationships reversed with increasing CV in

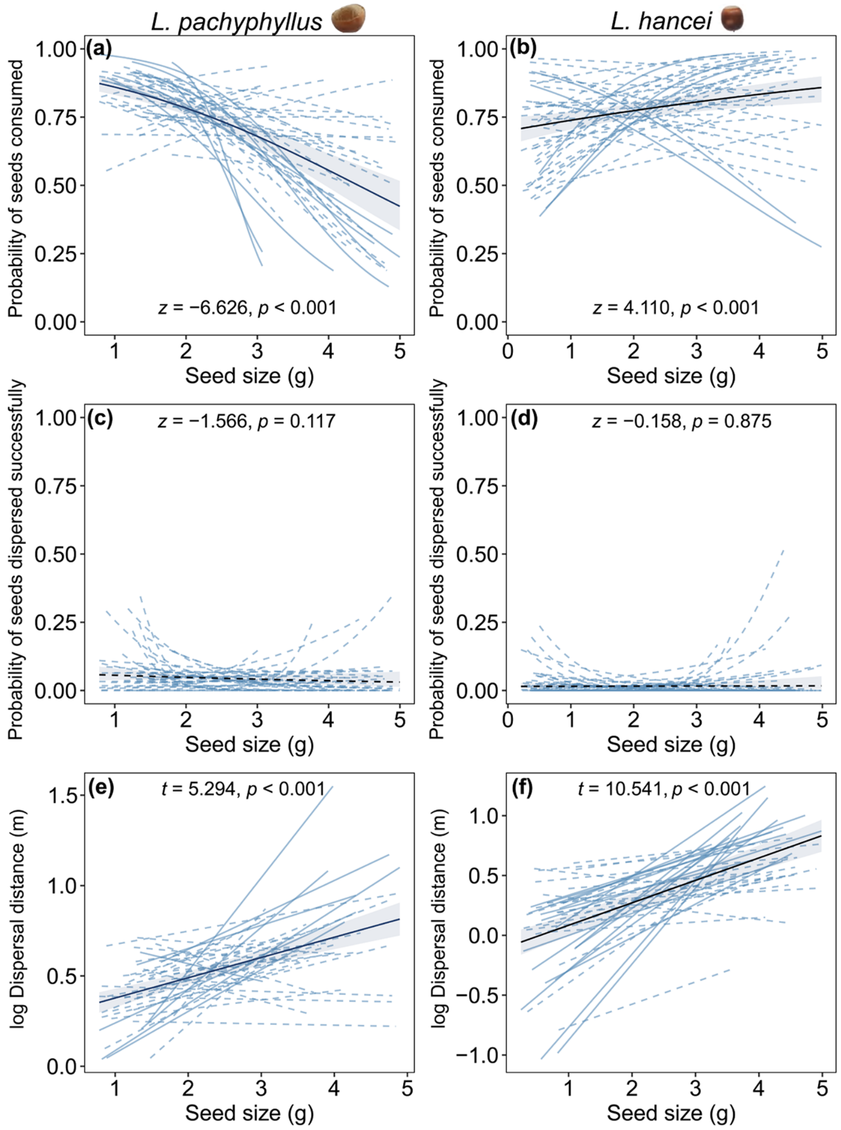

Figure 2. Individual size-dependent seed fate in *L. pachyphyllus* (left panels) and *L. hancei* (right panels): (a, b) probability of seeds being consumed, (c, d) probability of seeds being successfully dispersed, and (e, f) dispersal distance. Pale blue lines represent patch-specific relationships; dark blue lines show overall effects incorporating CV, skewness, and their interactions (full statistics in the Supporting information). Shaded areas indicate 95% confidence intervals.

left-skewed (negative → positive) versus right-skewed (positive → negative) patches (Fig. 3a–c). For *L. pachyphyllus*, the negative size–distance relationship became positive in left-skewed patches as CV increased, while the opposite occurred in right-skewed patches (Fig. 3d–f).

Discussion

Our study provides novel insights into how intraspecific seed size variation, characterized by coefficient of variation (CV) and skewness, mediates rodent–seed interactions through both patch-level and individual seed-level processes. The findings reveal that seed trait distributions not only influence overall seed fates but also modulate the strength and direction of rodent selection on individual seed size, offering a mechanistic explanation for the maintenance of seed size polymorphism in natural populations. These results align with emerging ecological frameworks emphasizing the role of trait heterogeneity in shaping species interactions and evolutionary dynamics (Berg and Ellers 2010, Vindenes and Langangen 2015, Crawford et al. 2019).

The positive relationship between seed size CV and predation probability in *L. pachyphyllus* suggests that more variable seed patches experience higher overall consumption rate. This pattern could emerge if heterogeneous patches attract more rodent activity or increase foraging efficiency, as rodents can selectively target larger seeds within mixed-size assemblages. While Shimada et al. (2015) reported a similar positive effect of CV on seed removal rate (combining both consumed and

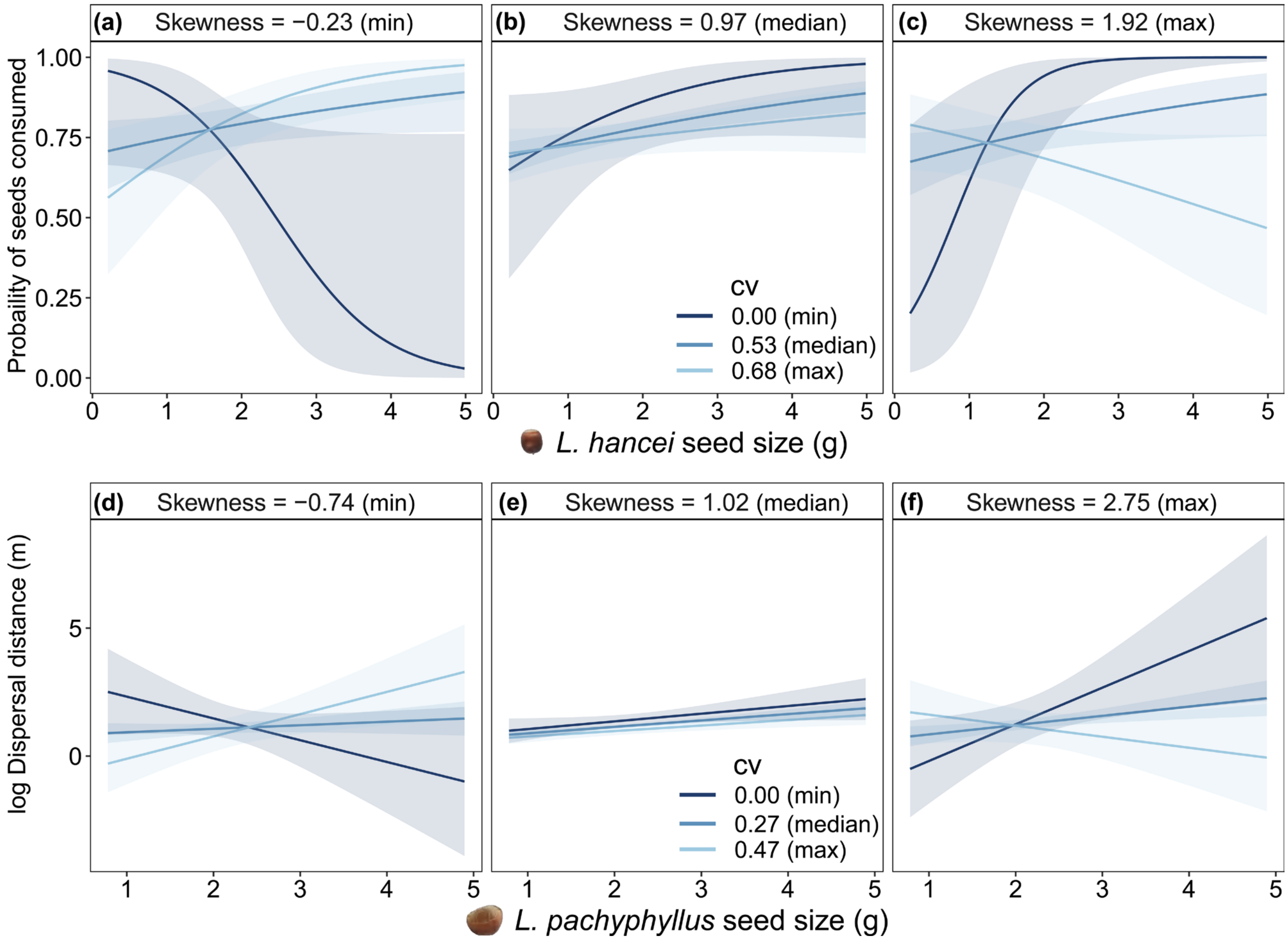

Figure 3. Partial relationships between individual seed size and seed fate when fixing CV and skewness at their maximums, minimums, and medians: (a–c) probability of seeds being consumed in *L. hancei* and (d–f) dispersal distance in *L. pachyphyllus*. Shaded bands represent 95% confidence intervals.

cached seeds), our refined approach reveals distinct fitness implications: higher CV increased predation risk without necessarily enhancing dispersal success. This critical distinction, enabled by our separate analysis of predation and dispersal outcomes, provides a more nuanced understanding of how seed size variation affects plant recruitment dynamics beyond simple removal metrics.

The negative relationship between CV and dispersal distance in *L. pachyphyllus* suggests an intriguing tradeoff in rodent foraging strategies. While high CV patches attracted more foraging activity and higher predation rates, the dispersed seeds tended to be moved shorter distances, supporting the rapid-sequestering hypothesis (Jenkins and Peters 1992, Jenkins et al. 1995). Alternatively, this pattern may reflect altered rodent movement patterns in response to patch heterogeneity, possibly because the presence of both highly desirable and less attractive seeds in variable patches might lead to more localized caching behavior as rodents balance energy acquisition and storage strategies (Cao et al. 2016).

The lack of significant CV effects in *L. hancei* reveals important interspecific differences in how seed traits mediate rodent interactions. Similar inter-specific variations have been reported in other studies focusing on seed–rodent interaction (Thein et al. 2021, Chen et al. 2022, Wu et al. 2024). While both species showed individual-level size selection, only *L. pachyphyllus* demonstrated clear patch-level responses to CV. This difference may relate to their distinct seed characteristics, as *L. hancei* seeds are generally smaller and may fall below a threshold where patch-level variation becomes ecologically meaningful to rodents. Alternatively, chemical defenses or other traits not measured in this study might override size distribution effects in *L. hancei*. These species-specific patterns emphasize that seed dispersal outcomes depend on complex interactions between multiple trait dimensions (Wang and Chen 2012, Gong et al. 2015). Interestingly, the lack of significant skewness effects in both species implies that rodents are more sensitive to the degree of variability than to distributional asymmetry, underscoring the pivotal role of CV in shaping patch-level foraging strategies.

Rodent selectivity for seed size varied dramatically across patches. For instance, in *L. hancei*, the direction of size–predation relationships reversed completely between left-skewed and right-skewed patches as CV increased; while for *L. pachyphyllus*, the negative size–distance relationship became positive in left-skewed patches as CV increased, while the opposite occurred in right-skewed patches (Fig. 3). These complex patterns demonstrate that rodent selection on seed size is not fixed but varies substantially depending on the local trait distribution context. This spatial heterogeneity in selection pressures creates a 'mosaic' of fitness landscapes, where no single seed size maximizes fitness across all patches (Wang and Ives 2017). Such conditional selection patterns provide a potential mechanism for maintaining seed size variation within populations through spatial variation in fitness landscapes, where the optimal seed size differs across patches with varying trait distributions. The significant three-way interactions among seed size, CV and skewness further emphasize the complexity of these ecological relationships. This nuanced pattern implies that seed traits experience spatially variable selection depending on their local neighborhood context offering crucial insights into the maintenance of genetic diversity in plant populations.

Our findings extend beyond seed dispersal systems to reveal a broader ecological principle: context-dependent selection mediated by intraspecific trait variation operates across diverse plant–animal interactions. For instance, nectarivores often prefer less variable food patches, showing variance-averse behavior when choosing between rewards with different variances (Herrera 2009, Nakamura and Kudo 2016). By analyzing 457 performance datasets across 53 insect herbivore species, Wetzel et al. (2016) demonstrated that intraspecific variation in plant nutritive traits substantially reduces mean herbivore performance. Moreover, pronounced intraspecific variation is ubiquitous across floral and foliar traits in natural ecosystems (Kuppler et al. 2020), representing a widespread phenomenon. The convergence across systems suggests that patch-level trait variation mediates selection, constituting a fundamental yet underappreciated ecological organizing principle.

While our models revealed significant effects of seed size variation on rodent foraging patterns, the relatively low R^2 values (Supporting information) indicate substantial unexplained variance, a common feature of ecological systems where multiple biotic and abiotic factors interact (Møller and Jennions 2002). This suggests that although CV and skewness represent important determinants of seed fate, additional factors (e.g. microhabitat characteristics, rodent community composition, or unmeasured seed traits) likely contribute to the observed patterns.

Several important questions remain for future research. First, how generalizable are these patterns across ecological contexts? Would similar relationships emerge in different ecosystems or with alternative rodent communities? Second, what is the relative importance of seed size variation compared to other trait variations (e.g. tannins, nutrients) in driving these patterns? Third, how do these patch-level processes interact with temporal variation in seed production to influence long-term plant population dynamics? Addressing these questions will require both broader comparative studies and longer-term monitoring of natural seed fate patterns. Fourth, future studies should incorporate the perspective of optimal foraging theory to better understand rodent decision-making processes. Our study focused primarily on how seed trait distributions (CV and skewness) affect seed fates, but rodent foraging behavior is ultimately driven by energy optimization (Vickery 1984). Investigating how seed trait distributions influence key foraging parameters, including handling time, patch residence time, and energy tradeoffs between immediate consumption and caching, could provide a more mechanistic explanation for the observed patterns. Furthermore, the conceptual framework developed here could potentially be extended to other plant-animal interaction systems, such as frugivory and pollination, where trait variation in rewards (e.g. fruit pulp or nectar) might similarly influence animal foraging decisions and mutualistic outcomes.

In conclusion, our study demonstrates that intraspecific variation in seed size – quantified through both CV and skewness – represents an important but understudied dimension of rodent–seed interactions. By showing that patch-level trait distributions modify both overall seed fates and individual-level selection patterns, we provide mechanistic insight into how seed size polymorphism might be maintained in natural populations. These findings advance ecological theory by highlighting the importance of considering trait distributions, not just individual traits, in understanding species interactions and selection dynamics in natural systems. Future work integrating these patch-level perspectives with community-level processes will further enhance our understanding of forest regeneration and biodiversity maintenance.

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Author contributions

Jinyu Zhang: Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (equal). **Bo Wang**: Conceptualization (lead); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.29606753 (Zhang and Wang 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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