Effects of Rodent-mediated Dispersal Limitation on Ridge Regeneration

Chao Ruan[1], Ganggang Zhang[1], Xiao Fan[1], Yang Wang[1], Deqing Meng[1], Xuyang Han[1], and Fei Yu[1]

[1]Henan Normal University

March 13, 2024

Abstract

Rodent-mediated seed dispersal largely affects the regeneration and colonization of the forest vegetation. However, due to the steep topography, complex terrains and the heavy anthropogenic logging from 1970s to 1990s, the secondary succession process of the forest is greatly inhibited where temperate deciduous broadleaf forests were the zonal vegetation. Previous studies have ignored the seed dispersal limitation mechanism among different slope positions in montane forests. We established 90 sample plots in Taihang Mountains among different slope positions (i.e., ridge, midslope and valley), and investigated the characteristics of seed removal rate, seed fate and seed dispersal distance of Quercus wutaishanica forest according to three slope positions. The results showed that only one from each of the three rodent species was captured at the ridge, while 52.1% and 43.8% of the small rodents were found in valley and midslope, respectively. Compared to the ridge whose almost all released seeds were intact in site, the seed removal rates were significantly higher in midslope and valley, and the proportions of scatter hoarded in ridge and midslope were significantly different, while both has no significant difference with that in valley. The average seed dispersal distance in midslope was 4.78 m, significantly greater than that in valley, while that of the ridge was only 2.09 m. Therefore, the midslope had the best seed dispersal, but the seed dispersal of ridge was severely restricted, providing the first empirical evidence for the Mid-domain Effect model and the Resource Availability Hypothesis. These results provide a better understanding of the dispersal limitation mechanism of the oak forest and the plant-animal interactions system in mountainous areas.

Introduction

Dispersal limitation is the failure of a seed to reach all regeneration sites suitable for its germination after leaving the parent. The failure reasons include seed factors (i.e., seed dispersal mode, dispersal ability, seed size, and yield) and environmental factors (i.e., wind, water flow, and topography) (Han and Wang, 2002; Thomson, 2011). Previous studies have shown that dispersal limitation played an important role in Changbai Mountain forests for the Jaccard coefficient of seed rain and neighboring mature trees decreased sharply with increasing neighborhood radius (Li *et al.* , 2012) and in the habitat fragmentation of tropical forest, where species diversity is rich and seeds are mainly dispersed by animals (Cordeiro *et al.* , 2009). Considering niche differentiation and dispersal limitation simultaneously may better explain successional mechanisms in tropical forests (Dalling *et al.* , 2002), and dispersal limitation may be more important than ecological niche differentiation in determining species composition in habitats where dispersers are scarce and forest cover is low (Dent and Estrada-Villegas, 2021). For example, dispersal limitation due to the disappearance of seed dispersers such as birds and mammals in tropical forests has been a major factor in the inability of later successional species to spread into young forests (Abbas *et al.* , 2021). Therefore, birds and mammals are believed to play an important role in seed dispersal (Willson, 1993; Glyphis *et al.* , 1981). Previous studies suggested that mammals and birds were probably the main dispersers of palm seeds (Zona & Henderson, 1989), and mainly focused on the effects of large mammals and birds on seed dispersal (Gosper *et al.* ,

1

2005). Seeds from excrement or seeds dropped during consumption by fruit-feeding primates could survive and germinate (Corlett & Lucas, 1990), and these seedlings had a higher survival rate (Pearson & Theimer, 2003). The composition and dynamics of large mammal and bird communities have undergone significant alterations, primarily attributable to pervasive overhunting and extensive habitat loss on a global scale (Carpenter *et al.*, 2020; Fernández-Palacios *et al.*, 2021). Furthermore, this has resulted in a significant reduction in the population of these large herbivores, leading to extinctions in certain cases, as well as a conspicuous reduction in the average body weight of large mammalian species. Evidenced by a shift from an average of approximately 14 kilograms at the 95th percentile to a mere 4 kilograms (Wenny & Levey, 1998), this trend underscores a substantial change in mammalian community structure. Consequently, this transformation has elevated the ecological significance of smaller fauna, particularly rodent species, in the process of seed dispersal.

While feeding on plant seeds and fruits, rodents carry some seeds and fruits to other places for storage to cope with food shortages (Zhang*et al.et al.*, 2015), and to help seeds escape predators, ultimately leading to successful seed dispersal and regeneration (Hirsch*et al.*, 2012). Therefore, dispersal hoarders, mainly rodents, are prominent seed dispersers of plants (Roth & Vander Wall, 2005). These rodents can spread viable seeds to different favorable environments (Jansen & Forget, 2001), some seeds buried can be retrieved by animals for food, while others would germinate successfully and achieve seedling settlement to a large extent. This animal storage behavior, especially decentralized storage, is profitable in reducing the competition for resources and space between seedlings and mother trees, to promote seed germination and seedling formation and to realize plant regeneration (Xiao & Zhang, 2016; Yang *et al.*, 2020). Food storage animals usually have an advantage over general foragers in finding storage food (Stapanian & Smith, 1978), this may be related to not only the difficulty of retrieval and the hidden conditions (Tamura *et al.*, 1999), but also the directional dispersal preference of certain storage animals. For example, scatter-hoarding rodents would transport seeds to high-density microsites (such as the tree canopy) and redistribute them for storage (Dimitri & Longland, 2017), resulting in the seed survival rate and the dispersal pattern, and ultimately affecting the regeneration pattern of vegetation (Yu *et al.*, 2017). The repeated movement of seeds and the distance to the habitat as the two main factors determining seed dispersal in rodents (Perea, 2011), and chemosensory information from predators and parasitoids also influence foraging decisions of storage rodents, and thus seed dispersal (Sunyer*et al.*, 2013).

Seed dispersal and seedling establishment are the key stages to the mountain forest succession and regeneration, and their failure would limit the recolonization of farmland (Standish *et al.*, 2007). Some studies exploring seed dispersal constraints are currently receiving increasing attention from naturalists, especially topography-specific structures (Muscarella *et al.*, 2020; Wang*et al.*, 2014; Freitas *et al.*, 2010). The topography in mountainous and hilly areas plays a significant role in regulating the distribution of the solar radiation and precipitation, this can effectively reveal the microclimatic state of the local environment and showcases variations in the soil depth and nutrient content across different locations (McDonald *et al.*, 1996). As an important topographical factor, slope position directly affects vegetation through geomorphic processes and controls the spatial redistribution of resource factors through morphological changes, thus indirectly affecting the distribution of vegetation (Kikuchi, 2001; Yang, 2005). Furthermore, slope position also has an effect on vegetation cover and its ability to recover after disturbance, with lower slopes having higher vegetation cover and height, while upper slopes are more susceptible to disturbances such as forest fire and deforestation (Pereira *et al.*, 2016). The higher the slope of the mountain, the more spatially isolated it is and the more susceptible it is to fire and logging disturbances (Han *et al.*, 2018). Furthermore, crop yields are generally lower in the upper slope than those in the lower slope due to differences in soil types (McPhee, 1997), and acorns on the upper slope are more susceptible to insects than those on the lower slope (Yu, 2003). Scatter hoarders also weigh the pros and cons of cache difficulty against the risk of theft, with higher risk of predation often implying higher seed establishment rates (Muñoz & Bonal, 2011; Steele *et al.*, 2014). Compared to the hilltop area, there are usually many exposed rocks and vegetation providing safe shelter for rodents in midslope (Meliyo *et al.*, 2014), this may lead to better seed storage and seedling regeneration. Treeline recruitment was seriously affected by the high rate of seed theft by rodents (Pansing *et al.*, 2007).

Therefore, the dispersal limitation is more pronounced on the upper slope than on the lower slope (Han *et al.* ,2018). However, the relationship between food storage rodents and their dispersal plants often changes depending on environmental conditions, with mutual benefits and seed predation occurring (Vander Wall, 2010), and there is no strict consistency.

As a result, differences in vegetation regeneration exist between different slope positions, yet the reasons for these disparities remain unknown. Could rodent-mediated seed dispersal serve as a critical factor in explaining the regeneration variations among slope positions? To quantitatively measure variations in seed dispersal across slope positions, the current study explored rodent abundance and tracked seed removal rate, seed fate, and seed dispersal distance by establishing experimental plots at different slope positions of the *Q. wutaishanica* -rodent ecosystem in the Dongling Mountains situated in the North of Taihang Mountains. Thus, addressing the following questions: 1) Do slope positions significantly influence rodent-mediated seed dispersal? 2) What about the seed dispersal efficiency among different slope positions? 3) Are there definite seed dispersal limitations among slope positions? Based on the aforementioned inquiries, we formulate the following preliminary hypotheses: 1) Concerning seed dispersal, in accordance with the Mid-domain Effect (MDE) Model (Colwell and Lees, 2000), the dispersal rate is expected to exhibit a unimodal pattern as slope position increases, characterized by an initial rise followed by a subsequent decline. 2) In terms of faunal and floral abundance, according to the Resource Availability Hypothesis (Coley, 1985), with increasing slope position, an equilibrium point of resource utilization is anticipated to exist, resulting in a pattern of initial abundance escalation followed by a subsequent decline.

Materials and Methods

Study region

The Beijing Forest Ecosystem Research Station (40°00'-40°03'N, 115°26'-115°30' E) was located in Dongling Mountains, the northern part of the Taihang Mountains. The region belongs to warm temperate semi-humid continental monsoon climate, and its average annual temperature is 5~10 and mean annual precipitation is 500~600 mm, mainly precipitate from July to August. The main soil type is brown soil and its depth is about 50 cm. The zonal vegetation is warm temperate deciduous broad-leaved and coniferous mixed forest, especially the *Q. wutaishanica* forest, which is widely distributed and plays a significant role in the conservation of water and soil, the maintenance of biodiversity and the regulation of climate in the Taihang Mountains. To minimize heterogeneity among forest types dominated by *Q. wutaishanica* , ten transects were established from the foot to the top of every mountain's western slope (i.e., each transect occupied a different elevation segment of the slopes), forming a single elevational gradient of montane forests (1020 m-1770 m) (Xu *et al.* , 2017). According to Parker's (1982) classification method widely used in previous studies (Coppoletta *et al.* , 2016; Guarin *et al.* , 2005; Clinton *et al.* , 1993) and the topographic characteristics of Dongling Mountains, the transects were divided into three slope positions: ridge, midslope, and valley, forming three continuous sampling lines of oak forest at the different slope positions.

Seed marking

The seed of *Q. wutaishanica* was collected during the mature period in 2020, and stored in the refrigerator at 4 for the germination rate of the oak seeds stored for seven days only slightly decreased and there was no significant difference compared to fresh seeds (Chen and Yan, 2019). Therefore, fresh and healthy seeds were selected within 48 hours by the water flotation and visual inspection method. The seed marking was completed by referring to the original method proposed by Zhang and Wang (2001) and made some necessary changes. A micro-drill was used to drill a small hole with a diameter of 0.3 mm at the bottom of the seed to avoid damaging the core. Small consecutively numbered plastic labels were made to track the seed fate, and 10 cm thick wires were used to pass through the holes in the seeds to connect the plastic labels with the seeds. Tags are generally exposed to the surface of the ground in most cases, so there is a high chance of finding them after the seeds have been buried by rodents. According to Kempter's (2018) research, labels have some influence on seed dispersal, but would not change with slope position and other factors concerned.

Seed release

The seeds were released in 10 transects set along the elevation gradient in the *Q. wutaishanica* forest in the Taihang Mountains from August 26 to October 14 in 2020. According to the elevation gradient, each transect line was classified into three slope positions: ridge (the upper 1/3 of each transect), midslope (the middle 1/3 of each transect), and valley (the lower 1/3 of each transect). In total, there were 90 seed stations, 10 transectsx3 slope positionsx3 seed stations, and there were 10 seeds released at each 1 m x 1 m seed station. For repeated experiments, the scale of concern was the community and the factor of interest was the slope position, with 30 seed stations set for each slope position. Considering that seed fates changed little after 15 days, observations were made only once a week. Therefore, it is observed two or three times a week in the early stage and only once a week after 15 days, in order to assess the harvest of the seeds and their removal by small rodents (Fig.1). Seed fates were classified as six types: (1) intact in situ (IIS), (2) eaten in situ (EIS), (3) eaten after removal (EAR), (4) intact after removal (IAR), (5) scatter hoarded (SH) or (6) missing (M). We recorded the seed code numbers, measured the distance between the tagged seed and its original seed station where the seed was removed, and marked the specific cache locations. During March and May of the following year, we investigated and identified the seedlings established from seeds scattered by rodents according to the tagged plastic labels.

Rodent composition structure

Trapping plots were set at about 500 m from the seed dispersal experiment region at each transect and its three slope positions in the Taihang Mountains to minimize interference. Three live traps, formed a trapping plot, were placed at each slope position in August 2019 and 2020, respectively. Rodents were captured using 40 cmx 25 cmx 20 cm live stell wire traps with peanuts as bait. The trapping experiment lasted one week per transect and slope position, and the trapping period was one month per year. From August to October 2020, an infrared camera was set up in each seed dispersal area of each slope position to monitor rodent activity.

Seedling surveys

We selected 10 transects to survey seedlings in the Taihang Mountains from October 3 to October 6 in 2019 before seed release experiment. Three slope positions (ridge, midslope and valley) were selected for each transect to investigate the abundance of *Q. wutaishanica* seedlings. The seedling survey experiment was repeated three times and a total of 90 (3 slope positions x 10 sample strips x 3 replicates) seedling data were obtained.

Data analysis

All statistical analysis were performed in R version 4.1.1 (R Core Team, 2021). The seed removal time of three slope positions was compared using Cox Regression Analysis, and seed fate and dispersal distance were analysed using seed tracking experiments. Differences in seed fate (i.e., IIS, EIS, EAR, IAR, SH and M) among three slope positions and the influence of the distance group on the removal distance were examined using a Generalized Linear Model (GLM). Tukey's HSD post hoc test was applied for multiple comparisons of seed fates, seed removal rate, and seed dispersal distance among three slope positions. The number of seedlings was analysed using One-way analysis of variance (ANOVA) with post hoc tests using the Least Significant Difference (LSD)method.

Results

Rodent species composition and abundance

There were 38, 32 and 3 captured rodents in valley, midslope, and ridge, respectively, including *Apodemus peninsulae* , *Apodemus agrarius* , *Sciurotamias davidianus* , *Tamiops swinhoei* , and *Sciurus vulgaris* (Table 1). *A. peninsulae* was the most common, accounting for 64.4% of the total, followed by *S. davidianus* and *T.s swinhoei* , and their percentages were 17.8% and 12.3%. Specifically, the first four rodent species mentioned above were captured in midslope and their relative abundances in the midslope were 68.6%, 3.1%, 9.4% and 18.8%, respectively. All five species of rodents were captured in valley, and *A. peninsulae* and *S. davidianus*

were common, accounting for 63.2% and 26.3%, respectively. Only three rodents were captured in ridge, including *A. peninsulae* , *A. agrarius* , and *T. swinhoei* .

Seed removal rate

Most of the seeds released in valley and midslope, except the ridge, were carried by rodents within 11 days (Fig.2). Cox regression analysis showed that seed removal rates were significantly higher in midslope (Z=10.69, P <0.001) and valley (Z=10.21,P <0.001) than that in ridge. Furthermore, the seed removal rate was significantly higher in midslope (Z=2.24P =0.0252) than in valley. The seed removal rates in midslope and valley almost had no change after 11 days and then became basically stable after 22 days.

Seed fate

Almost all seeds were kept intact (ISS) in ridge, while half of the seeds at valley and midslope were eaten by rodents (EAR, EIS) (Fig.3). The ratios of IIS, EIS, EAR, IAR and M in valley (IIS: t =14.112,df =87, P <0.001; EIS: t =6.504,df =87, P <0.001; EAR: t =8.619,df =87, P <0.001; IAR: t =2.707,df =87, P =0.0220; M: t =8.800, df =87,P <0.001) and midslope (IIS: t =13.363,df =87, P <0.0001; EIS: t =5.488,df =87, P <0.001; EAR: t =9.328,df =87, P <0.0001; IAR: t =4.410,df =87, P =0.0001; M: t =4.470, df =87,P =0.0001) differed significantly from those in ridge. The proportion of SH in ridge (t =1.892, df =87,P =0.1470) and midslope (t = 3.478, df = 87,P = 0.0023) had not significant difference with that in valley, while there was significant difference in the proportion of SH between ridge and midslope (t =3.379, df =87, P =0.0031).

Seed dispersal distance

The seeds dispersed by the rodent in ridge were all within 3 m and were mainly concentrated in 1-3 m (Fig.4). The maximum dispersal distance of midslope was almost 15 m, with a major concentration around 5 m. The average seed dispersal distance was significantly higher in midslope (t =3.449, df =207,P =0.002) than that in ridge, indicating that the seed was dispersed farther in midslope. In contrast, the dispersal distance of the seeds in ridge was finite.

Seedling survey

The mean value of seedling was 1.43 cm as a whole, while those in ridge, midslope and valley were 1.13 cm, 1.83 cm and 1.33 cm. The variance test statistic showed that the number of seedling in different slope positions were significantly different (F=4.567, P = 0.013<0.05). The number of seedling was significantly less in ridge than those in midslope (P =0.004, SE=0.239) and valley (P =0.039, SE=0.239). There were no significant differences for the number of seedling between midslope and valley (P =0.404, SE=0.239).

Discussion

Seedling regeneration

According to our investigation, the number of seedlings in ridge was lower than midslope and valley, this is consistent with the results of Takahashi *et al.* (2010) and O'Brien & Escudero (2022), supporting our hypothesis (2) as mentioned above. The reason is that soil in ridge is shallower and drier than other slope position, creating droughty and frost-prone conditions, which can be detrimental to seedling germination and early establishment (Fenner & Thompson, 2005; Takahashi *et al.* , 2010). Furthermore, as the ridge slope increased near the top, airflow velocity increased, increasing snow flux and snow transport, leading to an increase in snow accumulation (Toloui-Semnani & Johnson, 2019) and intensifying transpiration of pioneer seedlings (Renison *et al.* , 2015). This further exacerbates the challenges faced by seedlings trying to establish themselves in ridge. Seedlings at ridge showed wilting and needle discoloration due to low photosynthetic carbon gain, reduced soil water potential, low symbiotic infection of seedlings with mycorrhizal fungi, limited root growth, and ultimately seedling dehydration, which may explain the higher than ninety percent mortality rate of seedlings in the ridge region (Smith *et al.* , 2009). As long as the processes of freezing, tumbling, and burial persist at ridge, it will be very difficult to establish seedlings in these areas (Butler *et al.* , 2009). The ecosystem stability of mid-elevation zones at the altitude between 500 and 2000 m were particularly

stable, while high-elevation zones (above 2000 m) and low-elevation zones (below 500 m) were comparatively vulnerable (Geng et al., 2019). This is, the communities of middle region being more stable compared to the other two regions (Jin et al., 2022). Furthermore, the forest litter layer may act as a barrier, making it difficult for seeds to contact the soil, thus affecting tree regeneration in the Taihang Mountains (Yang et al., 2014). These natural challenges make ridge areas particularly inhospitable for seedling regeneration and survival. Therefore, topographic fragmentation, special climate and soil conditions lead to poor vegetation regeneration in Taihang Mountains, with simple layers and low coverage, especially at the ridge of the mountain.

Rodent abundance

Among the five recorded rodent species, the *Apodemus peninsulae* was the most common in the Taihang Mountains, and the midslope and valley had more rodents than ridge. According to the 'landscape of fear' theory, vegetated habitats can provide shelter and improve survival chances for animals, so animals prefer vegetated habitats over open high-risk habitats (Laundre *et al.* , 2001), small rodents were found in greater numbers in forested sparse grassland areas (Afonso, 2021), and nests around shrubs on the slopes could avoid the negative effects of rainfall and uphill runoff on burrows (Jiang *et al.* , 2017). Furthermore, plants generally exhibit better growth in midslope compared to ridge and valley (Liao *et al.* , 2021; Ohsawa & Ide, 2008), and the vertical structure of vegetation distribution on the mountain exhibits a central peak pattern (Lomolino, 2001). A similar feature was also found that the distribution of alpha diversity of plant community in the Taihang Mountains had unimodal distribution on the elevational gradient, which was in line with the theory of "diversity peaked at the intermediate altitude" (Liang, 2022). Therefore, the midslope and valley may have more rodents than the ridge. Significantly, the distribution of small mammals exhibits a mid-elevation peak, i.e., a single-peaked distribution at mid-elevation (McCain, 2010) according to the MDE (Colwell and Lees, 2000), meaning that the midslope should have more rodents than ridge and valley. Unfortunately, this study showed that there were more rodents in the valley, which is inconsistent with hypothesis (2), but there is little difference in rodent abundance between the valley and the midslope. This may be due to the limitation of plant growth by forest water sources as vegetation is primarily driven by energy supply (Roebroek *et al.* , 2020). According to the energy limitation hypothesis (Colwell and Lees, 2000), light, water and other conditions in mid-slope may be moderate, but not as abundant as in valley, some rodent species may adapt to this medium energy limitation environment, but other species may not adapt well, reducing their diversity and quantity. Our results of rodent abundance were obtained based on camera trap monitoring and traditional survey methods, the applicability of the high resolution, the large breadth, and the high sensitivity of infrared camera may allow better access to animal behavioral data and may improve the results in future.

Seed removal rate and seed fate

The seed removal rate and the seed collected proportion by rodents was lowest in ridges, which is consistent with our hypothesis (1). On the contrary, we found that the midslope had the highest seed removal rate and proportion collected. Seed removal rate is a critical metric for understanding the dynamics of seed dispersal and regeneration within an ecosystem, reflecting a composite of various ecological activities, including those of seed predators, primary seed dispersers, and secondary seed dispersers (Hambuckers *et al.* , 2020; Milotić *et al.* , 2018). So, this rate is not merely a quantitative measure but also provides insights into the qualitative aspects of seed dispersal mechanisms and their effectiveness under different environmental conditions (Carlo & Morales, 2016). Seeds in ridges exhibit limited dispersal, encountering challenges in germination primarily attributed to restricted movement towards suitable germination sites (Forget, 1990). The limitation in seed dispersal is chiefly due to the diminished or absent role of key seed dispersers, particularly rodents and birds. According to the niche limitation hypothesis (Romanuk & Kolasa, 2002), the scarcity of resources and lower temperatures at high elevations would increase the intensity of competition so that only rodent species adapted to these conditions and survived in these regions. Ecological niches at high altitudes may only be suitable for some specific rodent species. Previous studies highlight the importance of specific seed dispersers for large-seeded plants is underscored (Moreira *et al.* , 2017). For example, the critical function

of various bird sizes in seed dispersal (Godínez-Alvarez *et al.* , 2020), the interspecific interactions of rodents for enhancing seed dispersal effectiveness in Japanese walnut (Okawa *et al.* , 2023), and the dual reciprocal roles in pollination and seed dispersal of dispersal-storage rodents (Xiao, 2021). These studies emphasize the necessary contribution of vertebrates in overcoming the challenges of seed dispersal, confirming the integrated part of these animals in maintaining ecosystem balance and plant reproduction (La Mantia *et al.* , 2019). Thus, the limiting effects of the absence of dispersers on seed dispersal are evident, which not only hinders the movement of seeds to suitable germination sites, but may also has long-term effects on the balance of the ecosystem as a whole.

An interesting observation is that rodent-mediated seed dispersal was more active in midslope, instead of the valley and ridge. Within our study, the EIS of *Q. wutaishanica* on the mid-slope was found to be lower than the average EIS rate (74%) reported in previous studies (Li and Zhang, 2001). Midslope's higher seed removal rate and scatter-hoarding rate imply greater opportunities for seed dispersal and establishment. This is inconsistent with the idea that seed release at the top of the mountain was an order of magnitude greater than at the bottom of the mountain (Katul, 2012). This is mainly because: 1) the seeds are likely to roll downhill when they break away from the mother tree, which can lead to superimposed seed shadows from different mother trees (Ohsawa *et al.* , 2007; Schupp *et al.* , 2019) on midslope and valley. Furthermore, some valleys may accumulate seeds at the bottom or in valley areas, as they may be natural meeting points for wind or water. (Boland, 2017). 2) Rodents prefer to spread seeds horizontally or downward because it consumes less energy (Li and Zhang, 2003), but the absence of rodents may limit seed dispersal and seedling regeneration in ridge. Although birds are capable of dispersing and establishing seeds in high mountainous or other high-altitude areas (Watanabe, 1994), Quercus species are only moderately preferred as food by birds (Wright, 2022). Consequently, the impact of birds on the dispersal of Quercus seeds is quite limited.

Seed dispersal distance

The dispersal distance reflects rodent foraging strategies and dispersing effectiveness to some extent (Wang and Yan, 2017). We found that the dispersal distances of the seeds were longer in midslope and valley than those in ridge where the dispersal distance in ridge was extremely limit (Fig.4). This phenomenon further validates the reasonableness of our hypothesis (1). Although seeds would tend to accumulate on lower slopes due to gravity and topography, and then valley had a higher seed density (Yamase and Sekioka, 2006), rodent-mediated seed dispersal is a central driver of horizontal seed dispersal as it requires less energy (Wang *et al.* , 2018), while in the vertical direction is just the opposite. Compared to the ridge and valley, the better vegetation and less disturbance on midslope attract more rodents to feed, and provide more diverse habitats for rodents to meet their requirements of spreading over a longer distance while avoiding predation (Bergstedt and Milberg, 2001). Furthermore, long-distance dispersal increases reproduction rates by allowing seeds to escape the high density of conspecifics in the vicinity of the mother tree, reducing competition and predators, and providing them with the opportunity to find suitable colonization sites (Novaes *et al.* , 2020) according to the negative density-dependent hypothesis (Metz *et al.* , 2010; Jansen *et al.* , 2014). In our study, the dispersal distance was concentrated within 15 m, which is consistent with previous studies (Chen *et al.* , 2022). The dispersal distance was mostly around and within 5 m, and the seed removal rate exhibited an initial rapid decline followed by a gradual slowdown, indicating that the rodents accelerated the possession of food, which might be caused by competition (Jenkins and Peters, 1992).

These results, as mentioned above, were helpful in understanding the dispersal of seeds mediated by rodents in the *Q. wutaishanica* population at different slope positions. Further research still needs to interpret the seed dispersal and vegetation regeneration pattern at a larger temporal and spatial scale (Nathan and Muller-Landau, 2000). For example, *Q. wutaishanica* interannual variation and its subsequent effects on vegetation structure might have been overlooked (Wang and Smith, 2002).

5. Conclusions

Slope position did significantly affect rodent-mediated seed dispersal, leading to differences in vegetation regeneration among different slopes, which supports our hypothesis that there was a significant seed dispersal

7

limitation in the ridge region, which may act as an important influence on forest regeneration in ridge. Also interesting was that seed dispersal and regeneration were best in midslope, providing the best evidence for the long standing suppositions named Mid-domain Effect and the Resource Availability Hypothesis. These findings emphasize the key role of rodents in seed dispersal, and elucidate to some extent the mechanism of rodent storage feeding on the regeneration pattern of *Q. wutaishanica* forest communities from a slope perspective, providing a scientific basis for further explaining the regeneration dynamics of mountain forests and improving the theoretical system of plant and animal interactions. Future research is still needed to explore the specific causes of seed dispersal limitation and how to improve the restoration and regeneration strategies of forest ecosystems.

REFERENCES

Abbas, S., Nichol, J. E., Zhang, J., Fischer, G. A., Wong, M. S., & Irteza, S. M., (2021). Spatial and environmental constraints on natural forest regeneration in the degraded landscape of Hong Kong. Science of the Total Environment. 752, 141760. https://doi.org/10.1016/j.scitotenv.2020.141760

Afonso, B. C., Swanepoel, L. H., Rosa, B. P., Marques, T. A., Rosalino, L. M., Santos-Reis, M., & Curveira-Santos, G., (2021). Patterns and drivers of rodent abundance across a South African multi-use landscape. Animals. 1(9), 2618. https://doi.org/10.3390/ani11092618

Alcántara, J. M., Rey, P. J., Sánchez-Lafuente, A. M., Valera, F., (2000). Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. Oikos. 8(2), 362-370. https://doi.org/10.1034/j.1600-0706.2000.880215.x

Bergstedt, J., Milberg, P., (2001). The impact of logging intensity on field-layer vegetation in Swedish boreal forests. Forest Ecology and Management. 154: 105-115. https://doi.org/10.1016/S0378-1127(00)00642-3

Bogoni, J. A., Peres, C. A., Ferraz, K. M., (2020). Extent, intensity and drivers of mammal defaunation: a continental-scale analysis across the Neotropics. Scientific Reports. 10(1), 1-16. https://doi.org/10.1038/s41598-020-72010-w

Boland, J.M., (2017). Linking seedling spatial patterns to seed dispersal processes in an intermittent stream. Madroño, 64(2): 61-70. https://doi.org/10.3120/0024-9637-64.2.61

Butler, D.R., Malanson, G.P., Resler, L.M., Walsh, S.J., Wilkerson, F.D., Schmid, G.L., Sawyer, C.F. (2009). Geomorphic patterns and processes at alpine treeline. Developments in earth surface processes. 12: 63-84. https://doi.org/10.1016/S0928-2025(08)00204-6

Carlo, T.A., Morales, J.M., (2016). Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. Ecology, 97(7): 1819-1831. https://doi.org/10.1890/15-2147.1

Carpenter, J.K., Wilmshurst, J.M., McConkey, K.R., Hume, J.P., Wotton, D.M., Shiels, A.B., Burge, O.R., Drake, D.R.,(2020). The forgotten fauna: native vertebrate seed predators on islands. Functional Ecology. 34(9): 1802-1813. https://doi.org/10.1111/1365-2435.13629

Chen, J., Chen, W.W., Lu, Z.Y., Wang, B., (2022). Canopy openness of individual tree promotes seed dispersal by scatter-hoarding rodents. Forest Ecology and Management. 507, 120016. https://doi.org/10.1016/j.foreco.2022.120016

Clinton, B. D., Boring, L. R., & Swank, W. T., (1993). Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology. (5), 1551-1558. https://doi.org/10.2307/1940082

Coley, Phyllis D., John P. Bryant, and F. Stuart Chapin III. (1985). "Resource availability and plant antiherbivore defense." Science 230.4728: 895-899. 10.1126/science.230.4728.895

Colwell, R. K., & Lees, D. C., (2000). The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology and Evolution. 15(2), 70-76. https://doi.org/10.1016/S0169-5347(99)01767-X

Coppoletta, M., Merriam, K. E., & Collins, B. M., (2016). Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications. 26(3), 686-699. https://doi.org/10.1890/15-0225

Cordeiro, N. J., Ndangalasi, H. J., McEntee, J. P., Howe, H. F., (2009). Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. Ecology. 90(4), 1030-1041. https://doi.org/10.1890/07-1208.1

Corlett, R. T., Lucas, P. W., (1990). Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaques (*Macaca fascicularis*). Oecologia. 82(2): 166-171. https:/doi.org/10.1007/BF00323531

Dalling, J. W., Muller-Landau, H. C., Wright, S. J., Hubbell, S. P., (2002). Role of dispersal in the recruitment limitation of neotropical pioneer species. Journal of Ecology. 90(4), 714-727. https://doi.org/10.1046/j.1365-2745.2002.00706.x

Dent, D. H., & Estrada-Villegas, S., (2021). Uniting niche differentiation and dispersal limitation predicts tropical forest succession. Trends in Ecology and Evolution. 36(8), 700-708. https://doi.org/10.1016/j.tree.2021.04.001

Dimitri, L.A., Longland, W.S., (2017). Distribution of western juniper seeds across an ecotone and implications for dispersal. Western North American Naturalist. 77: 212-222. https://doi.org/10.3398/064.077.0209

Fenner, M., & Thompson, K. (2005). The ecology of seeds. Cambridge university press.

Fernandez-Palacios, J.M., Kreft, H., Irl, S.D.H., Norder, S., Ah-Peng, C., Borges, P.A., Burns, K.C., de Nascimento, L., Meyer, J.Y., Montes, E., Drake, D.R., (2021). Scientists' warning–The outstanding biodiversity of islands is in peril. Global Ecology and Conservation. 31: e01847. https://doi.org/10.1016/j.gecco.2021.e01847

Forget, P. (1990). Seed-dispersal of *Vouacapoua americana*(Caesalpiniaceae) by caviomorph rodents in French Guiana. Journal of Tropical Ecology 6(4), 459-468. https://doi.org/10.1017/S0266467400004867

Freitas, S.R., Hawbaker, T.J., Metzger, J.P., (2010). Effects of roads, topography, and land use on forest cover dynamics in the Brazilian Atlantic. Forest. Forest Ecology and Management. 259(3): 410-417. https://doi.org/10.1016/j.foreco.2009.10.036

Glyphis, J. P., Milton, S. J. Siegfried, W. R., (1981). Dispersal of*Acacia cyclops* by birds. Oecologia. 48, 138–141. https://doi.org/10.1007/BF00347002

Godinez-Alvarez, H., Rios-Casanova, L., Peco, B., (2020). Are large frugivorous birds better seed dispersers than medium-and small-sized ones? Effect of body mass on seed dispersal effectiveness. Ecology and Evolution, 10(12): 6136-6143. https://doi.org/10.1002/ece3.6285

Gosper, C. R., Stansbury, C. D., Vivian-Smith, G., (2005). Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. Diversity and Distributions. 11(6): 549-558. https://doi.org/10.1111/j.1366-9516.2005.00195.x

Guarin, A., & Taylor, A. H., (2005). Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. Forest Ecology and Management. 218(1-3), 229-244. https://doi.org/10.1016/j.foreco.2005.07.014

Hambuckers, A., Trolliet, F., Simon, A., Cazetta, E., & Rocha-Santos, L. (2020). Seed removal rates in forest remnants respond to forest loss at the landscape scale. Forests. 11(11), 1144. https://doi.org/10.3390/f11111144

Han J, Shen Z, Li Y, Luo C, Xu Q, Yang K, Zhang Z. (2018). Beta diversity patterns of post-fire forests in Central Yunnan Plateau, Southwest China: Disturbances intensify the priority effect in the community assembly. Frontiers in Plant Science. https://doi.org/10.3389/fpls.2018.01000

Hirsch, B. T., Kays, R., Pereira, V. E., Jansen, P. A., (2012). Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent. Ecology Letters. 15(12), 1423-1429. https://doi.org/10.1111/ele.12000

Hongzhu, L., Lili, L.I.U., Hui, G.A.O., et al. (2022). Altitudinal distribution pattern and its driving factors of plant diversity in the middle section of the eastern slope of the Taihang Mountain. Chinese Journal of Eco-Agriculture, 30(7): 1091-1100. 10.12357/cjea.20210863

Jansen, P. A., Forget, P. M., (2001). Scatter hoarding rodents and tree regeneration. Nouragues: dynamics and plant-animal interactions in a neotropical rainforest, pp. 275-288. https://doi.org/10.1007/978-94-015-9821-7_26

Jansen, P. A., Visser, M. D., Joseph Wright, S., Rutten, G., & Muller-Landau, H. C., (2014). Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. Ecology Letters. 17(9), 1111-1120. https://doi.org/10.1111/ele.12317

Jenkins, S.H., Peters, R.A., (1992). Spatial patterns of food storage by Merriam's kangaroo rats. Behavioral Ecology 3(1), 60-65. https://doi.org/10.1093/beheco/3.1.60

Jiang, L., Wang, X., Li, L., Shi, Z., & Yang, X., (2017). Spatial association of shrubs and their interrelation to burrowing site preference of subterranean rodents on dune slope in the Otindag Sandy Land, China. Sustainability, 9(10), 1729. https://doi.org/10.3390/su9101729

Jin S S, Zhang Y Y, Zhou M L, et al. (2022). Interspecific association and community stability of tree species in natural secondary forests at different altitude gradients in the southern Taihang Mountains. Forests, 13(3): 373. https://doi.org/10.3390/f13030373

Katul, G.G., Poggi, D., (2012). The effects of gentle topographic variation on dispersal kernels of inertial particles. Geophysical Research Letters. 39(3). https://doi.org/10.1029/2011GL050811

Kempter, I., Nopp-Mayr, U., Hausleithner, C., Gratzer, G., (2018). Tricky to track: comparing different tagging methods for tracing beechnut dispersal by small mammals. Ecological Research. 33, 1219-1231. https://doi.org/10.1007/s11284-018-1640-y

Kikuchi, T., (2001). Vegetation and Landforms. Tokyo: University of Tokyo Press.

Laundre, J. W., Hernandez, L., & Altendorf, K. B., (2001). Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology. 79(8), 1401-1409. https://doi.org/10.1139/z01-094

Li, B., Hao, Z., Bin, Y., Zhang, J., Wang, M., (2012). Seed rain dynamics reveals strong dispersal limitation, different reproductive strategies and responses to climate in a temperate forest in northeast China. Journal of Vegetation Science. 23(2), 271-279. https://doi.org/10.1111/j.1654-1103.2011.01344.x

Li, H.J., Zhang, Z.B., (2003). Effects of rodents on acorn dispersal and survival of the Liaodong oak (*Quercus wutaishanica* Koidz.). Forest Ecology and Management. 176 387-396. https://doi.org/10.1016/S0378-1127(02)00286-4

Liao, C., Li, H., Lv, G., Tian, J., Liu, B., Tian, M., You G., Xu, Y. (2021). Can ecological restoration improve soil properties and plant growth in valley-slope sand dunes on southern Tibetan Plateau? Physical Geography. 42(2), 143-159. https://doi.org/10.1080/02723646.2020.1735859

Lomolino, M.V., (2001). Elevation gradients of species-density: historical and prospective views. Global Ecology and biogeography, 10(1): 3-13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

McCain, C. M., (2010). Global analysis of reptile elevational diversity. Global Ecology and Biogeography. 19(4), 541-553. https://doi.org/10.1111/j.1466-8238.2010.00528.x

McDonald, D. J., Cowling, R. M., & Boucher, C. (1996). Vegetation-environment relationships on a species-rich coastal mountain range in the Fynbos Biome (South Africa). Vegetatio. 123, 165-182. https://doi.org/10.1007/BF00118269

McPhee, K. E., Muehlbauer, F. J., & Spaeth, S. C., (1997). Seed yield and residue production of lentil cultivars grown at different slope positions. Journal of Production Agriculture. 10(4), 602-607. https://doi.org/10.2134/jpa1997.0602

MeliyoJ. L., MassaweB. H., MsanyaB. M., KimaroD. N., HieronimoP., MulunguL. S., KihupiN. I., DeckersJ. A., GulinckH., & LeirsH. (2014). Landform and surface attributes for prediction of rodent burrows in the Western Usambara Mountains, Tanzania. Tanzania Journal of Health Research. 16(3). https://doi.org/10.4314/thrb.v16i3.5

Metz, M. R., Sousa, W. P., & Valencia, R., (2010). Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. Ecology, 91(12), 3675-3685. https://doi.org/10.1890/08-2323.1

Milotić, T., Baltzinger, C., Eichberg, C., et al. (2019). Functionally richer communities improve ecosystem functioning: Dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. Journal of Biogeography, 46(1): 70-82. https://doi.org/10.1111/jbi.13452

Mitsui, Y., Isagi, Y., Setoguchi, H., (2010). Multiple spatial scale patterns of genetic diversity in riparian populations of *Ainsliaea faurieana* (Asteraceae) on Yakushima Island, American Journal of Botany. 97(1): 101-110. https://doi.org/10.3732/ajb.0800220

Moreira, J.I., Riba-Hernández, P., Lobo, J.A., (2017). Toucans (*Ramphastos ambiguus*) facilitate resilience against seed dispersal limitation to a large-seeded tree (*Virola surinamensis*) in a human-modified landscape. Biotropica, 49(4): 502-510. https://doi.org/10.1111/btp.12427

Munoz, A., & Bonal, R. (2011). Linking seed dispersal to cache protection strategies. Journal of Ecology. 99(4), 1016-1025. https://doi.org/10.1111/j.1365-2745.2011.01818.x

Muscarella, R., Kolyaie, S., Morton, D. C., Zimmerman, J. K., Uriarte, M., (2020). Effects of topography on tropical forest structure depend on climate context. Journal of Ecology. 108(1), 145-159. https://doi.org/10.1111/1365-2745.13261

Nathan, R., Muller-Landau, H.C., (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution. 15(7): 278-285. https://doi.org/10.1016/S0169-5347(00)01874-7

Novaes, L. R., Calixto, E. S., de Oliveira, M. L., Alves-de-Lima, L., de Almeida, O., & Torezan-Silingardi, H. M., (2020). Environmental variables drive phenological events of anemocoric plants and enhance diaspore dispersal potential: A new wind-based approach. Science of the Total Environment. 730, 139039. https://doi.org/10.1016/j.scitotenv.2020.139039

O'Brien, M. J., & Escudero, A. (2022). Topography in tropical forests enhances growth and survival differences within and among species via water availability and biotic interactions. Functional Ecology. 36(3), 686-698. https://doi.org/10.1111/1365-2435.13977

Ohsawa, T., & Ide, Y. (2008). Global patterns of genetic variation in plant species along vertical and horizontal gradients on mountains. Global Ecology and Biogeography. 17(2), 152-163. https://doi.org/10.1111/j.1466-8238.2007.00357.x

Ohsawa, T., Tsuda, Y., Saito, Y., Sawada, H., & Lde, Y., (2007). Steep slopes promote downhill dispersal of *Quercus crispula* seeds and weaken the fine-scale genetic structure of seedling populations. Annals of Forest Science. 64(4), 405-412. https://doi.org/10.1051/forest:2007017

Okawa, R., Saitoh, T., Noda, T., (2023). Interactive effects of two rodent species on the seed dispersal of *Japanese walnut* . Scientific Reports, 13(1): 18098. https://doi.org/10.1038/s41598-023-44513-9

Pansing, E.R., Tomback. D.F., Wunder, M.B., French, J.P., Wagner, A.C., (2017). Microsite and elevation zone effects on seed pilferage, germination, and seedling survival during early whitebark pine recruitment. Ecology and Evolution. 7: 9027-9040. https://doi.org/10.1002/ece3.3421

Parker, A. J., (1982). The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. Physical Geography. 3(2), 160-168. https://doi.org/10.1080/02723646.1982.10642224

Pearson, K.M. & Theimer, T.C., (2003). Seed-caching responses to substrate and rock cover by two Peromyscus species: Implications for pinyon pine establishment. Oecologia. 141, 76–83. https://doi.org/10.1007/s00442-004-1638-8

Perea, R., San Miguel, A., Gil, L., (2011). Acorn dispersal by rodents: the importance of re-dispersal and distance to shelter. Basic and Applied Ecology. 12(5): 432-439. https://doi.org/10.1016/j.baae.2011.05.002

Pereira, P., Cerda, A., Lopez, A. J., Zavala, L. M., Mataix-Solera, J., Arcenegui, V., Misiune L., Keesstra S., Novara, A. (2016). Short-term vegetation recovery after a grassland fire in Lithuania: The effects of fire severity, slope position and aspect. Land Degradation and Development. 27(5), 1523-1534. https://doi.org/10.1002/ldr.2498

Prats, S. A., Sierra-Abrain, P., Morana-Fontan, A., & Zas, R., (2022). Effectiveness of community-based initiatives for mitigation of land degradation after wildfires. Science of the Total Environment. 810, 152232. https://doi.org/10.1016/j.scitotenv.2021.152232

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Renison, D., Chartier, M. P., Menghi, M., Marcora, P. I., Torres, R. C., Giorgis, M., ... & Cingolani, A. M. (2015). Spatial variation in tree demography associated to domestic herbivores and topography: Insights from a seeding and planting experiment. Forest Ecology and Management. 335, 139-146. https://doi.org/10.1016/j.foreco.2014.09.036

Roebroek, C.T.J., Melsen, L.A., Hoek, van Dijke, A.J., et al. (2020). Global distribution of hydrologic controls on forest growth. Hydrology and Earth System Sciences, 24(9): 4625-4639. https://doi.org/10.5194/hess-24-4625-2020

Romanuk, T.N., Kolasa, J., (2002). Abundance and species richness in natural aquatic microcosms: a test and refinement of the Niche-Limitation Hypothesis[J]. Community Ecology, 3(1): 87-94. https://doi.org/10.1556/comec.3.2002.1.10

Roth, J.K., Vander Wall, S.B., (2005). Primary and secondary seed dispersal of bush chinquapin (Fagaceae) by scatter hoarding rodents. Ecology. 86(9): 2428-2439. https://doi.org/10.1890/04-0791

Schupp, E. W., Zwolak, R., Jones, L. R., Snell, R. S., Beckman, N. G., Aslan, C., Cavazos B. R., Effiom E., Fricke E. C., Montano-Centellas F., Poulsen J., Razafindratsima O. H., Sandor M. E., Shea, K., (2019). Intrinsic and extrinsic drivers of intraspecific variation in seed dispersal are diverse and pervasive. AoB Plants. 11(6), plz067. https://doi.org/10.1093/aobpla/plz067

Smith, W.K., Germino, M.J., Johnson, D.M., Reinhardt, K., (2009). The altitude of alpine treeline: a bellwether of climate change effects. The Botanical Review. 75: 163-190. https://doi.org/10.1007/s12229-009-9030-3

Standish, R. J., Cramer, V. A., Wild, S. L., Hobbs, R. J., (2007). Seed dispersal and recruitment limitation are barriers to native recolonization of old-fields in western Australia. Journal of Applied Ecology. 44(2), 435-445. https://doi.org/10.1111/j.1365-2664.2006.01262.x

Stapanian, M.A., Smith, C.C., (1978). A model for seed scatter hoarding: coevolution of fox squirrels and black walnuts. Ecology. 59(5): 884-896. https://doi.org/10.2307/1938541

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? Behavioral Ecology 25(1), 206-215. https://doi.org/10.1093/beheco/art107

Sun, S.C., Chen, L.Z., (2000). Seed demography of *Quercus wutaishanica* in Dongling Mountain Region. Acta Phytoecologia Sinica. 24, 215-221.

Sunyer, P., Munoz, A., Bonal, R., Espelta, J. M., (2013). The ecology of seed dispersal by small rodents: a role for predator and conspecific scents. Functional Ecology., 27(6), 1313-1321. https://doi.org/10.1111/1365-2435.12143

Takahashi, K., Arii, K., & Lechowicz, M. J. (2010). Codominance of *Acer saccharum* and *Fagus grandifolia* : the role of Fagus root sprouts along a slope gradient in an old-growth forest. Journal of Plant Research. 123, 665-674. https://doi.org/10.1007/s10265-010-0312-y

Tamura, N., Hashimoto, Y., Hayashi, F., (1999). Optimal distances for squirrels to transport and hoard walnuts. Animal Behaviour. 58(3): 635-642. https://doi.org/10.1006/anbe.1999.1163

Thomson, F. J., Moles, A. T., Auld, T. D., Kingsford, R. T., (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. Journal of Ecology. 99(6), 1299-1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

Toloui-Semnani, M., & Johnson, E. A. (2019). Processes that cause natural unforested areas in Canadian Rockies below temperature treeline. Geomorphology. 347, 106857. https://doi.org/10.1016/j.geomorph.2019.106857

Vander Wall, S. B. (2010). How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. Philosophical Transactions of The Royal Society B-biological Sciences. 365(1542), 989-997. https://doi.org/10.1098/rstb.2009.0205

Villalobos, A., Schlyter, F., Olsson, G., Witzell, J., & Lof, M., (2020). Direct seeding for restoration of mixed oak forests: Influence of distance to forest edge, predator-derived repellent and acorn size on seed removal by granivorous rodents. Forest Ecology and Management. 477, 118484. https://doi.org/10.1016/j.foreco.2020.118484

Wang, B.C., Smith, T.B., (2002). Closing the seed dispersal loop. Trends in Ecology and Evolution. 17(8): 379-386. https://doi.org/10.1016/S0169-5347(02)02541-7

Wang, J., Yan, Q., Zhang, T., Lu, D., Xie, J., Sun, Y., Zhang, J., Zhu, J., (2018). Converting larch plantations to larch-walnut mixed stands: Effects of spatial distribution pattern of larch plantations on the rodent-mediated seed dispersal of *Juglans mandshurica* . Forests. 9(11), 716. https://doi.org/10.3390/f9110716

Wang, J., Yan, Q.L., (2017). Effects of disturbances on animal-mediated seed dispersal effectiveness of forest plants: A review. Chinese Journal of Applied Ecology. 28(5): 1716-1726. 10.13287/j.1001-9332.201705.033

Wang, Z. F., Lian, J. Y., Ye, W. H., Cao, H. L., Wang, Z. M., (2014). The spatial genetic pattern of *Castanopsis chinensis* in a large forest plot with complex topography. Forest Ecology and Management. 318, 318-325. https://doi.org/10.1016/j.foreco.2014.01.042

Watanabe S., (1994). Tree specia, Tokyo Univ. Press, Tokyo. (in Japanese).

Wei, X., Meng, H., Jiang, M., (2013). Landscape genetic structure of a streamside tree species *Euptelea pleiospermum* (Eupteleaceae): Contrasting roles of river valley and mountain ridge. PLoS One. 8(6): e66928. https://doi.org/10.1371/journal.pone.0066928

Wenny, D.G., Levey, D.J., (1998). Directed seed dispersal by bellbirds in a tropical cloud forest. Proceedings of the National Academy of Sciences. 95(11): 6204-6207. https://doi.org/10.1073/pnas.95.11.6204

Willson, M.F., (1993). Mammals as seed-dispersal mutualists in North America. Oikos. 159-176. https://doi.org/10.2307/3545106

Wright, J. R., Matthews, S. N., Pinchot, C. C., & Tonra, C. M., (2022). Preferences of avian seed-hoarders in advance of potential American chestnut reintroduction. Forest Ecology and Management. 511, 120133. https://doi.org/10.1016/j.foreco.2022.120133

Xiao, Z., (2022). Dual ecological functions of scatter-hoarding rodents: pollinators and seed dispersers of *Mucuna sempervirens*(Fabaceae). Integrative Zoology, 17(5): 918-929. https://doi.org/10.1111/1749-4877.12603

Xiao, Z.S., Zhang, Z.B., (2016). Contrasting patterns of short-term indirect seed-seed interactions mediated by scatter-hoarding rodents. Journal of Animal Ecology. 85(5): 1370-1377. https://doi.org/10.1111/1365-2656.12542

Xu, G., Lin, Y., Zhang, S., Zhang, Y., Li, G., & Ma, K. (2017). Shifting mechanisms of elevational diversity and biomass patterns in soil invertebrates at treeline. Soil Biology and Biochemistry. 113, 80-88. http://dx.doi.org/10.1016/j.soilbio.2017.05.012

Yamase, K., Sekioka, H., (2006). Comparison of topsoil seedbank potential at the 3 districts in Hyogo Prefecture. Journal of the Japanese Society of Revegetation Technology. 32: 266-269. https://doi.org/10.7211/jjsrt.32.266

Yang, X., Yan, D., Liu, C., (2014). Natural regeneration of trees in three types of afforested stands in the Taihang Mountains, Chin. PloS one, 9(9): e108744. https://doi.org/10.1371/journal.pone.0108744

Yang, X.F., Yan, C., Gu, H. F. Zhang, Z.B., (2020). Interspecific synchrony of seed rain shapes rodent-mediated indirect seed–seed interactions of sympatric tree species in a subtropical forest. Ecology Letters. 23: 45-54. https://doi.org/10.1111/ele.13405

Yang, Y., (2005). Vegetation structure in relation to micro-landform in Tiantong National Forest Park, Zhejiang, China. Acta Ecologica Sinica. 25, 2830-2840. https://doi.org/10.3321/j.issn:1000-0933.2005.11.006

Yi, X.F., Liu, C.Q., (2014). Retention of cotyledons is crucial for resprouting of clipped oak seedlings. Scientific Reports. 4: 5145. https://doi.org/10.1038/srep05145

Yu, F., Shi, X.X., Zhang, X., Yi, X.F., Wang, D.X., Ma, J.M., (2017). Effects of selective logging on rodent-mediated seed dispersal. Forest Ecology and Management. 406, 147-154. https://doi.org/10.1016/j.foreco.2017.10.001

Yu, X., Zhou, H., & Luo, T., (2003). Spatial and temporal variations in insect-infested acorn fall in a *Quercus liaotungensis* forest in North China. Ecological Research. 18(2), 155-164. https://doi.org/10.1046/j.1440-1703.2003.00543.x

Zhang, H., Yan, C., Chang, G., Zhang, Z., (2016). Seed trait-mediated selection by rodents affects mutualistic interactions and seedling recruitment of co-occurring tree species. Oecologia. 180(2), 475-484. https://doi.org/10.1007/s00442-015-3490-4

Zhang, S., Xia, C., Li, T., Wu, C., Deng, O., Zhong, Q., Xu X., Jia, Y., (2016). Spatial variability of soil nitrogen in a hilly valley: Multiscale patterns and affecting factors. Science of the Total Environment. 563, 10-18. https://doi.org/10.1016/j.scitotenv.2016.04.111

Zhang, Z.B., (2019). Studies on the rodent-seed interactions of forest ecosystems: Exploring the secret of cooperation between antagonists (1st Edition). Beijing: Science Press.

Zhang, Z.B., Wang, F.S., (2001). Effect of rodents on seed dispersal and survival of wild apricot (*Prunus armeniaca*). Acta Ecologica Sinica. 21(5), 839-845.

Zona, S., Henderson, A., (1989). A review of animal-mediated seed dispersal of palms. Selbyana. 6-21. https://www.jstor.org/stable/41759760

Figure captions

Fig. 1 Schematic illustration of the seed dispersal experiment.

Fig. 2 Seed removal rates for *Quercus wutaishanica* after release at different slope positions. The data were represented as mean +- standard error (SE).

Fig. 3 Seed fates of *Quercus wutaishanica* after primary dispersal by rodents. The data were represented as mean +- standard error (SE). IIS: Intact in situ; EIS: eaten in situ; EAR: eaten after removal; IAR: intact but not buried after removal to another location; SH: scatter hoarded after removal; M: missing; Primary dispersal: the initial movement of seeds from the seed station.

Fig. 4 Seed dispersal distances of *Quercus wutaishanica* after primary dispersal from the seed stations in the three slope positions. Note: The data were represented as mean +- standard error (SE). The number above the boxplot represents the p-value.
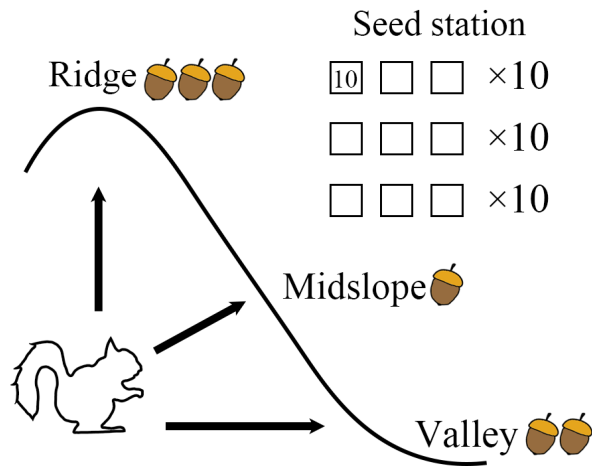
Fig. 1

Fig. 2

Fig. 3

Fig. 4

Table captions

Table 1 Abundance and composition of rodents. Note: "*" represents the number of rodents photographed by infrared cameras or visually observed during the experience of seed release.

Table 1

Species	Valley	Midslope	Ridge	Total

Apodemus peninsulae	24(63.2%)	22(68.6%)	1(33.3%)	47(64.4%)
Apodemus agrarius	1(2.6%)	1(3.1%)	1(33.3%)	3(4.1%)
Sciurotamias davidianus	5*+5(26.3%)	3*(9.4%)	0(0)	13(17.8%)
Tamiops swinhoei	2(5.3%)	5*+1(18.8%)	1(33.3%)	9(12.3%)
Sciurus vulgaris	1*(2.6%)	0(0)	0(0)	1(1.4%)
Total	38(52.1%)	32(43.8%)	3(4.1%)	73(100%)