Does Animal-Mediated Seed Dispersal Facilitate the Formation of Pinus armandii-Quercus aliena var. acuteserrata Forests?

Fei Yu¹, Dexiang Wang¹*, Xianfeng Yi², Xiaoxiao Shi³, Yakun Huang¹, Hongwu Zhang¹, XinPing Zhang¹

¹ College of Forestry, Northwest A & F University, Yangling, Shaanxi, China, ² College of Life Sciences, Jiangxi Normal University, Nanchang, Jiangxi, China, ³ College of Animal Science and Technology, Northwest A & F University, Yangling, Shaanxi, China

Abstract

The Pinus armandii and Quercus aliena var. acuteserrata mixed forest is one of the major forest types in the Qinling Mountains, China. P. armandii is considered to be a pioneer species during succession and it is usually invaded by late successional Q. aliena var. acuteserrata. However, the mechanism that underlies its invasion remains unclear. In the present study, we tracked seed dispersal of P. armandii and Q. aliena var. acuteserrata using coded plastic tags in the western, middle and eastern Qinling Mountains to elucidate the invasion process in the mixed forests. Our results indicated that the seeds of both P. armandii and Q. aliena var. acuteserrata were removed rapidly in the Qinling Mountains, and there were no differences in the seed removal rates between the two species. There were significant differences in rodent seed-eating and caching strategies between the two tree species. For P. armandii, seeds were more likely to be eaten in situ than those of Q. aliena var. acuteserrata in all plots. By contrast, the acorns of Q. aliena var. acuteserrata were less frequently eaten in situ, but more likely to be removed and cached. Q. aliena var. acuteserrata acorns had significantly longer dispersal distances than P. armandii seeds in all plots. Although P. armandii seeds were less likely to be dispersed into the Q. aliena var. acuteserrata stands, over 30% of the released acorns were transported into the P. armandii stands where they established five seedlings. Based on the coupled recruitment patterns of P. armandii and Q. aliena var. acuteserrata, we suggest that the animal-mediated seed dispersal contributes to the formation of Pinus armandii-Quercus aliena var. acuteserrata forests.

Introduction

Natural forest regeneration and succession may depend on the arrival of animal- or wind-dispersed seeds [1–4]. Many rodent species, as well as jays, play important roles in the secondary dispersal of pine or oak species via their hoarding behaviors in temperate zonal forests [5–7]. Seed removal by rodents has indirect effects on regeneration and colonization in plant populations, thereby affecting plant community structure [8]. It is generally believed that Quercus can colonize the understory of pine forests via the jay- or rodent-mediated dispersal of acorns [9–11]. Oaks depend entirely on animals for the dispersal of their seeds because they have not evolved wind-dispersal structures [12]. By contrast, most Pinus species rely on seed dispersal by wind, which is facilitated by their small seeds with attached wings [13–15]. However, some Pinus species (e.g., Pinus armandii and Pinus koraiensis) depend on animals for seed dispersal [16–18]. It is not clear whether these animal-dispersed Pinus species can colonize or establish successfully in the understory of oak forests.

It is widely accepted that the successional changes in pine-oak forests follow the patterns of vegetation dynamics described for the Mediterranean Basin, where Pinus species are considered to be pioneer species during succession, and are usually invaded by late-successional Quercus species [9,19]. However, the mechanism that underlies the invasion is not well understood. In this framework, mixed forests are usually considered to be a successional stage of initial post-disturbance pine forests [19–21]. Evidence has accumulated that pine recruits occur at a higher frequency and at a greater abundance under the canopies of their congener, whereas oak species usually exhibit greater regeneration than pine species in pine-dominated stands and mixed oak-pine forests [22–24]. In central China, the Pinus armandii and Quercus aliena var. acuteserrata mixed forest is one of the major forest types in the Qinling Mountains [21,25]. Studies have shown that oak seedlings had a comparable abundance to pine seedlings in P. armandii forests [21,26]. By contrast, P. armandii seedlings are rare in oak forests in the mosaic distribution regions between P. armandii and Q. aliena var. acuteserrata forests [21,27]. The explanation for this phenomenon remains unclear and we have little knowledge of how the seed dispersal of these two species contributes to this phenomenon. Moreover, few studies have focused on how P. armandii is invaded by the late successional Q. aliena var. acuteserrata in the oak-pine forest belt.

In the present study, we tracked individual seeds of P. armandii and Q. aliena var. acuteserrata using coded plastic tags and explored the effects of small rodents on the dispersal of the seeds of these
two species in the middle, eastern and western Qinling Mountains. The aims of this study were as follows: (1) To explain the patterns where oak seedlings are often observed in the P. armandii forest, whereas P. armandii seedlings are seldom found in oak forests in the mosaic distribution regions. (2) To explore why P. armandii stands are usually invaded by late successional Quercus aliena var. acuteserrata. We hypothesized that the rodent-mediated seed dispersal of Q. aliena var. acuteserrata into P. armandii stands might explain the succession mechanism in Pinus armandii-Quercus aliena var. acuteserrata mixed forests in the Qinling Mountains, China. Thus, we aimed to elucidate the succession mechanism in oak-pine mixed forests and provide valuable information to support the development of effective forest management and restoration plans.

Materials and Methods

Ethics statement

This study was carried out in strict accordance with the current laws of China. The protocol was approved by the Administrative Panel on the Ethics of Huoditang Forest, Northwest A & F University. We signed a contract with the Huoditang Forest in 2012, and the contract included the permissions to access the study site and conduct this study.

Study site

We conducted the experiments on south-facing slopes within Qinling Mountains. Three experimental plots were established in (1) the western region of the Qinling Mountains (WQ) on Xiaolong Mountain, Gansu Province, (2) the middle region of the Qinling Mountains (MQ) at the Qinling National Forest Ecosystem Research Station in Huoditang Forest, Ningshan County, Shaanxi Province, and (3) the eastern region of the Qinling Mountains (EQ) in Luonan County, Shaanxi Province (Table 1). Three identical experiments were carried out in these three plots to test the same question in different regions of the mountains. The Qinling Mountains run east-west and form the basin divider between the two longest rivers in China, the Yellow River and the Yangtze River. The Qinling Mountains are situated in the transitional zone between two macroclimatic regimes (subtropical and warm-temperate zones) where the annual precipitation ranges from 950 to 1,200 mm, most of which falls between July and September. Snow cover usually lasts five or more months (from November to March), and the mean annual temperature ranges from 6 to 11°C below 2,000 m and from 1 to 6°C above 2,000 m above sea level [28]. The natural vegetation types in the Qinling Mountains are deciduous broad-leaved forests (below 2,000 m), mixed conifer and deciduous forests (800–2,500 m), and conifer forests (above 2,500 m). The dominant tree species are Q. aliena var. acuteserrata, P. armandii, Betula albosinensis, B. luminifera, P. tabulaeformis, Populus davidiana, Populus davidiana, Toxicodendron vernicifluum, and Acer davidii. The P. armandii and Q. aliena var. acuteserrata mixed forest belt covers a quarter of the Qinling Mountains. Several rodent species coexisted in the study site and the dominant species are Apodemus draco, Sciurus variegatus, and Neontamias davidiana and Neontamias davidiana. Previous studies show that these rodents are likely to affect the natural regeneration of the main tree species [17,29].

Identification of seed removers

To determine the abundance of rodents that could potentially remove the released seeds, 50 live steel-wire traps (30 cm × 25 cm × 20 cm) baited with peanuts were placed in each plot along each of the two transects at an interval of 3 m apart during October 8–11, 2012 (MQ, EQ and WQ). The traps were

| Study site | Longitude (E) | Latitude (N) | Location in China | Average annual temperature (°C) | Average annual rainfall (mm) | Dominant species |
|------------|--------------|--------------|-------------------|-----------------|-----------------------------|-----------------|
| MQ         | 108° 21′–108° 39′ | 33° 16′–33° 28′ | Ningshan County, Shaanxi | 12.7 | 1,130 | Quercus aliena var. acuteserrata, Pinus armandii, Betula albosinensis, B. luminifera, P. tabulaeformis, Populus davidiana, Toxidendron vernicifluum, and Acer davidii |
| EQ         | 104° 44′–106° 43′ | 33° 52′–34° 25′ | Luonan County, Shaanxi | 11.5 | 779 | Quercus aliena var. acuteserrata, Pinus armandii, Betula albosinensis, B. luminifera, P. tabulaeformis, Populus davidiana, Toxidendron vernicifluum, and Acer davidii |
| WQ         | 104° 2′–106° 40′ | 33° 30′–34° 49′ | Tianshui City, Gansu | 10.9 | 5185 | Quercus aliena var. acuteserrata, Pinus armandii, Betula albosinensis, B. luminifera, P. tabulaeformis, Populus davidiana, Toxidendron vernicifluum, and Acer davidii |

MQ: study area located in the western Qinling Mountains; MQ: study area located in the middle Qinling Mountains; EQ: study area located in the eastern Qinling Mountains.
checked twice a day at sunrise and sunset. The captured animals were weighed and released immediately in situ. We did not mark the captured animals to identify recaptures. Trapping was conducted for three consecutive days. The total number of trapping days and nights was 150 (30 traps × 3 days and nights) for each plot.

**Seed dispersal experiment**

We selected plots that each measured about 3.0 ha at the experimental plots in MQ, EQ, and WQ, i.e., the western, eastern and middle regions of the Qingsheng Mountains, respectively. Mature and fresh seeds of Q. aliena var. acuteserrata and P. armandii were collected from the ground outside our experimental plots for field release during the first fortnight of October 2012. We used water flotation to distinguish between sound and insect-damaged/empty seeds. We randomly selected 600 fresh sound seeds of P. armandii seeds (1.30 ± 0.78 cm, 0.36 ± 0.03 g, n = 100) and Q. aliena var. acuteserrata acorns (1.69 ± 1.40 cm, 1.70 ± 0.04 g, n = 100) from each of the three plots, respectively (in total, 3,600 seeds), and labeled them using slight modifications of the methods reported by Zhang and Wang [30] and Li and Zhang [31]. A tiny hole measuring 0.3 mm in diameter was drilled through the husk near the germinial disc of each seed, without damaging the cotyledon and the embryo. A white flexible plastic tag (3.0 ± 1.0 cm, <0.1 g) was tied through the hole in each seed using a thin 10 cm long steel thread. To ensure that each seed could be relocated and identified easily, each seed was numbered consecutively and discriminatively with a tag. When rodents buried the seeds in the soil or litter, the tags were often still visible on the surface of the ground, which made them easy to find. Tagging has been shown to have a negligible effect on seed removal and hoarding by rodents [30,32].

In each plot, 20 seed stations were established on the forest edges between P. armandii and Q. aliena var. acuteserrata forests, spaced 30 m apart along a transect line (Fig. 1). We used Whitmoror’s [33] characterization of the forest mosaic to distinguish between two types of patches, i.e., P. armandii forests dominated by P. armandii (patch 1) and Q. aliena var. acuteserrata forest dominated by Q. aliena var. acuteserrata (patch 2). We placed 30 tagged seeds of each species in separate batches (2–5 m apart) at each seed station (Fig. 1). The total number of seeds released was 20 (stations) × 30 (seeds) × 2 (species) × 3 (plots) = 3,600 seeds. Starting the day after placement, we checked for seed removal on a daily basis until all of the seeds were removed or consumed. During each visit, we randomly searched the area around each seed station and recorded the status of all released seeds. The post-dispersal seed fates were classified using six categories: 1) intact in situ (IS); 2) eaten in situ (EIS); 3) eaten after removal (EAR); 4) intact after removal to another location (IAR); 5) eaten after removal (CAR); and 6) missing where their true fates were unknown (MI). When a cache was discovered, we carefully recorded the seed code numbers, measured the distance of the tagged seeds from their original seed stations, and determined the cache location using a chopstick to mark the cache location, which was coded with the same number as the tag. The sticks were placed 25 cm from the seed caches. If the seeds were scatter-hoarded, we recorded whether they were cached under the canopy of P. armandii or Q. aliena var. acuteserrata. During the next visit, we also checked all of the caches that were relocated in previous visits until the caches were removed or eaten by rodents. If a marked cache was removed, the area around the cache (radius <30 m) was searched randomly. These experiments were conducted during October 15–November 17, 2012. Seed germination was surveyed during the following spring in 2013.

Figure 1. Sketch map of the locations of seed stations in the experimental plots. doi:10.1371/journal.pone.0089886.g001

**Seed rain survey**

We measured the seed rain of Q. aliena var. acuteserrata and P. armandii forests using three plots (separate plots in MQ, EQ, and WQ). We used water flotation to distinguish between sound and insect-damaged/empty seeds. We randomly selected 600 fresh sound seeds of P. armandii seeds (1.30 ± 0.78 cm, 0.36 ± 0.03 g, n = 100) and Q. aliena var. acuteserrata acorns (1.69 ± 1.40 cm, 1.70 ± 0.04 g, n = 100) from each of the three plots, respectively (in total, 3,600 seeds), and labeled them using slight modifications of the methods reported by Zhang and Wang [30] and Li and Zhang [31]. A tiny hole measuring 0.3 mm in diameter was drilled through the husk near the germinial disc of each seed, without damaging the cotyledon and the embryo. A white flexible plastic tag (3.0 ± 1.0 cm, <0.1 g) was tied through the hole in each seed using a thin 10 cm long steel thread. To ensure that each seed could be relocated and identified easily, each seed was numbered consecutively and discriminatively with a tag. When rodents buried the seeds in the soil or litter, the tags were often still visible on the surface of the ground, which made them easy to find. Tagging has been shown to have a negligible effect on seed removal and hoarding by rodents [30,32].

In each plot, 20 seed stations were established on the forest edges between P. armandii and Q. aliena var. acuteserrata forests, spaced 30 m apart along a transect line (Fig. 1). We used Whitmoror’s [33] characterization of the forest mosaic to distinguish between two types of patches, i.e., P. armandii forests dominated by P. armandii (patch 1) and Q. aliena var. acuteserrata forest dominated by Q. aliena var. acuteserrata (patch 2). We placed 30 tagged seeds of each species in separate batches (2–5 m apart) at each seed station (Fig. 1). The total number of seeds released was 20 (stations) × 30 (seeds) × 2 (species) × 3 (plots) = 3,600 seeds. Starting the day after placement, we checked for seed removal on a daily basis until all of the seeds were removed or consumed. During each visit, we randomly searched the area around each seed station and recorded the status of all released seeds. The post-dispersal seed fates were classified using six categories: 1) intact in situ (IS); 2) eaten in situ (EIS); 3) eaten after removal (EAR); 4) intact after removal to another location (IAR); 5) cached after removal (CAR); and 6) missing where their true fates were unknown (MI). When a cache was discovered, we carefully recorded the seed code numbers, measured the distance of the tagged seeds from their original seed stations, and determined the cache location using a chopstick to mark the cache location, which was coded with the same number as the tag. The sticks were placed 25 cm from the seed caches. If the seeds were scatter-hoarded, we recorded whether they were cached under the canopy of P. armandii or Q. aliena var. acuteserrata. During the next visit, we also checked all of the caches that were relocated in previous visits until the caches were removed or eaten by rodents. If a marked cache was removed, the area around the cache (radius <30 m) was searched randomly. These experiments were conducted during October 15–November 17, 2012. Seed germination was surveyed during the following spring in 2013.

**Data analysis**

SPSS for Windows (Version 17.0) was used for the statistical analyses. One-way ANOVA was used to detect the difference in the seed crops among three plots. The proportions of remaining, eaten, and cached seeds were arcsine square root transformed before the statistical analysis. Cox regression was used to test for differences in the seed removal rates between the two species. Two-way ANOVA was used to test for difference in the seed
dispersal distances and the proportion of the seed fates between *P. armandii* and *Q. aliena var. acuteserrata*.

**Results**

Rodent abundance and seed availability

Although several traps triggered false, a total of 23, 44, and 37 rodents were captured in WQ, MQ, and EQ, respectively (Table 2). In WQ, four rodent species were trapped during 150 trap nights. By contrast, only three species were captured in MQ and EQ (Table 2).

The seed crops of *Q. aliena var. acuteserrata* and *P. armandii*, respectively, in each plot were: 30.58±4.95 m² and 14.28±2.94 m² in MQ; 7.75±1.71 m² and 6.58±1.03 m² in WQ (mean ± SE). There were significant differences in seed crops among three plots (*P*<0.001, respectively).

Removal rates of the two seed species at seed stations

The investigations of *P. armandii* and *Q. aliena var. acuteserrata* seed dispersal demonstrated that 100% of the tagged seeds were removed by small rodents within seven days after their release in all plots (Fig. 2). Cox regression analysis detected no significant difference in the seed removal rates of the two species in all plots (*Wald* = 3.923, *df* = 1, *P* = 0.051 in WQ; *Wald* = 0.010, *df* = 1, *P* = 0.922 in MQ; *Wald* = 0.254, *df* = 1, *P* = 0.614 in EQ).

Seed fates

Significantly more *P. armandii* seeds were eaten in situ (EIS) than *Q. aliena var. acuteserrata* seeds in all plots (33.0% compared to 10.4% in WQ, 50.7% compared to 20.7% in MQ, and 26.3% compared to 8.3% in EQ (all *P*<0.001), while more *Q. aliena var. acuteserrata* seeds were cached after removal (CAR) in all plots (30.8% compared to 7.7% in WQ, 35.3% compared to 17.7% in MQ, and 48.6% compared to 29.3% in EQ (all *P*<0.001) (Fig. 3). The eaten in situ (EIS), cached after removal (CAR), and eaten after removal (EAR) seed fate proportions were also affected significantly by plot (EIS: *F* = 3.676, *df* = 2, *P* = 0.032; CAR: *F* = 10.380, *df* = 2, *P* < 0.001; EAR: *F* = 11.032, *df* = 2, *P* < 0.001) (Fig. 3), while there were no significant interactions between seed species and plot (EIS: *F* = 0.526, *df* = 2, *P* = 0.594; CAR: *F* = 1.729, *df* = 2, *P* = 0.180; EAR: *F* = 0.579, *df* = 2, *P* = 0.564).

Seed dispersal distance

Most of the seeds were dispersed less than 20 m in all plots (Fig. 4). The average dispersal distance was affected significantly by seed species (*F* = 158.215, *df* = 1, *P* < 0.001) and plot (Table 2).

| Species               | WQ      | MQ      | EQ      |
|-----------------------|---------|---------|---------|
|                       | Trapped individuals | Proportion (%) | Trapped individuals | Proportion (%) | Trapped individuals | Proportion (%) |
| Apodemus peninsulae   | 13      | 56.5    | 29      | 65.9    | 21      | 56.8              |
| Apodemus draco        | 5       | 21.7    | 9       | 20.5    | 7       | 18.9              |
| Sciurotamias davidianus | 3      | 13.0    | 6       | 13.6    | 9       | 24.3              |
| Apodemus agrarius     | 2       | 8.7     |         |         |         |                   |
| Total                 | 23      | 100     | 44      | 100     | 37      | 100               |

Table 2. Number of small rodents captured (*n* = 150 trap days and nights) in the three experimental plots.

WQ: study area located in the western Qinling Mountains; MQ: study area located in the middle Qinling Mountains; EQ: study area located in the eastern Qinling Mountains.

doi:10.1371/journal.pone.0089886.t002
While the interaction between seed species and plot was not significant (F = 0.451, df = 2, P = 0.637), the average dispersal distances of *Q. aliena* var. *acuteserrata* seeds (6.98 ± 0.40 m in WQ; 7.31 ± 0.46 m in MQ; 9.41 ± 0.58 m in EQ) were much greater than those of *P. armandii* (2.63 ± 0.23 m in WQ; 3.19 ± 0.33 m in MQ; 4.66 ± 0.31 m in EQ) in all plots (all P < 0.001). The maximum dispersal distances for *Q. aliena* var. *acuteserrata* and *P. armandii* seeds were 30.0 m and 17.1 m in WQ, 31.9 m and 11.0 m in MQ, and 35.4 m and 13.1 m in EQ, respectively. Only a few *P. armandii* seeds were transported into the *Q. aliena* var. *acuteserrata* stands in all plots (2.6% in WQ, 2.0% in MQ, and 1.3% in EQ). By contrast, over 30% of the *Q. aliena* var. *acuteserrata* seeds were transported into the *P. armandii* forest in all plots (36.7% in WQ, 35.0% in MQ, and 30.3% in EQ).

Survival of cached seeds

A total of 46, 53, and 73 seeds of *Q. aliena* var. *acuteserrata* in primary caches were found to be recovered and subsequently re-cached in WQ, MQ, and EQ, respectively, which further extended the cache distributions and the mean dispersal distances increased from 6.98 m for primary caches to 11.10 m for secondary caches in WQ (n = 46), from 7.31 to 9.62 m in MQ (n = 53) and from 9.41 to 13.93 m in EQ (n = 73). By contrast, almost all of *P. armandii* seeds in primary caches were found to be recovered and subsequently consumed. Only seeds of *Q. aliena* var. *acuteserrata* survived during our final survey. The total numbers of scatter-hoarded *Q. aliena* var. *acuteserrata* seeds that remained under the canopy were 22 in WQ, 29 in MQ, and 37 in EQ for the *P. armandii* forest, while the total numbers of seeds that remained under the canopy in the *Q. aliena* var. *acuteserrata* forest were 21 in WQ, 15 in MQ, and 35 in EQ. During spring 2013, a few *Q. aliena* var. *acuteserrata* seedlings emerged from the tagged seeds within the study area, i.e., under the canopy of *P. armandii* forest: one seedling in WQ, no seedlings in MQ, and three seedlings in EQ under the canopy of *Q. aliena* var. *acuteserrata* forest: one seedling in WQ, one seedling in MQ, and three seedlings in EQ.

**Discussion**

In our study, the rapid seed removal of *P. armandii* and *Q. aliena* var. *acuteserrata* from the seed stations and the lack of difference between the two species demonstrate the importance of small rodents for the seed dispersal effectiveness in the Qinling...
Mountains. Our observations agree with previous studies where fallen seeds were removed rapidly by rodents [14,18,29,34–37]. We found different patterns of seed predation and dispersal in Q. aliena var. acuteserrata and P. armandii, which were both affected by small rodents. More seeds of P. armandii were eaten by small rodents, whereas Q. aliena var. acuteserrata producing relatively heavy seeds were more frequently dispersed by animals. Small rodents tended to scatter-hoard more Q. aliena var. acuteserrata seeds in all study sites. Previous studies have indicated that basic seed traits (e.g., seed size, nutrition content, and defensive secondary compounds, etc.) may be primary factors that affect the eating and caching strategies of rodents [15,36,38–39]. Seed size is considered to be a decisive factor for scatter-hoarding rodents in the choice between seed predation and caching [39]. Previous quantitative studies have suggested that small seeds are more likely to be eaten immediately, whereas large acorns are more likely to be cached by rodents for future use [34–37,40–41]. Clearly, our results support the idea that the role of rodents during tree seed removal vary with tree species, although they are mainly dependent on seed size [42].

We also found that the seed dispersal distance was affected significantly by seed species, i.e., larger seeds were dispersed longer distances than small seeds. Our results clearly support the hypothesis of Jansen et al. [40] that larger seeds are dispersed further from their parent trees (or seed stations). Over 30% of the released acorns were moved into the P. armandii stands, whereas P. armandii seeds were rarely dispersed into the Q. aliena var. acuteserrata stands. These findings agree with other studies, which have shown that oaks can colonize the understory of pine forests via jay- or rodent-mediated dispersal of acorns [10,11]. Our data support the previous prediction that Pinus species are pioneer species that are usually replaced by late successional Quercus species [9,19]. Therefore, our results strengthened the hypothesis that rodent-mediated seed dispersal of Q. aliena var. acuteserrata into P. armandii stands facilitates the succession of the oak-pine mixed forests in Qinling Mountains, China. Q. aliena var. acuteserrata is known to establish successfully in the P. armandii forest in Qinling Mountains [21,26]; however, only a few Q. aliena var. acuteserrata seedlings were germinated from our tagged seeds in the study area. Seed crop may have an important impact on seed survival and subsequent establishment [41,43–44]. Our study indicated that seed fate and seed survival were different between plots, reflecting the spatial effects on seed dispersal and seed predation [45]. Previous studies have shown that scatter-hoarding and dispersal distances are enhanced during mast years compared with those during non-mast years (e.g., Pinus ponderosa, Pinus contorta, and Pinus jeffreyi) often depend on gaps for establishment [49–51]. A number of these species have dormant seeds that wait for a new gap to form, but dormancy also involves the risk of high attrition (e.g., the loss of dormant seeds to animals, fungi, and deep burial) [51]. Thus, Quercus species seem to have a higher competitive ability compared with Pinus species, which is supported by their current distribution in northern China [52].

In summary, we found that P. armandii had limited seed dispersal and experienced heavy predation by small rodents, whereas Q. aliena var. acuteserrata colonized the understory of pine forests and established successfully via the rodent-mediated dispersal of acorns. Although natural forest regeneration and succession may be influenced by many factors (e.g., post-dispersal seed survival) [8,31,53,54], our study highlights the importance of the dispersal behavior of small rodents and their potential contribution to the invasion of oak into pine forests, better explaining the succession patterns in oak-pine mixed forests in the Qinling Mountains of China.

Acknowledgments

The authors thank two anonymous reviewers for valuable comments on the manuscript and Dr Duncan E. Jackson for improving the earlier version of the manuscript. We also thank Qinling National Forest Ecosystem Research Station at Huoditang, Ningshaan County, Shaanxi Province for considerable support during our field investigation. Ziliang Zhang, Ganggang Zhang, Tingdong Guo and Dongyuan Zhang provided important help in the field.

Author Contributions

Conceived and designed the experiments: FY DW XY. Performed the experiments: FY DW XY XS HZ YH XZ. Analyzed the data: FY XY XS. Contributed reagents/materials/analysis tools: FY XY XS. Wrote the paper: FY DW XY XS.

References

1. Da Silva JMC, Uhlig C, Murray G (1996) Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Conserv Biol 10: 491–503
2. Nepstad DC, Uhlig C, Pereira CA, Da Silva JMC (1996) A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76: 25–39
3. Mendoza I, Gomez-Aparicio L, Zanor R, Matías L (2009) Recruitment limitation of forest communities in a degraded Mediterranean landscape. J Veg Sci 20: 367–376
4. Caves EM, Jennings SB, HilleRisLambers J, Trevaskis JF, Rogers HS (2013) Natural experiment demonstrates that bird loss leads to cessation of dispersal of native seeds from intact to degraded forests. Plos One 8(S): e65618
5. Steele MA, Smallwood PD (2002) Acorn dispersal by birds and mammals (In: Oak Forest Ecosystems: Ecology and Management for wildlife, Eds W McShea, WM Healy). Johns Hopkins University Press, Baltimore, pp 182–195
6. Hollander JL, Vander Wall SB (2004) Effectiveness of six species of rodents as dispersers of singleleaf pinon pine (Pinus monophylla). Oecologia 138: 57–65
7. Perez R, Miguel AS, Martinez-Jauregui M, Valbuena-Carabana M, Gil L (2012) Effects of seed quality and seed location on the removal of acorns and beechnuts. Eur J Forest Res 131: 625–631
8. Zhang HM, Chen Y, Zhang ZB (2008) Differences of dispersalfitness of large and small acorns of Liaodong oak (Quercus liaotungensis) before and after seed caching by small rodents in a warm-temperate forest, China. For Ecol Manag 255: 1243–1250
9. Barbéro M, Leisler R, Quaérell P, Richardson DM, Romane F (1998) Pines of the Mediterranean Basin. In: Richardson DM (Ed), Ecology and Biogeography of Pines. Cambridge University Press, Cambridge: 153–170

10. Mosandl R, Klement A (1998) Development of oaks (Quercus petraea (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (Pinus silvestris L.) stands. For Ecol Manag 105: 36–44

11. Gómez JM (2003) Spatial patterns in long-distance dispersal of Quercus ilex acorns by Jays in a heterogeneous landscape. Ecology 84: 573–584

12. Jemison TS, Nielsen OF (1986) Rodent as seed dispersers in a heath—oak woodland succession. Oecologia 70: 214–221

13. Greene DF, Johnson EA (1993) Seed mass and dispersal capacity in wind-dispersed diaspores. Oikos 67: 69–74

14. Vander Wall SB (1993) Cache site selection by chipmunks (Tamias spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (Pinus jeffreyi). Oecologia 96: 246–252

15. Vander Wall SB (2003) Effects of seed size of wind-dispersed pines (Pinus) on secondary seed dispersal and the caching behavior of rodents. Oikos 100: 25–34

16. Yi XF, Xiao ZS, Zhang ZB (2008) Seed dispersal of Korean pine (Pinus koraiensis) labeled by two different tags in a northern temperate forest, northeast China. Ecol Res 23(2): 379–384

17. Chang G, WangKF, Wang Z (2012) Effect of forest rodents on predation and dispersal of Pinus arundinacea seeds in Qinling Mountains. Acta Ecologica Sinica 32(10): 3177–3181 (in Chinese, English abstract).

18. Yu F, Shi XX, Yi XF, Wang DX (2013) Effect of relative abundance of Quercus mongolica acorns on seed dispersal of five tree species in Xaidong’an Mountain. Chinese Journal of Applied Ecology 24(6): 1531–1535 (in Chinese with English abstract).

19. Gracia M, Retana J, Roig P (2002) Mid-term successional patterns after fire of mixed pine-oak forests in NE Spain. Acta Oecologica 23: 405–411

20. Xu HC (1995) Chinese pine Pinus tabuliformis. China Forestry Publishing House, Beijing, pp 113–115

21. Yu F, Wang DX, Shi XX, Chen LL, Huang QF et al. (2013) Species composition and regeneration characteristics of main woody plant seedlings in a pine-oak mixed forest in Qinling Mountains. Acta Bot. Boreal. -Occident.Sin 33(3): 0592–0598 (in Chinese with English abstract).

22. Galindo-Jaimes L, González-Espinosa M, Quintana-Ascencio P, García-Parrioso L (2002) Tree composition and structure in disturbed stands with varying dominance by Pinus spp. in the highlands of Chiapas, Mexico. Plant Ecol 162: 259–272

23. Pons J, Pausas JG (2006) Oak regeneration in heterogeneous landscapes: the case of fragmented Quercus ilex forests in the eastern Iberian Peninsula. For Ecol Manag 231: 196–204

24. Uribeta IR, García L, Zavala MA, Marañón T (2011) Mediterranean pine and oak distribution in southern Spain: Is there a mismatch between regeneration and adult distribution? J Veg Sci 22: 18–31

25. Liu GQ, Tu XN, Zhao SD, Sun SH, Gravenhorst G (2001) Distributional characteristics of biomass and nutrient elements of pine-oak forest belt in Mt. Qinling. Scientia Silvae Sinicae 37(1): 25–36 (in Chinese with English abstract)

26. Zhang YQ (1989) Shaanxi Forest. Xi’an Science and Technology Press, Xi’an, pp 242–244

27. Kang B, Liu SR, Wang DX, Zhang Y, Liu HB et al. (2011) Regeneration characteristics of woody plant seedlings in typical secondary forests in Qinling Mountains. Chinese Journal of Applied Ecology 22(12): 3123–3130 (in Chinese with English abstract)

28. Dang H, Jiang Q, Zhang Y (2007) Growth responses of subalpine fir (Abies tabuliformis) to climate variability in the Qinling Mountains, China. For Ecol Manag 240: 143–150

29. Chang G, Jin TZ, Pei JF, Chen XN, Zhang B et al. (2012) Seed dispersal of three sympatric oak species by forest rodents in the Qinling Mountains, Central China. Plant Ecol 215: 1637–1642

30. Zhang ZB, Wang FS (2001) Effect of rodents on seed dispersal and survival of wild apricot (Prunus armeniaca). Acta Ecologica Sinica 21: 839–845

31. Li HJ, Zhang ZB (2003) Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in Pinus armandii. Acta Ecologica Sinica 23(3): 0592–0598 (in Chinese with English abstract)

32. Xiao ZS, Jansen PA, Zhang ZB (2006) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. For Ecol Manag 223: 18–23

33. Whitmore TC (1978) Gaps in the forest canopy. In: Tomlinson PB, Zimmerman MH (eds) Tropical Trees as Living Systems. Cambridge University Press, New York, pp. 639–655

34. Jansen PA, Forget PM (2001) Scattering-hoarding rodents and tree regeneration. In: Bongers F, Charles-Dominique P, Forget PM, Théry M(Eds), Dynamics and Plant–Animal Interactions in a Neotropical Rainforest. Nouragues: Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 275–300

35. Vander Wall SB (1990) Food Hoarding in Animals. University of Chicago Press, Chicago

36. Xiao ZS, Zhang ZB, Wang YS (2005) The effects of seed abundance on seed predation and dispersal by rodents in Castanopsis fargesii (Fagaceae). Plant Ecol 177: 249–257

37. Caccia FD, Chaneton EJ, Kitzberger T (2006) Trophic and nontrophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. Oikos 113: 469–480

38. Steele MA, Knowles T, Bielle K, Samms EL (1993) Tannins and partial consumption of acorns: implication for dispersal of oaks by seed predators. Am Midl Nat 130:229–238

39. Wang B, Chen J (2009) Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. Ecology 90:3023–3032

40. Jansen PA, Bartholomew M, Bongers F, Elzinga JA, Ouden, J et al. (2002) The role of seed size in dispersal by a scatterhoarding rodent. In: Levey D, Silva WR, Galetti M (Eds), Seed Dispersal and Frugivory: Ecology, Evolution and Conservation. CAB Publishing, Wallingford, pp 209–225

41. Jansen PA, Hemerik L, Bongers F (2004) Seed mass and mast seedling enhancement dispersal by a neotropical scatter-hoarding rodent. Ecol Monogr 74: 569–589

42. Price MV, Jenkins SH (1996) Rodents as seed consumers and dispersers. In: Murray, DR (Ed), Seed Dispersal. Academic Press, Sydney, Australia, pp 191–235

43. Vander Wall SB (2002) Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83: 3508–3516

44. Li HJ, Zhang ZB (2007) Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in Pinus armandii (Rosaceae). For Ecol Manag 242: 511–517

45. Meng L, Gao X, Chen J, Martin K (2012) Spatial and temporal effects on seed dispersal and seed predation of Medicago sativa in southern Yunnan, China. Integr Zool 7: 30–40

46. DeMattia EA, Curran LM, Rathcke B (2004) Effects of small rodents and large mammals on neotropical seeds. Ecology 85: 2161–2170

47. Xiao ZS, Zhang ZB, Krebs CJ (2013) Long-term seed survival and dispersal dynamics in a rodent-dispersed tree: testing the predator satiation hypothesis and the predator dispersal hypothesis. Journal of Ecology 101: 1256–1264

48. Lookingbill T, Zavala MA (2000) Spatial pattern of Quercus ilex and Quercus faginea recruitment in Pinus halepensis dominated woodlands. J Veg Sci 11: 607–612

49. Augspurger CK (1984) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. J Ecol 72(3): 777–795

50. Brokaw NVL (1983) Gap-phase regeneration in a tropical forest. Ecology 64(3): 682–687

51. Schupp EW, Howes HF, Augspurger CK, Levey DJ (1989) Arrival and survival in tropical treefall gaps. Ecology 70: 562–564

52. Liu H, Cui H, Yu P (2002) The origin of remnant forest stands of Pinus tabuliformis in southeastern Inner Mongolia. Plant Ecol 158: 139–151

53. Barcelona AR, Bobrowiec PED, Sanaei-TM, Gribel R (2013) Seed germination from lowland tapir (Tapirus terrestris) fecal samples collected during the dry season in the northern Brazilian Amazon. Integr Zool 8: 63–73

54. Capece PI, Aliaga-Rossel E, Jansen PA (2013) Viability of small seeds found in feces of the Central American tapir on Barro Colorado Island, Panama. Integr Zool 8: 57–62