Forest Ecology and Management 507 (2022) 120016

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Canopy openness of individual tree promotes seed dispersal by scatter-hoarding rodents

Jie Chen [a], Wenwen Chen [a,b], Zhiyun Lu [c,d], Bo Wang [a,b,*]

[a] School of Resources and Environmental Engineering, Anhui University, Hefei, Anhui 230601, China
[b] Anhui Province Key Laboratory of Wetland Ecosystem Protection and Restoration (Anhui University), Hefei, Anhui 230601, China
[c] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China
[d] Ailaoshan Station of Subtropical Forest Ecosystem Studies, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Jingdong, Yunnan 676209, China

ARTICLE INFO

Keywords:
Canopy openness
Plant-animal interaction
Seed predation
Seed removal
Tree-to-tree variation

ABSTRACT

Scatter-hoarding rodents are important seed predators and dispersers in various forest ecosystems and significantly influence the seed fate and seedling regeneration of many tree species. Canopy openness is believed to have an important influence on the foraging behavior of scatter-hoarding rodents, mainly because of the variation in predation risk between open and canopy microsites. Most of the current studies have mainly focused on the spatial variation in canopy openness within a forest or on comparisons among forests; however, the question of how variation in canopy openness at the individual tree scale affects seed-rodent interaction has received little attention, although tree-to-tree variation in canopy openness is ubiquitous. In this study, we measured the individual canopy openness of 45 trees belonging to three species in a subtropical forest, and compared seed dispersal and predation by rodents under the selected trees by labeling and tracking 4,500 seeds. Our results showed that canopy openness differed among individual trees both within and across species. More importantly, our results proved that individual tree variation in canopy openness significantly affected seed dispersal and predation by rodents, although not all species followed a consistent pattern. Seeds under trees with larger canopy openness were more likely to be removed rather than eaten *in situ* and dispersed farther. Our study highlights the pattern that individual tree characteristics (e.g., canopy openness) have profound effects on rodent-mediated seed dispersal services, which may further lead to tree-to-tree variation in seed fate and seedling regeneration. Our results also provide important implications for forest conservation and management: crown pruning can promote seed dispersal by rodents and natural seedling regeneration.

1. Introduction

In forest ecosystems, the canopy of trees blocks most of the sunlight that directly influences the photosynthesis and energy accumulation of underground vegetation, especially for tree seedlings (Brooks et al., 1996, Robakowski et al., 2004, Giertych et al., 2015). Furthermore, high density of seeds and seedlings under the canopies usually leads to a disproportionate mortatily of seeds and seedlings around mother trees because of its huge attraction for specialist enemies (Janzen, 1970, Connell, 1971, Chesson, 2000, Comita et al., 2014). Therefore, canopy openness plays a crucial role in a series of ecological processes in forest regeneration such as seed germination, seedling growth and survival, and biodiversity maintenance (Winkler et al., 2005, Goodale et al., 2014, Lu et al., 2018). Furthermore, canopy openness can also affect the foraging behavior of forest-dwelling animals (e.g., herbivores, seed predators, and dispersers) mainly because of the variation in shelter and predation risk between open and canopy microsites (Iida, 2006, Perea et al., 2011, Zhang et al., 2017), thus in turn influencing forest regeneration indirectly (Basset et al., 2001, Yang et al., 2016, Barrere et al., 2021).

Scatter-hoarding rodents are important seed predators and dispersers in various forest ecosystems, and significantly influence the seed fate and seedling regeneration of many tree species (Vander Wall, 2010, Cao et al., 2016, Wang and Ives, 2017, Bogdziewicz et al., 2020). Canopy openness is believed to have an important influence on the foraging behavior of scatter-hoarding rodents, mainly because of the variation in predation risk between open and canopy microsites (Iida, 2006, Pérez-Ramos et al., 2008, Perea et al., 2011). For example, the giving-up

* Corresponding author at: School of Resources and Environmental Engineering, Anhui University, Hefei, Anhui 230601, China.
E-mail address: yangblue@ahu.edu.cn (B. Wang).

https://doi.org/10.1016/j.foreco.2022.120016
Received 11 November 2021; Received in revised form 5 January 2022; Accepted 6 January 2022
Available online 15 January 2022
0378-1127/

densities, the densities at which foraging at a site is given up, of rodents were lower under the tree canopies compared to open sites, and rodents preferred to cache seeds at open sites because the high predation risks may reduce the cache pilferage (Steele et al., 2014, 2015); while some other studies found that seeds cached in open microsites were detected and removed faster than those under canopies (Dimitri and Longland, 2021).

Current studies discussing the effects of canopy openness on rodent-seed interaction have mainly focused on one of two scales of comparison: (i) the among-forest scale, with comparisons among forests with different canopy densities, such as logged forest vs. unlogged forest, and thinned forest vs. unthinned forest (Lambert et al., 2005, Zhang et al., 2016, Wang et al., 2019); or (ii) the within-forest scale, with comparisons among sites within the same forest, such as inner vs. edge of the forest, forest understory vs. canopy gaps, and among sites with different distances to the base of the tree or canopy gaps (Chen et al., 2017; Greenler et al., 2019; Smit et al., 2008; Steele et al., 2015; Yu et al., 2014).

In both these comparisons, the environments under the canopies of different trees in the forest are treated equally and the canopy openness effect is explored at the community level, while the variation in canopy openness under individual trees is ignored. However, trees in the forest often differ substantially in height, crown size, foliage luxuriance, and spatial arrangement of branches and leaves (King, 1998, Reinhardt and Kuhlemeier, 2002, Rosell et al., 2009, Shenkin et al., 2020, Santopuoli et al., 2022), all of which may lead to tree-to-tree variation in canopy openness. Furthermore, because of the high density of seeds during the fruiting season, rodents often show much more activity under tree crowns. Therefore, the effects of canopy openness on rodent foraging behavior under trees may be much stronger than that in open sites. Moreover, focusing on the effect of canopy openness at the individual tree scale may also provide some new perspectives; for example, the tree-to-tree variation in canopy openness may consequently lead to variation in seed predation and dispersal by rodents and, in turn, the fitness of individual trees. Surprisingly, the question of how variation in canopy openness at the individual tree scales affects seed-rodent interaction has so far received little attention.

In this study, we measured the individual canopy openness of 45 trees belonging to three species in a subtropical forest, and compared the seed dispersal and predation by rodents under the selected trees by labeling and tracking 4,500 seeds. We aimed to address the following questions: 1) Does canopy openness differ among individual trees? 2) Does tree-to-tree variation in canopy openness affect seed predation and dispersal by rodents? 3) If so, do the species follow the same rules?

2. Material and methods

2.1. Study site

The field experiment was conducted in 2020 in a subtropical evergreen broadleaf forest in the Ailao Mountains, southwestern China (24°32′ N, 101°01′ E, altitude 2045 m). The mean annual temperature is 11.7 ℃ and precipitation is 1,923 mm. The dominant tree species were of the Fagaceae family (e.g., *Lithocarpus xylocarpus* and *Lithocarpus hancei*), all of which depend on scatter-hoarding rodents for seed dispersal. The dominant rodent species were *Niviventer confucianus*, *Apodemus ilex*, and *Niviventer excelsior*, all of which could both scatter-hoard and larder-hoard plant seeds, and were responsible for the cosumption and dispersal of our experimental seeds (Feng et al., 2021; Lang and Wang, 2016; Wang et al., 2018; Xiao and Zhang, 2012, unpblished camera-trap data).

2.2. Study species and experimental design

Three stone oak species were selected for the study: *Lithocarpus xylocarpus*, *Lithocarpus hancei*, and *Lithocarpus pachyphyllus*. In November 2020, intact seeds were collected directly from the forest floor, and the woody-enclosed receptacles were removed manually. A 0.6 mm hole was drilled in each seed at the base end of the seed and connected with a white plastic tag (3.5 cm × 2.5 cm) by a 15 cm long steel line (0.2 mm in diameter), and each tag was numbered for individual seed identification (Xiao et al., 2006, Wang and Ives, 2017).

Fifteen adult trees of each target species, spaced >30 m apart from each other, were chosen from the forest. Under the canopy of each tree, one seed releasing point was randomly established. At each point, 100 conspecific seeds were placed along a circle (30 cm in diameter), with tags pointing outwards. In total, 4,500 seeds were released (100 seeds × 15 trees × 3 species) in December 2020. The released seeds did not differ in seed mass among the individual trees for all the three species (one-way ANOVA test, all p values > 0.09). The canopy openness for each tree was monitored with a hemispheric camera placed 1 m above the seed releasing point. The Gap Light Analyzer software was used to analyze the canopy photos and calculate the percentage of canopy openness (Frazer et al., 1999).

The overwinter fate of each seed was checked in the May month of the following year. Rodents usually transport seeds over distances that are <30 m in our study forest (Feng et al., 2021; Lang and Wang, 2016, unpublished data). Therefore, we conducted an intensive and complete search around each tree with a radius of 30 m, beyond which we performed a haphazard search to locate as many seeds that were removed as possible. Seed fates were first classified as seeds eaten by rodents *in situ*, seeds removed by rodents, and seeds left intact at the releasing points. The removed seeds included seeds that were eaten after being transported, seeds that were not found with their fates unknown (i.e., missing seeds), and seeds that were dispersed successfully (seeds deposited on the ground or buried in the soil intact after being removed by rodents). When a removed seeds was relocated (including both the seeds eaten after removal and seeds dispersed successfully), the dispersal distance to its original point was measured.

2.3. Data analysis

A GLM (general linear model) was used to analyze the differences in canopy openness and seed fates among trees and among species. Pearson's correlation coefficient was used to evaluate the correlation between individual tree canopy openness and the seed fates under each tree (i.e., the proportions of seeds eaten *in situ*, removed, and successfully dispersed, and the dispersal distance). We first analyzed all the trees together and we then analyzed the trees of each species separately. All statistical analyses were conducted using the statistical software R (version 3.6.1).

3. Results

3.1. General pattern of canopy openness

The mean canopy openness differed among the 45 trees, ranging from 3.8% to 8.2%. The canopy openness showed significant differences among tree species (GLM: $F_{2,42} = 3.408$, $p = 0.043$): the canopy openness of *L. xylocarpus* was 5.20 ± 0.75 (Mean ± SD), with the range being 3.76–6.43; the canopy openness of *L. hancei* was 5.68 ± 1.17, with the range being 4.23–8.06; and the canopy openness of *L. pachyphyllus* was 6.14 ± 0.99, with the range being 4.94–8.21.

3.2. General pattern of seed fates

Of the 4,500 seeds released, 1,020 (22.7%) were eaten *in situ*, 3,478 (77.3%) were removed by rodents, and only two seeds were left intact under the canopy. Of the 3,478 seeds removed, 1197 (34.4%) were eaten, 87 (2.5%) were cached and survived overwinter (i.e., being successfully dispersed), and the remaining 2,194 seeds (63.1%) were missing (Fig. 1). The mean dispersal distance was 2.73 ± 2.89 m, with

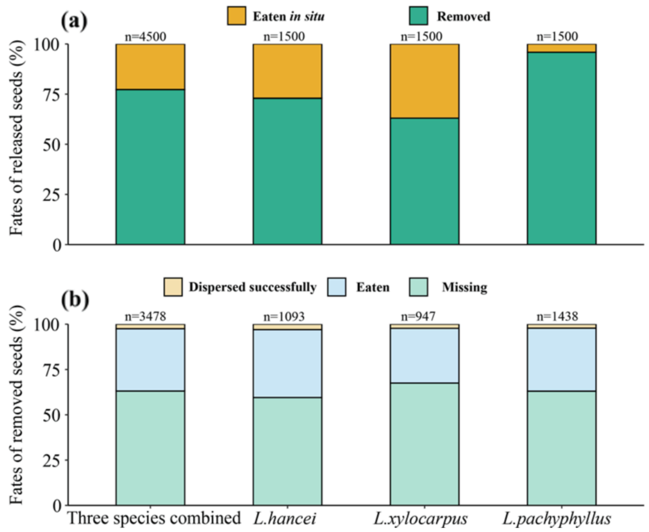

Fig. 1. Seed fates at the original releasing points (a) and after being removed by rodents (b). Numbers above the bars are the sample sizes.

the range being 0–27.33 m.

3.3. Effects of canopy openness on seed eaten in situ

The proportion of seeds eaten *in situ* differed considerably among the 45 trees, ranging from 0% to 83%. A significantly negative relationship was detected between canopy openness and the proportion of seeds eaten *in situ* ($r = -0.453$, $p = 0.002$), with the result that seeds under the trees with larger canopy openness were less likely to be eaten by rodents *in situ* (Fig. 2a). When analyzing each tree species separately, a negative trend was detected among the trees of *L. pachyphyllus* ($r = -0.583$, $p = 0.023$), but not among the trees of either *L. hancei* ($r = -0.430$, $p = 0.11$) or *L. xylocarpus* ($r = -0.121$, $p = 0.668$) (Fig. 2a).

3.4. Effects of canopy openness on seed removal

The proportion of seeds removed differed among trees, ranging from 17% to 100%. A significantly positive relationship was detected between canopy openness and the proportion of seeds removed ($r = 0.453$, $p = 0.002$), suggesting that seeds under trees with larger canopy openness were more likely to be removed by rodents (Fig. 2b). When analyzing each tree species separately, a positive trend was detected among the *L. pachyphyllus* trees ($r = 0.583$, $p = 0.023$), but not among the trees of either *L. xylocarpus* ($r = 0.121$, $p = 0.668$) or *L. hancei* ($r = 0.430$, $p = 0.11$) (Fig. 2b).

3.5. Effects of canopy openness on successful dispersal

The proportion of seeds dispersed successfully differed among trees, ranging from 0% to 40%. There was no significant relationship between canopy openness and proportion of seeds dispersed successfully ($r = 0.051$, $p = 0.739$) (Fig. 2c). Similarly, when analyzing each tree species separately, none of the species showed a clear trend between canopy openness and seed successful dispersal (all p values > 0.2) (Fig. 2c).

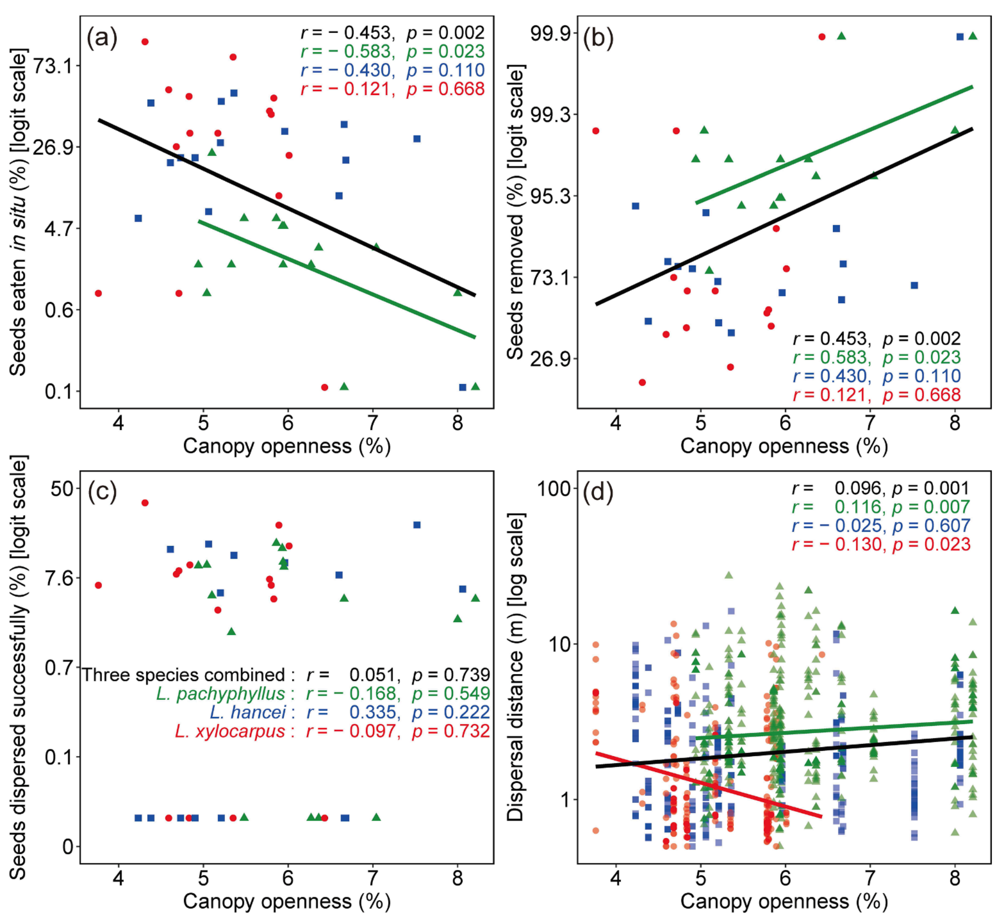

Fig. 2. The Pearson's correlation between the individual tree canopy openness and the proportion of seeds eaten *in situ* (a), removed (b), successfully dispersed (c) and dispersal distance (d).

3.6. Effects of canopy openness on dispersal distance

The dispersal distance of seeds differed substantially among trees (GLM: $F_{44,1239} = 6.544$, $p < 0.001$), ranging from 0.6 ± 0.3 m to 6.7 ± 5.8 m. A significantly positive relationship was detected between canopy openness and dispersal distance ($r = 0.096$, $p = 0.001$), suggesting that seeds under the trees with larger canopy openness were dispersed farther (Fig. 2d). When analyzing each tree species separately, a positive trend was detected among the trees of *L. pachyphyllus* ($r = 0.116$, $p = 0.007$) but a negative trend was detected for *L. xylocarpus* ($r = -0.130$, $p = 0.023$). No clear trends were detected for *L. hancei* tree species. ($r = -0.025$, $p = 0.607$) (Fig. 2d).

4. Discussion

Overall, our study showed that canopy openness differed among individual trees both within and across species. More importantly, our results suggested that individual tree variation in canopy openness significantly affected seed dispersal and predation by rodents, although not all species followed a consistent pattern. Seeds under trees with larger canopy openness were more likely to be removed rather than eaten *in situ* and to be dispersed at a further distance.

Canopy openness affects seed dispersal and predation by rodents, mainly because of the effects of light conditions on rodent foraging behavior, which lead to different predation risks (Pérez-Ramos et al., 2008, Perea et al., 2011). As discussed previously, most of the current studies have mainly focused on the spatial variation in canopy openness within a forest or on comparisons among forests, while ignoring the canopy openness variation among individual trees (Lambert et al., 2005, Steele et al., 2015, Zhang et al., 2016, Greenler et al., 2019). However, our results showed that the canopy openness also differed among individual trees. Furthermore, the individual tree variation in canopy openness affected the foraging behavior of scatter-hoarding rodents, which in turn led to tree-to-tree variation in seed fate. Our study indicated that the canopy openness could promote seed dispersal effectiveness by increasing seed removal probabliltiy and dispersal distance. In this case, trees with larger canopy openness may benefit more in the seed dispersal process, with may further translate into the following seedling establishment process. Furthermore, such findings occurred both within and across species; therefore, we may expect that the effect of individual tree canopy openness on seed dispersal plays an important role in seedling regeneration at both population and community level.

Several studies have attempted to test the individual tree variation in seed dispersal and predation; however, all of these studies have mainly focused on the effects of the variation on seed production and seed traits (e.g., seed size and tannin content) among trees (Shimada et al., 2015, Xiao et al., 2015, Wang and Ives, 2017). Our results indicated that even after the seeds are dropped from their mother tree, their seed dispersal and predation processes are subsequently affected by the different light conditions (i.e., canopy openness) provided by the mother tree. In this case, the canopy openness, seed production, as well as seed traits of the mother tree co-influenced seed dispersal and predation, which may lead to an unequal contribution of seedling regeneration among individual trees. A trade-off can be expected: on the one hand, a larger crown and more branches and leaves may enable the production of more energy and more number of seeds, and a higher density of seeds may result in either a higher survival rate (Predator satiation hypothesis, Kelly and Sork, 2002, Xiao et al., 2013) or better dispersal service with more seeds being dispersed and further dispersal distances (Predator dispersal hypothesis, Vander Wall, 2002; Wang et al., 2021). On the other hand, a large luxuriant crown may decrease the canopy openness, which may in turn increase the probability of seeds being eaten *in situ* but decrease the probability of seeds being dispersed and reduce the dispersal distance. Such a trade-off may reduce the tree-to-tree variation in terms of the contribution of seedling regeneration, so that many trees, with large or small canopies, have the probability to produce their own seedlings and the population may maintain a high level of genetic diversity. In such a case, an interesting question that can be asked is: which side of this trade-off has a greater impact on tree-to-tree variation in terms of seed predation and dispersal by rodents? It is difficult to address this question based on the findings of the current study, as we only focused on the effects of individual variations in canopy openness. However, tree-to-tree variation in seed production and seed traits usually varies substantially among years (Vander Wall, 2002, Xiao et al., 2013, Wang and Ives, 2017), while the individual variation in canopy openness does not often change considerably. Therefore, we may expect that the relative magnitudes of the two sides of this trade-off are dynamic.

The effects of canopy openness did not follow the same pattern among species, indicating that the effect of canopy openness on seed dispersal and predation by rodents may be species-specific. Similar interspecific variation has also been reported in other seed-rodent interaction studies, for example, the density effect on seed predation by rodents (Wang, 2020), and the fine-scale spatiotemporal variation in seed dispersal and predation by rodents (Feng et al., 2021). The interspecific variation in seed traits may be a potential explanation, as it can determine the rodent foraging preference for multiple species of seeds (Gong et al., 2015; Lichti et al., 2017; Vander Wall, 2010). Nevertheless, the species-specific variation in canopy openness effects on seed-rodent interaction may influence, at least to a certain extent, the seedling composition of the community, especially when extreme weather events occur (e.g., extreme snow and drought), and the canopy openness changes rapidly because of the death of trees and damage to crowns. Because seed-rodent interactions respond to canopy changes differently among tree species, a consequent change in the species-specific variation in seed survival and seedling regeneration can be expected, which may further change the species composition of the whole seedling community.

In addition, our results are also helpful in understanding the fine-scale spatial variation in seed dispersal and predation by rodents, for example, similar seeds often suffer different fates (predation vs. dispersal) at different sites or under different trees (Feng et al., 2021; Shimada et al., 2015; Wang and Chen, 2008). Logically, the individual tree variation in canopy openness does not change dramatically over time, especially in primary forests dominated by evergreen tree species; therefore, we undertook this experiment for only one year. However, our one-year results clearly indicate that the tree-to-tree variation in canopy openness, which has been usually ignored by relevant studies, plays an important role in seed-rodent interactions.

5. Conclusion

Our study highlights the pattern that individual tree characteristics (e.g., canopy openness) have profound effects on rodent-mediated seed dispersal services, which drive plant recruitment of diverse forest ecosystems. The tree-to-tree variation in canopy openness detected in our study forest ranged from 3% to 8%; however, such moderate variation could still lead to tree-to-tree variation in seed-rodent interactions, thus affecting the seed fates of individual trees. In some other forests, especially temperate forests, such variation in canopy openness may be even larger, and a stronger effect on seed-rodent interaction can be expected. Our results provide important implications for forest conservation and management; crown pruning can promote seed dispersal by rodents and natural seedling regeneration.

Data archiving statement

All data used in the manuscript are available in the supplementary material.

CRediT authorship contribution statement

Jie Chen: Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Wenwen Chen:** Investigation, Writing – review & editing.

Zhiyun Lu: Investigation, Writing – review & editing. **Bo Wang:** Conceptualization, Methodology, Formal analysis, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Mr Xiang Zhang and Mr Tianjie Lin for the help with field data collection, and Ailaoshan Station of Subtropical Forest Ecosystem Studies for logistical support in the field work.

Funding

This study was supported by the National Natural Science Foundation of China (31971444, 32171533 and 31901218).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120016.

References

Basset, Y., Charles, E., Hammond, D.S., Brown, V.K., 2001. Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. J. Appl. Ecol. 38, 1045–1058.
Barrere, J., Petersson, L.K., Boulanger, V., Collet, C., Felton, A.M., Löf, M., Saïd, S., 2021. Canopy openness and exclusion of wild ungulates act synergistically to improve oak natural regeneration. For. Ecol. Manage. 487, 118976. https://doi.org/10.1016/j.foreco.2021.118976.
Bogdziewicz, M., Crone, E.E., Zwolak, R., Rees, M., 2020. Do benefits of seed dispersal and caching by scatterhoarders outweigh the costs of predation? An example with oaks and yellow-necked mice. J. Ecol. 108 (3), 1009–1018.
Brooks, J.R., Sprugel, D.G., Hinckley, T.M., 1996. The effects of light acclimation during and after foliage expansion on photosynthesis of *Abies amabilis* foliage within the canopy. Oecologia 107 (1), 21–32.
Cao, L., Wang, Z., Yan, C., Chen, J., Guo, C., Zhang, Z., 2016. Differential foraging preferences on seed size by rodents result in higher dispersal success of medium-sized seeds. Ecology 97 (11), 3070–3078.
Chen, Q., Tomlinson, K.W., Cao, L., Wang, B., 2017. Effects of fragmentation on the seed predation and dispersal by rodents differ among species with different seed size. Integr. Zool. 12 (6), 468–476.
Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31 (1), 343–366.
Comita, L.S., Queenborough, S.A., Murphy, S.J., Eck, J.L., Xu, K., Krishnadas, M., Beckman, N., Zhu, Y., 2014. Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J. Ecol. 102, 845–856.
Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer, P.J., Gradwell, G.R. (Eds.), Dynamics of Populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, pp. 298–312.
Dimitri, L.A., Longland, W.S., 2021. Pilfering of western juniper seed caches by scatter-hoarding rodents varies by microsite and canopy type. Integr. Zool. 00, 1–14.
Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
Feng, L., Chen, S., Wang, B., 2021. Fine-scale spatiotemporal variation in seed-rodent interactions: A potential contribution to species coexistence. For. Ecol. Manage. 498, 119566. https://doi.org/10.1016/j.foreco.2021.119566.
Giertych, M.J., Karolewski, P., Oleksyn, J., 2015. Carbon allocation in seedlings of deciduous tree species depends on their shade tolerance. Acta Physiol. Plant 37, 1–15.
Gong, H., Tang, C., Wang, B., 2015. Post-dispersal seed predation and its relations with seed traits: a thirty-species-comparative study. Plant Spec. Biol. 30 (3), 193–201.
Goodale, U.M., Berlyn, G.P., Gregoire, T.G., Tennakoon, K.U., Ashton, M.S., 2014. Differences in survival and growth among tropical rain forest pioneer tree seedlings in relation to canopy openness and herbivory. Biotropica 46 (2), 183–193.
Greenler, S.M., Estrada, L.A., Kellner, K.F., Saunders, M.R., Swihart, R.K., 2019. Prescribed fire and partial overstory removal alter an acorn–rodent conditional mutualism. Ecol. Appl. 29 (7), e01958. https://doi.org/10.1002/eap.v29.710.1002/eap.1958.
Iida, S., 2006. Dispersal patterns of *Quercus serrata* acorns by wood mice in and around canopy gaps in a temperate forest. For. Ecol. Manage. 227 (1-2), 71–78.
Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104 (940), 501–528.
Kelly, D., Sork, V.L., 2002. Mast seeding in perennial plants: why, how, where? Annu. Rev. Ecol. Syst. 33 (1), 427–447.
King, D.A., 1998. Relationship between crown architecture and branch orientation in rain forest trees. Ann. Bot. 82, 1–7.
Lambert, T.D., Malcolm, J.R., Zimmerman, B.L., 2005. Effects of mahogany (*Swietenia macrophylla*) logging on small mammal communities, habitat structure, and seed predation in the southeastern Amazon Basin. For. Ecol. Manage. 206 (1-3), 381–398.
Lang, Z., Wang, B., 2016. The effect of seed size on seed fate in a subtropical forest, southwest of China. iForest 9 (4), 652–657.
Lichti, N.I., Steele, M.A., Swihart, R.K., 2017. Seed fate and decision-making processes in scatter-hoarding rodents. Biol. Rev. 92 (1), 474–504.
Lu, D., Wang, G.G., Zhang, J., Fang, Y., Zhu, C., Zhu, J., 2018. Converting larch plantations to mixed stands: Effects of canopy treatment on the survival and growth of planted seedlings with contrasting shade tolerance. For. Ecol. Manage. 409, 19–28.
Perea, R., González, R., San Miguel, A., Gil, L., 2011. Moonlight and shelter cause differential seed selection and removal by rodents. Anim. Behav. 82 (4), 717–723.
Pérez-Ramos, I.M., Urbieta, I.R., Marañón, T., Zavala, M.A., Kobe, R.K., 2008. Seed removal in two coexisting oak species: ecological consequences of seed size, plant cover and seed-drop timing. Oikos 117 (9), 1386–1396.
Reinhardt, D., Kuhlemeier, C., 2002. Plant architecture. EMBO Rep 3 (9), 846–851.
Robakowski, P., Wyka, T., Samardakiewicz, S., Kierzkowski, D., 2004. Growth, photosynthesis, and needle structure of silver fir (*Abies alba* Mill.) seedlings under different canopies. For. Ecol. Manage. 201 (2-3), 211–227.
Rosell, J.R., Llorens, J., Sanz, R., Arnó, J., Ribes-Dasi, M., Masip, J., Escolà, A., Camp, F., Solanelles, F., Gràcia, F., Gil, E., Val, L., Planas, S., Palacín, J., 2009. Obtaining the three-dimensional structure of tree orchards from remote 2D terrestrial LIDAR scanning. Agr. Forest Meteorol. 149 (9), 1505–1515.
Santopuoli, G., Vizzarri, M., Spina, P., Maesano, M., Scarascia Mugnozza, G., Lasserre, B., 2022. How individual tree characteristics and forest management influence occurrence and richness of tree-related microhabitats in Mediterranean mountain forests. For. Ecol. Manage. 503, 119780. https://doi.org/10.1016/j.foreco.2021.119780.
Shenkin, A., Bentley, L.P., Oliveras, I., Salinas, N., Adu-Bredu, S., Marimon-Junior, B.H., Marimon, B.S., Peprah, T., Choque, E.L., Trujillo Rodriguez, L., Clemente Arenas, E. R., Adonteng, C., Seidu, J., Passos, F.B., Reis, S.M., Blonder, B., Silman, M., Enquist, B.J., Asner, G.P., Malhi, Y., 2020. The influence of ecosystem and phylogeny on tropical tree crown size and shape. Front. For. Glob. Change 3, 501757. https://doi.org/10.3389/ffgc.2020.501757.
Shimada, T., Takahashi, A., Shibata, M., Yagihashi, T., Brody, A., 2015. Effects of within-plant variability in seed weight and tannin content on foraging behaviour of seed consumers. Funct. Ecol. 29 (12), 1513–1521.
Smit, C., Ouden, J., Díaz, M., 2008. Facilitation of *Quercus ilex* recruitment by shrubs in Mediterranean open woodlands. J. Veg. Sci. 19 (2), 193–200.
Steele, M.A., Contreras, T.A., Hadj-Chikh, L.Z., Agosta, S.J., Smallwood, P.D., Tomlinson, C.N., 2014. Do scatter hoarders trade off increased predation risks for lower rates of cache pilferage? Behav. Ecol. 25 (1), 206–215.
Steele, M.A., Rompré, G., Stratford, J.A., Zhang, H., Suchocki, M., Marino, S., 2015. Scatterhoarding rodents favor higher predation risks for cache sites: the potential for predators to influence the seed dispersal process. Integr. Zool. 10 (3), 257–266.
Vander Wall, S.B., 2002. Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83 (12), 3508–3516.
Vander Wall, S.B., 2010. How plants manipulate the scatter-hoarding behavior of seed-dispersing animals. Philos. Trans. R. Soc. B. 365, 989–997.
Wang, B., Chen, J., 2008. Tannin concentration enhances seed caching by scatterhoarding rodents: An experiment using artificial 'seeds'. Acta Oecol. 34 (3), 379–385.
Wang, B., Ives, A.R., 2017. Tree-to-tree variation in seed size and its consequences for seed dispersal versus predation by rodents. Oecologia 183 (3), 751–762.
Wang, B., 2020. Seed density affects post-dispersal seed predation: evidence from a seed removal experiment of 62 species. Integr. Zool. 15 (2), 135–143.
Wang, Z., Wang, B., Yi, X., Yan, C., Cao, L., Zhang, Z., 2018. Scatter-hoarding rodents are better pilferers than larder-hoarders. Anim. Behav. 141, 151–159.
Wang, J., Yan, Q., Lu, D., Diao, M., Yan, T., Sun, Y., Yu, L., Zhu, J., 2019. Effects of microhabitat on rodent-mediated seed dispersal in monocultures with thinning treatment. Agr. Forest Meteorol. 275, 91–99.
Winkler, M., Hulber, K., Hietz, P., 2005. Effect of canopy position on germination and seedling survival of epiphytic bromeliads in a Mexican humid montane forest. Ann. Bot. 95, 1039-1047.
Wang, J., Zhang, B., Han, N., Feng, T., Hou, X., An, X., Chen, X., Chang, G., 2021. Effects of mast seeding and insect infestation on predation and dispersal of *Castanea mollissima* nuts by rodents in the Qinling Mountains of China. For. Ecol. Manage. 499, 119630. https://doi.org/10.1016/j.foreco.2021.119630.
Xiao, Z., Jansen, P.A., Zhang, Z., 2006. Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. For. Ecol. Manage. 223 (1-3), 18–23.
Xiao, Z., Zhang, Z., 2012. Behavioural responses to acorn germination by tree squirrels in an old forest where white oaks have long been extirpated. Anim. Behav. 83 (4), 945–951.

Xiao, Z., Zhang, Z., Krebs, C.J., Whitney, K., 2013. Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. J. Ecol. 101 (5), 1256–1264.
Xiao, Z., Zhang, Z., Krebs, C.J., 2015. Seed size and number make contrasting predictions on seed survival and dispersal dynamics: a case study from oil tea *Camellia oleifera*. For. Ecol. Manage. 343, 1–8.
Yang, Y., Zhang, M., Yi, X., 2016. Small rodents trading off forest gaps for scatter-hoarding differs between seed species. For. Ecol. Manage. 379, 226–231.
Yu, F., Shi, X., Wang, D., Wang, T., Yi, X., Lou, Y., 2014. Seed predation patterns favor the regeneration of dominant species in forest gaps compared with the understory in an oak-pine mixed forest. Acta theriologica 59 (4), 495–502.
Zhang, M., Wang, Z., Liu, X., Yi, X., 2017. Seedling predation of *Quercus mongolica* by small rodents in response to forest gaps. New Forest. 48 (1), 83–94.
Zhang, Y., Yu, J., Sichilima, A.M., Wang, W., Lu, J., 2016. Effects of thinning on scatter-hoarding by rodents in temperate forest. Integr. Zool. 11 (3), 182–190.