Forest Ecology and Management 433 (2019) 625–632

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Proximity to roads reduces acorn dispersal effectiveness by rodents: Implication for forest regeneration and management

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ARTICLE INFO

Keywords:
Barrier effect
Forest regeneration
Road effect zone
Rodent
Seed dispersal effectiveness

ABSTRACT

Globally, the aggregate length of roads exceeds 64 million km and 90.7% of protected areas are disturbed by road penetration, and therefore understanding how road networks impact species and ecosystem processes is highly relevant to applied conservation ecology. Among various effects on wildlife, roads may disrupt the interaction between plants and their animal-mediated seed dispersers, compromising forest regeneration and composition. Here, using the acorn-rodent system, we quantified to what extent rodent functions on seed dispersal are modified by roads over two years (i.e. 2013 and 2014). Road had negative effects on seed-dispersal services provided by rodents, with an approximate 30% reduction of seed dispersal effectiveness (SDE) and 50% reductions of dispersal distance in proximity to the road. These detrimental effects gradually declined along a gradient from the roadside towards forest interior. Declines of rodent abundance in proximity to the road seem to induce these depressed seed dispersal functions. Although the influential magnitudes of roads on SDE were similar in both years, its influential magnitudes on seed dispersal were stronger in 2014 which indicates the more negative impacts of road encroachment on seed dispersal services. Crucially, no tagged seeds were dispersed across the road, implying that it imposed a barrier effect on animal-mediated seed dispersal and plant recruitment. Given wildlife's key roles in plant recruitment, we conclude that the ever-expanding effect of roads on animal-mediated seed dispersal may ultimately cause profound changes in forest composition and structure across diverse ecosystems, on a global scale.

1. Introduction

Road network can promote social and economic development by connecting people and their societies, and facilitating exchange of information and resources between urban and countryside (Leonard and Hochuli, 2017; Watts et al., 2007). However, the current unprecedented expansion of global roads enhances human access into previously remote areas, potentially exacerbating human-caused disturbances to wildlife through direct and indirect environmental impacts (Forman and Alexander, 1998; Van der Ree et al., 2015). Notably, among terrestrial ecosystems, 90.7% of world's protected areas (including forests) are disturbed by road penetration (Ibisch et al., 2016). This potentially threats the composition, structure, and function of forest ecosystems (Laurance et al., 2009), raising a critical issue for forest conservation and management.

Within the framework of Human-Induced Rapid Environmental Change, road network presents one of the most pervasive human-mediated habitat transformations (Van der Ree et al., 2015). A striking impact of road encroachment in forest ecosystems is causing rapid decline of many vertebrate species because of their marked avoidance behavior and roadkill (Torres et al., 2016). The meta-analysis of 49 studies across the globe found that species abundance of birds and mammals decreased by 28–36% and 25–38% within 2.6 km and 17 km from roads and other infrastructure, respectively (Benítez-López et al., 2010). Road networks act as barriers to dispersal and connectivity for remnant individuals, and cause modification to wide strips of road-side habitat that can fragment populations and alter ecological community composition at the landscape level (Laurance et al., 2009; Van der Ree et al., 2015). Thus, remnant individuals are likely to be imposed to alter behavior for adapting the disturbed road habitat, such as the shift in dietary composition and spatial movement (Bautista et al., 2004; Siemers and Schaub, 2011). The population declines and behavior alterations have caused detrimental impacts on the ecosystem services (e.g. dispersing seeds) they provide (McConkey and O'Farrill, 2016), and potentially increased the extinction risk for plant species (Caughlin et al., 2015). This would further alter ecological process and species

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https://doi.org/10.1016/j.foreco.2018.11.029
Received 7 April 2018; Received in revised form 14 November 2018; Accepted 16 November 2018

composition (Zhou et al., 2013b), and trigger biomass and carbon storage collapse (Peres et al., 2016; Sobral et al., 2017).

Zoochorous seed dispersal, a critical ecological process, determines the plant recruitment template and shapes subsequent seedling establishment and regeneration success, thus playing a vital role in ecosystem functionality and the persistence of biodiversity (Jansen et al., 2014; Levine and Murrell, 2003). It associates the reproductive cycle of adult plants with the establishment of individual offspring (Wang and Smith, 2002), and can facilitate recruitment success by allowing offspring to avoid distance- and density-dependent mortality and colonize favorable sites (Connell, 1971; Janzen, 1970). However, the process of seed dispersal is being disrupted worldwide (McConkey and O'Farrill, 2016). Previous studies revealed that roads have caused the negative impacts on seed dispersal: (1) barrier effects for dispersing seeds (Lambert et al., 2014; Niu et al., 2018), and (2) declined seed dispersal function near roadside compared with forest interior (Hosaka et al., 2014; Niu et al., 2018; Suhonen et al., 2017). In several circumstances, roads may enhance the movement of large animals with abundant food resources (e.g. elephants; Wadey et al., 2018; Yamamoto-Ebina et al., 2016), and act as corridors for seeds of fleshy-fruited shrub dispersed by carnivores and rabbits, and thus facilitate fleshy-fruited shrub recruitment and establishment (Suárez-Esteban et al., 2013). Nevertheless, these road-side zones often support pioneer plant communities involving colonisation by invasive/exotic species at the cost of regeneration of former dominant species (Suárez-Esteban et al., 2016). Several factors, including habitat alteration (e.g. canopy gap) during road construction, noise, chemical and light pollution from vehicle and road use, may cause these impacts near roadside (Laurance et al., 2009; Leonard and Hochuli, 2017). Indeed, the influencing magnitudes of these factors exhibit the gradient decline from the roadside towards the forest interior, and have largely been ignored in assessing the road networks on seed dispersal function.

Here, we develop the road-effect paradigm beyond effects due to traffic collisions with wildlife (e.g., Bíl et al., 2017; Seshadri and Ganesh, 2011), or how roads simply act as barriers to dispersal (e.g. Lugo and Gucinski, 2000; Niu et al., 2018), fragmenting ecological communities (e.g., Laurance et al., 2009; Zhou et al., 2013a). Rather we investigate how seed dispersal function may be depressed by alterations in habitat and by changes to the behavior of seed dispersing species along the 'road-effect' gradient. We focus on the interaction between rodents and oak acorns, the former of which act as conditional mutualists in this system because they both predate upon and disperse acorns (Chen et al., 2017b; Sawaya et al., 2018). Some acorns encountered by rodents are eaten immediately, whereas others are dispersed and hoarded, which potentially promotes germination and survival compared with undispersed acorns, if the cached acorns are not recovered (Cao et al., 2016; Kelly and Sork, 2002). Rodents thus are important proxies for dispersal of seed plants (Lichti et al., 2017), in particular at the "road-effect" zone, where they tolerate road disturbances better than large-body seed dispersers because of their high reproductive rates, small home ranges, and avoidance of road surface regardless of traffic volume (Rytwinski and Fahrig, 2012).

Disturbance caused by road encroachment in forest ecosystems impacts food availability and energetic intake to primary consumers (a 'bottom-up' ecological process, Power, 1992). This risks three important (and possibly counteractive) effects on the interaction between rodents and oak acorns, influential on acorn dispersal and fate: (1) more open canopy adjacent to roads may have negative or positive effects (Laurance et al., 2009) on perceived predation risk and/or on predator abundance ('top-down' processes, Power, 1992), causing changes in rodent activity, vigilance and acorn dispersal behavior (Lichti et al., 2017); (2) more light reaching the forest floor can enhance the density of understory vegetation (Tinya and Ódor, 2016), providing improved ground-level cover for rodents and causing more acorns to be dispersed (Lichti et al., 2017); and (3) the 'road-effect' gradient may skew rodents' distribution (Benítez-López et al., 2010) and/or acorn dispersal behavior.

To quantify how roads affect forest regeneration by influencing the seed dispersal along the 'road-effect' gradient, we use the sharptooth oak (*Quercus aliena* var. *acuteserrata*) acron-rodent system in proximity to a major road bisecting Shennongjia World Natural Heritage Site in Central China as a study paradigm. By tracking acorn fate in three transects at different distances to the road (10 m, 100 m and 200 m) and in the forest interior (control transects, at least 3 km from the nearest unpaved dirt road) over two years, we test the following hypotheses that: (i) seed dispersal function may be depressed due to typically negative effects of roads on rodents caused by either 'bottom-up' and/or 'top-down' ecological process (reviewed by Van der Ree et al., 2015); (ii) the impacts may gradually decline along an gradient from the roadside towards the forest interior (the 'road-effect' gradient; Leonard and Hochuli, 2017). After the completion of this acron dispersal experiment, a survey of rodent abundances were undertook in our sampling sites to identify changes that may affect acorn predation and dispersal. Finally, we consider the implications of our findings in terms of forest management and the sustainable development of transport infrastructures to accommodate and mitigate this novel road-side anthropogenic forest ecosystem.

2. Materials and methods

2.1. Study site and road characteristics

This study was conducted at the Shennongjia World Natural Heritage Site (31°19′N, 110°29′E), north-west of Hubei Province, in central China (Fig. 1). It is an important biodiversity hotspot in both China and the globe, harboring exceptional biodiversity, the highest concentration of global temperate genera of trees and deciduous woody species. This region is a key habitat for numerous relics, rare, endangered and endemic species, and presents a typical example of mountain altitudinal biological zones in the Oriental Deciduous Forest Biogeographical Province (Zhou et al., 2017). The climax vegetation is montane evergreen and deciduous broad-leaved mixed forest, including *Quercus* spp., *Fagus* spp., *Castanea* spp., and *Cyclobalanopsis* spp. The climate is a typical subtropical monsoon, characterized by four distinct seasons including a hot, humid summer (June-August) and a cold winter (December-February). The annual precipitation is 1350 mm and annual mean temperature is 10.6 °C (Xie, 2012).

National Road 209 permeates to the Shennongjia World Natural Heritage Site and splits it into two parts, impeding species movement and habitat connectivity (Fig. 1; Zhou et al., 2017). It was constructed from a gravel road (4.5–7.5 m wide) in 1966 and then upgraded to a paved (bitumen) standard (Grade II of the Chinese National Road classification) in 1990. In 2001, the road was re-paved with bitumen-based asphalt due to a large increase in traffic (Zhu, 2011). There is only a single lane of traffic in each direction, with no barrier dividing opposing lanes. For our experiments, we established two sampling sites along stretches of National Road 209 that comprised homogeneous patches of the sharptooth oak forests, which were reserved as forest tree provenance and thus were subject to little non-road related human disturbance (Xie, 2012; Zhu, 2011). Three transects (300 m long) in each of the two road sampling sites were delineated at 10 m, 100 m and 200 m from the road edge, and two control forest transects were chosen within old-growth and mature forest located at Longmenhe National Forest Park (ca. 5 km far from the road sampling sites). The established control transects (1.5 km apart) were at least 3 km from the nearest unpaved dirt road and little traffic noise could be heard (Fig. 1). These four forest sites with canopies dominated by the sharptooth oak (up to 90%, Chen, 2004; Xie, 2012).

2.2. Study species and acorn marking

Our focus species, the sharptooth oak, is a keystone and widespread

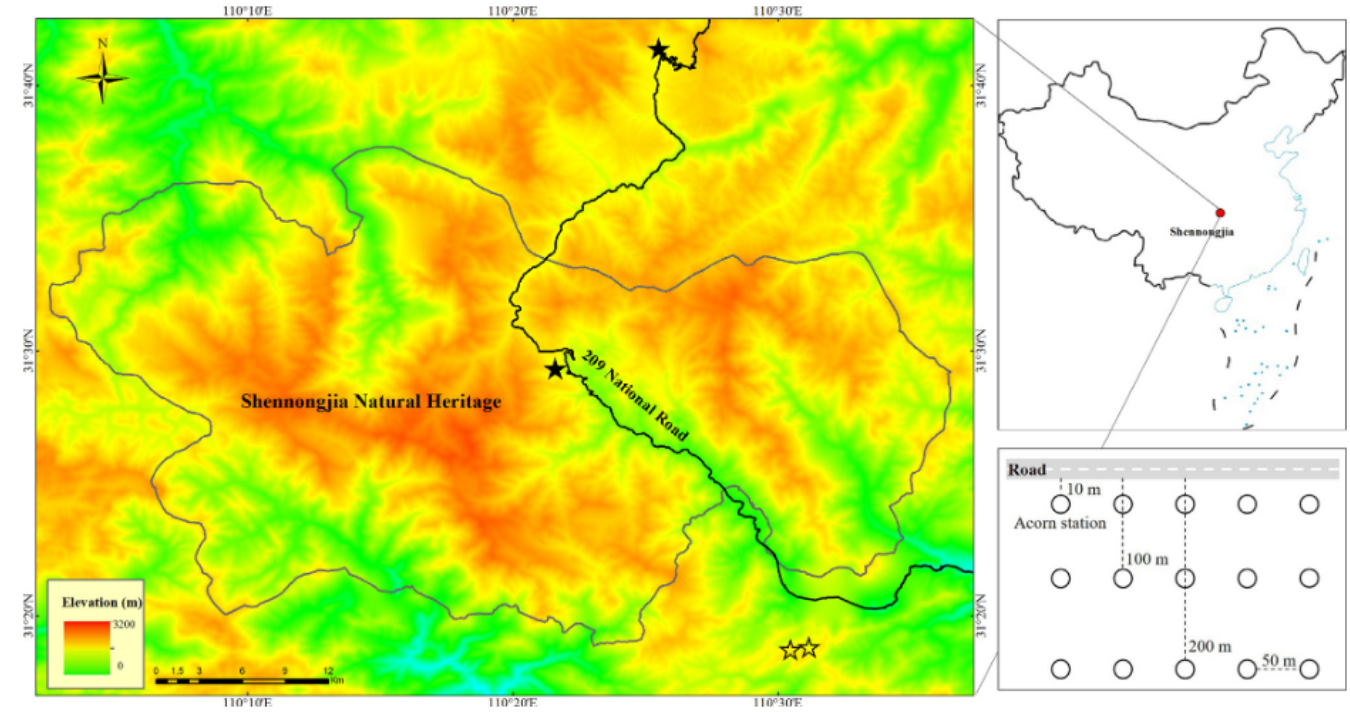

Fig. 1. Map of the study area in the Shennongjia World Natural Heritage Site, illustrating two sampling sites along stretches of National Road 209 (solid black asterisk) and two control forest transects within old-growth and mature forest (white asterisk). The locations of the Heritage Site within China (upper right plot) and three transects in each of the two road sampling sites (low right plot) are indicated in the inset.

tree species existed in the montane subtropical and temperate forests in Asia (including China) (Chen, 2004), which can grow up to 30 m in height within our study area (Chen et al., 2017b). It produces wind-pollinated catkins from March to April, and bears mature fruits (i.e., acorns) from October to November. It is a mast seeding species, showing intermittent and synchronous production of heavy seed crops in certain years (e.g. a mast seeding year during our study period in 2014). Although most of thirty-one species of Fagaceae recorded in Shennongjia region have the mast seeding phenology, they are not synchronous (but generally 2–9 year cycles). A previous study conducted in our study site indicated the sharptooth oak exhibits a 2-year cycle of mast seeding with ca. 4 times acorn production in mast seeding year relative to non-mast seeding year (Fig. S1, Chen, 2004). The sharptooth oak is the dominant component of the canopy (up to 90%) and the density of adult trees can be up to 50 individuals per 400 m^2 plot in our sampling sites (Chen, 2004). Thirty-one species of Rodentia have been recorded for the study area (Chen et al., 2017c), of which many rely on acorns and nuts as important food sources. Of these, at least seven species from genus *Apodemus*, *Niviventer*, and *Leopoldamys* were found to hoard and disperse the acorn of sharptooth oak at our (Chen et al., 2017b) and other study sites (Yu et al., 2017).

In late October of 2013 and 2014, mature acorns of the sharptooth oak were collected from the ground at our experimental sites. Their quality was visually ascertained, and then empty and insect-damaged acorns were subsequently removed using water floatation (Chen et al., 2017b). A hole with 0.6 mm in diameter was drilled in the base of each acorn, and a numbered white plastic tag (length × width: 3.6 × 2.5 cm) was tied with the acorn through the hole by using a 10 cm long and 0.3 mm wide stainless steel wire. When acorns were buried, the tags were often left on the surface, which allowed us to follow its exact fate and spatial location (Xiao et al., 2006).

2.3. Acorn dispersal and fate

In each transect, we established five acorn provisioning stations (50 m apart), where 50 acorns were set equidistant along the perimeter of ca. 15-cm radius circle (Fig. 1) in November of 2013 and 2014. Thus, a total of 4000 acorns were offered (road sampling sties, 2 sites × 3 transect × 5 stations × 50 acorns × 2 years; control transects, 2 transect × 5 stations × 50 acorns × 2 years). After winter (i.e. early-April of the subsequent year), we intensively searched the area within a 25 m radius around each provisioning station to retrieve the removed acorns and record acorn fates, because the acorns of sharptooth oak were removed typically within a distance of 10 m and very few acorns were dispersed farther than 20 m at our (Chen et al., 2017b) and other study sites (Yu et al., 2017). When we found some acorns were dispersed over 25 m at one provisioning station, the search radius was increased to 50–60 m until we could not retrieve acorns within this area. In total, we found 99.3% (n = 1933) of acorns and acorn fragments distributed within 25 m of provisioning stations; only 14 (0.7%) of 1947 dispersed acorns were farther than 25 m (see Section 3).

For all provisioning sites along transects within 10 m from the road, we intensively searched for acorns potentially transported across the road by repeating the same protocol as described above. We found that most acorns (90.0%, n = 450) were dispersed within 10 m along transects within 10 m from the road (see Section 3); and most of dispersed acorns trended to be transported towards forest interior (Chen W, personal observation). Indeed, rodents were typically evidenced to avoid paved roads and move towards forest interior (see Grilo et al., 2018 for reviews). Collectively, these procedures suggest that the probability of tagged acorns transported across the road was very low.

Acorns found at the provisioning station were categorized as remaining (non-dispersed and uneaten), consumed (seed fragments with dental marks found) and removed. When a removed acorn was found, we recorded its tag number and measured its distance (in centimeters) to its origin station. The fate of recovered acorns was further categorized as intact (i.e. post-dispersal survival) and consumed.

2.4. Rodent abundance

To assess how proximity to road affects the abundance of rodent communities, we set up 100 live traps (30 × 25 × 20 cm) as a 10 × 10

grid with an interval of 2–3 m at each provisioning station at nightfall and checked them in the next morning. Granivore abundance may fluctuate across different years (Cao et al., 2016; Kellner et al., 2016), but our previous 4-year data did not reveal a significant annual variation over this short-term period in our study area (Chen et al., 2017b). We thus set the traps within two weeks after the seed dispersal experiment to minimize the potential effect of trapping on the experimental rodent community. Moreover, these 4-year monitoring data indicated that the widely used baits, peanuts, could trap more rodent individuals than two local tree seeds, acorns and seguin chestnuts (*Castanea seguinii*) (Zhang, 2014; Zhong, 2012). Peanuts were thus used as baits to obtain high trapping rate (Chen et al., 2017c). All captured individuals were identified to species based on pelage (e.g., color, texture, and length) and morphological characteristics (e.g., shape, body size, tail and foot length) (Smith and Xie, 2009), and then immediately released at their respective sites of capture. Species belonging to same genus (i.e., *Apodemus chevrieri* vs. *A. draco*, and *Niviventer confucianus* vs. *N. fulvescens*) that might be confused, were determined by comparison with the pervious reference specimens collection that were kept at zoological specimen room in the National Observation and Research Station for Forest Ecosystem in Shennongjia (Zhang, 2014; Zhong, 2012). In addition, hairs from captured individuals, identified by microscopic morphological analysis, were used to differentiate species if required.

2.5. Data variables and analysis

Acorn dispersal and fate data were assessed at four metrics: (i) the number of acorns dispersal, (ii) acorns survived at cache sites, (iii) seed (acorn) dispersal effectiveness (SDE), and (iv) the dispersal distance of acorns. These parameters showed the probability of acorns being dispersed from the source to other sites with the potential for seed germination and further seedling establishment (Chen et al., 2017b; Kellner et al., 2016). For the metric (i), the number of acorns removed from provisioning stations was recorded to assess the probability of acorns dispersal. The number of intact acorns at cache sites over winter was calculated as the metric (ii). Caching seeds can ensure an even supply of food throughout the year for rodents, but this could promote seed germination, seedling survival if the cached acorns are not recovered, and further enhance seed dispersal fitness (Lichti et al., 2017). Similar to the metric (i), the distances (the metric [iv]) to which acorns were removed from provisioning stations were assessed.

Metrics (i) and (ii) were recorded as binary data, and fitted to generalized linear mixed models (GLMM) with a binomial distribution. The distance parameters (log-10 transformed to meet assumptions of the statistical models) were analyzed using linear mixed models (LMM). The distance to the road, year, and their interaction were included as fixed factors in above models, and the provisioning station was incorporated as a random effect. When a statistically significant interaction was found, we further ran separate models for each sampling year to better understand the structure of the relationship (Aiken et al., 1991). Inference for all models was based on χ^2-values, unless noted otherwise, and associated *p*-values from Wald type-II tests (Fox and Weisberg, 2011).

We applied the "Seed dispersal effectiveness (SDE)" framework, developed by Schupp et al. (2010, 2017), which is a more ecologically relevant parameter for evaluating the contribution of seed dispersal to plant recruitment. SDE is calculated as the product of the quantity and quality components of seed dispersal, and high SDE for a plant species implies increasing seedling recruitment (Kellner et al., 2016; Schupp et al., 2010). For seed dispersal by scatter-hoarding rodents, SDE relating to the qualitative probability of being cached rather than consumed immediately, can be replaced by the 'quality of seed treatment in mouth and gut' (Cui et al., 2018; Gómez et al., 2008; Schupp et al., 2010). For the metric (iii), SDE was thus estimated as the product of the probability of acorns removal (quantity component) from provisioning stations (ρ) and the probability of acorns survival (quality component) at cache sites (ψ_ρ) (Kellner et al., 2016; Lichti et al., 2014). We simulated 1000 posterior estimates of ρ and ψ_ρ from the fitted models for each stratum (i.e., stand and year). We then calculated the product of each pair of simulated probabilities to yield a posterior distribution for SDE. Significant differences in SDE among different distance to the road and between years were tested by bootstrapping a 95% confidence interval (CI) for the difference between strata means and determining if the interval overlapped zero (Chen et al., 2017b; Kellner et al., 2016).

The differences in rodent community were examined as the species richness and abundance of each species. These parameters were recorded as count data, and fitted to GLMM following a Poisson distribution, with the distance to the road as a fixed factor and the trap station as a random effect. The analysis of rodent abundance was only applied for *Niviventer confucianus* and *Apodemus draco* owing to the small sample size of other rodents. In addition, the multivariate generalized linear models (Manyglm) with Poisson error structure and 999 Monte-Carlo permutations were used to test for significant effects of distance to the road on community composition. The likelihood ratio test based on 999 Monte-Carlo permutations were used for multiple comparisons among transects (Wang et al., 2012). To correct for multiple hypothesis testing, *p* values were adjusted by controlling a false-discovery rate of 5% using the Benjamini-Hochberg false-discovery-rate method.

All statistical analyses were performed in *R* version 3.4.0 and associated packages. GLMMs and LMM were constructed in the *lme4* packages, and χ^2 and associated *p*-values obtained in the *car* package. Restricted maximum likelihood (REML) *t*-tests and associated *p* values were calculated using Satterthwaite approximations to degrees of freedom for Post-hoc comparison in LMM (the *lmerTest* package). Manyglm were constructed with the package *mvabund*, and *p*-value corrections were conducted by using the *p.adjust* function in *R*'s base package.

3. Results

3.1. Acorn dispersal and fate

Overall, 1092 (788 vs. 304 in 2013 and 2014) tagged acorns at provisioning station were eaten, and 2908 (1212 vs. 1696) of 4000 tags originally tethered to acorns were ultimately removed (namely, no acorns remained at provisioning station over winter); of these removed acorns, 1947 (896 vs. 1051) were eventually recovered (either in an acorn or alone) and 191 (77 vs. 114) acorns were intact at cache sites following the winter after seed displacement. Moreover, no tags originally tethered to acorns were relocated across the road, indicating that it imposed a barrier effect on rodent-mediated acorn dispersal.

More acorns were removed ($\chi^2 = 271.860$, $p < 0.001$; Fig. 2a) and subsequently survived (marginally significant, $\chi^2 = 2.846$, $p = 0.092$; Fig. 2b) in 2014 than 2013. No significant difference was found for the probability of acorns removed from provisioning stations ($\chi^2 = 1.306$, $p = 0.728$) among different transects in road and control forest sampling sites, but a marginal significance was found for survival probability at cache sites ($\chi^2 = 7.055$, $p = 0.070$). These results indicated that proximity to road did not alter acorn removal but has slight negative impact on subsequent survival (Fig. 2a, b).

Mean SDE was 0.07 ± 0.01 across all strata (i.e. distance to the road and years). Overall, SDE was significantly higher in 2014 (0.09 ± 0.01) than 2013 (0.05 ± 0.01; Fig. 2c) (the 95% bootstrap CI did not overlap zero in all cases, Table 1). Compared with the control transects, 38.3%, 45.6% and 7.2% reductions in SDE were found in transects at 10 m, 100 m and 200 m proximity to the road in 2014, respectively. In terms of the effects of road proximity, SDE was significantly lower on transects within 10 m and 100 m proximity to the road compared with transects 200 m away in 2014, while SDE did not differ between transects within 10 m and 100 m (Table 1). The direction

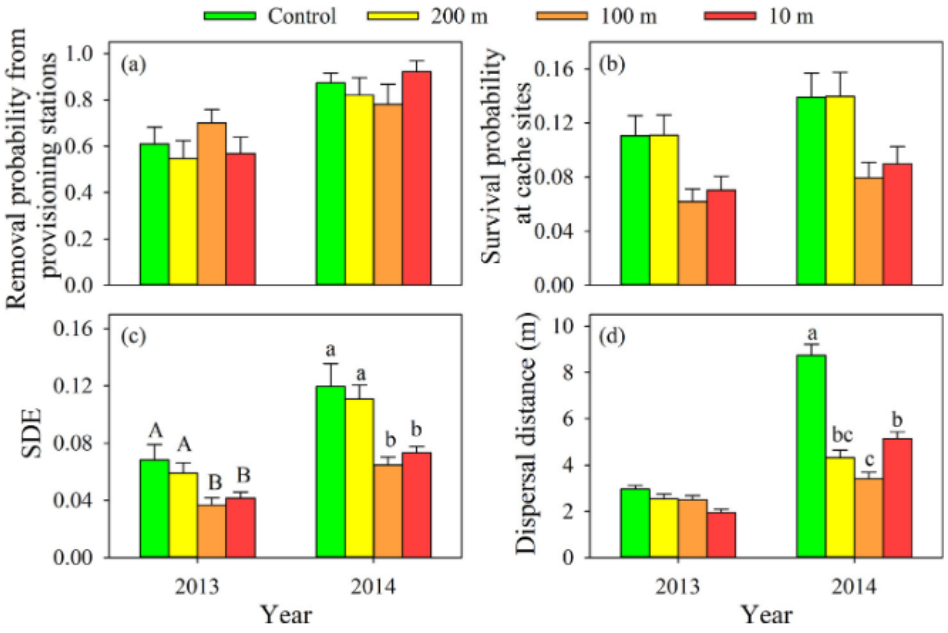

Fig. 2. Acorn dispersal and fate at different distance to the road and within the control forest in 2013 and 2014. (a) the probability of acorns that were removed from provisioning stations, (b) the survival probability of acorns that were cached, (c) seed dispersal effectiveness (SDE, the product of probability of acorn removal and probability of post-dispersal survival at cache sites), (d) dispersal distance for acorns that were removed from provisioning stations. Different letters above bars indicate significant differences.

Table 1
Mean differences (d) and 95% bootstrap confidence interval (CI) of seed dispersal effectiveness at different distances to the road and within the control forest in 2013 and 2014. **Statistical significances were tested by bootstrapping 95% CI for the difference between strata means and determining if the interval overlapped zero (Chen et al., 2017b; Kellner et al., 2016).

Multiple comparisons	d	CI
2013 vs. 2014		
Control	−0.051**	(−0.093, −0.016)
200 m	−0.052**	(−0.075, −0.03)
100 m	−0.028**	(−0.043, −0.015)
10 m	−0.032**	(−0.044, −0.02)
2013		
Control – 200 m	0.009	(−0.015, 0.034)
Control – 100 m	0.031**	(0.008, 0.054)
Control – 10 m	0.026**	(0.004, 0.048)
200–100 m	0.022**	(0.006, 0.04)
200–10 m	0.017**	(0.001, 0.034)
100–10 m	−0.005	(−0.017, 0.008)
2014		
Control – 200 m	0.009	(−0.027, 0.045)
Control – 100 m	0.054**	(0.022, 0.087)
Control – 10 m	0.046**	(0.012, 0.079)
200–100 m	0.046**	(0.025, 0.069)
200–10 m	0.037**	(0.017, 0.058)
100–10 m	−0.009	(−0.02, 0.005)

of the road effect in 2013 was generally consistent with that in 2014, but the influential magnitudes were lower (Table 1; Fig. 2c).

Mean dispersal distance for acorns was 4.1 ± 0.1 m, maximum up to 38.5 m. The dispersal distance differed between 2013 and 2014 ($\chi^2 = 232.785$, $p < 0.001$), and among different transects in road and control forest sampling sites ($\chi^2 = 18.474$, $p < 0.001$), and the interaction was significant ($\chi^2 = 60.135$, $p < 0.001$). Longer dispersal distance was found in 2014 than 2013 ($t = 12.538$, $p < 0.001$; Fig. 2d). Compared with the control forest, significant reductions in dispersal distance were found proximity to the road in 2014 (50.6%, 60.7% and 40.9% reduction at 200 m, 100 m and 10 m distance to the road, respectively), while they did not show statistical significance in 2013 (Table 2), indicating that roads have stronger negative impacts in seed dispersal distance in 2014 than 2013 (Fig. 2d). Among transects proximity to the road, the only significant decline in dispersal distance was found in 100 m transect comparing with 10 m transect in 2014 ($t = 2.111$, $p = 0.042$).

Table 2
Parameter estimates for covariate effects on dispersal distance of acorns. Fixed factors in bold indicate significant difference ($p < 0.05$).

Parameters	Estimate	SE	*t*	*p*-value
2013				
Intercept	**2.290**	**0.065**	**35.329**	**< 0.001**
200 m	−0.135	0.092	−1.462	0.152
100 m	−0.090	0.091	−0.993	0.327
10 m	−0.146	0.091	−1.594	0.120
2014				
Intercept	**2.754**	**0.068**	**40.220**	**< 0.001**
200 m	**−0.327**	**0.098**	**−3.354**	**0.002**
100 m	**−0.448**	**0.098**	**−4.577**	**< 0.001**
10 m	**−0.242**	**0.096**	**−2.512**	**0.017**

3.2. Rodent abundance

Among 4000 traps, we captured 124 rodent individuals belonging to 7 species (Table 3). Mean species richness was 1.7 per 100 trapping-days, and no significant differences were found in the species richness among transects in road and control forest sampling sites ($\chi^2 = 2.685$, $p = 0.443$). Abundance of *N. confucianus* did not differ among transects ($\chi^2 = 0.789$, $p = 0.852$), while *A. draco* showed a declining pattern ($\chi^2 = 13.760$, $p = 0.003$) with 63.6% ($z = 2.107$, $p = 0.035$), 72.7% ($z = 2.435$, $p = 0.015$) and 90.9% ($z = 3.058$, $p = 0.002$) reduction at 200 m, 100 m, and 10 m proximity to the road, respectively, compared with the control forest (Table S1). At community level, road disturbance had significant effects on community composition ($\chi^2 = 43.556$, $p = 0.002$, *anova.manyglm* function in *mvabund*). Community abundance declined significantly with decreased distance to road (Table S1).

4. Discussion

Our field experiments indicate that proximity to roads have negative impacts on seed dispersal services provided by rodents, which potentially affect the process of seedling establishment and forest regeneration (Chen et al., 2017b; Jansen et al., 2014). Although no significant differences were found in the probability of acorns dispersed

Table 3
Abundance, species richness and body mass of rodents captured from 4000 trapping-days in control forest and at different distance to the road. Their home range sizes and roles as seed predator/disperser were derived from references.

Species	Abundance				Body mass (g)	Home range size (ha)	Seed predator/disperser
	Control	200 m	100 m	10 m			
Apodemus chevrieri	2	0	0	2	42.6	0.01–2.02[a]	+/+[d]
Apodemus draco	22	8	6	2	31.1	0.22–0.50[b]	+/+[d]
Leopoldamys edwardsi	2	3	0	1	322.4	2.08–9.83[a]	+/+[d]
Niviventer confucianus	18	19	19	14	64.1	0.02–0.72[c]	+/+[d]
Niviventer fulvescens	0	2	0	0	94.2	0.02–2.02[a]	+/+[e]
Rattus nitidus	0	0	0	1	82.4	0.22–1.9[a]	+/+[e]
Typhlomys cinereus	0	1	1	1	18.9	–	+/Unknown[d]
Total	44	33	26	21			
Species richness	4	5	3	6			

[a] Due to paucity of information, data are presented from the similar, *A. sylvaticus*, *A. agrarius*, *A. flavicollis*, *A. draco*, *A. speciosus*, *L. sabanus*, *N. coninga*, *N. confucianus*, and *R. rattus* (Shen, 2011; Wilson et al., 2017).
[b] Wilson et al. (2017).
[c] Shen (2011).
[d] Chen et al. (2017b).
[e] Xiao et al. (2006).

and survived at cache sites, reductions in seed dispersal effectiveness (SDE) and dispersal distance near roads implied the depressed seed dispersal services (hypotheses i). This negative impact decreased with increasing distance to the road (hypotheses ii); and, at 200 m distance to the road, the SDE was less disrupted by roads despite of a marked reduction in dispersal distance.

Seed dispersal is a complicated process and affected by several factors, including habitat structure, environmental pressure, food availability, and the size and composition of the disperser community (Chen et al., 2017b; Lichti et al., 2017). In our study, the road cutting in which the road was constructed imposed a 5.5–8.5 m wide break in canopy cover, which led to an increase in understory cover because of an increase in the density of understory vegetation (Zhu, 2011). Under such circumstances, the predation risk perceived by rodents is lower, and they can trade vigilance for longer or more frequent foraging bouts (Chen et al., 2017b; Kellner et al., 2016) which induced their ecological function shift from seed dispersers to predators (Chen et al., 2017a; Morán-López et al., 2015). Thus, a higher understory cover may contribute to the reduced cached acorn survival, which resulted in low SDE proximity to road.

Our hypothesis (ii) (i.e., the 'road-effect' gradient) was partly supported in SDE, but not in seed dispersal distance. The influential magnitude and features from road construction, vehicle and road use may explain these patterns. In our study, the road was built through Shennongjia by blasting away rock. This resulted in numerous gravel piles with soils and litters extending up to 150 m into roadside habitat (Zhu, 2011), which contribute the high cover and density of understory vegetation. As discussed above, higher understory cover lead to the shift of rodents' ecological function from seed dispersers to predators, which may further cause SDE reductions in transects at 10 m and 100 m distance to the road relative to 200 m distance. Behavioral (e.g., home range rearrangements, dietary shift; Chen et al., 2017a; Grilo et al., 2018; McConkey and O'Farrill, 2016) and morphological (e.g., small body size; Galantinho et al., 2017) acclimation to road disturbance for remnant wildlife populations near roads may also be relevant because over the 30 years since initial road construction, behavioral codes and morphological characteristics of small mammals have re-established at Shennongjia near roads (Zhang, 2014; Zhong, 2012). Home ranges of rodents in our study area are generally very small and are less than 200 m in radius (Table 3), indicating that seed dispersal in transects at 10 m and 100 m distance to the road may be performed by same rodent individuals, but not for 10 m and 200 m. Indeed, we observed a typical response, where rodent seed dispersal functions were similar in transects at 10 m and 100 m distance to the road, and were lower relative to 200 m and control transects which were also similar (Fig. 2). These declined seed dispersal may be also induced by behavioral shift from dispersing seeds to eating seeds of remnant rodents near roads (Chen et al., 2017a). Therefore, both immediate (e.g. rodent community alteration) and long-term (e.g. acclimation of remnant wildlife populations) effects of road installation may together cause the 'road-effect' gradient (Forman and Alexander, 1998; Van der Ree et al., 2015).

By contrast, seed dispersal distances were not longer in transects at 200 m distance to the road relative to 10 m, and 100 m, and it is likely due to the large influential extent of noise and air pollution from motorized vehicles and road use. Air pollution in roadside ecosystems is implicated as a key source for inducing the "masking effect" to the detriment of olfaction communication in wildlife (Leonard and Hochuli, 2017; Yi et al., 2016), which increase rodents' energetic cost to relocate seeds (Li et al., 2018). Thus, the reduced dispersal distance could allow rodents to spend more time on seed searching as proposed by the "search time relocation hypothesis" (Jorge et al., 2012). Additionally, traffic noise can induce distraction and elevated stress for remnant individuals near roads (Swaddle et al., 2015). These could result in an increase in vigilance behaviors and perceived predation risks by rodents, contributing to a reduction in dispersal distance near roads as an effective cache protection (Sunyer et al., 2013). Notably, a longer seed dispersal distance was found in transects at 10 m distance to the road relative to 100 m and 200 m transects. It is likely explained by several potential, interacting (and possibly counteractive) factors: acorn production relative to granivore abundance, habitat alteration, and physical and chemical disturbances from road and vehicle use (see above). Collectively, to better understand how roads influence ecological function of rodents, it would be interesting (but difficult) to figure out the rodents' foraging decisions and responses to competitive and environmental pressures proximity to roads (Lichti et al., 2017).

Despite the similar trends of road impacts on seed dispersal services provided by rodents, the patterns in 2014 were stronger than in 2013, indicating that the road impacts on seed dispersal were significant in seed abundant year (i.e. 2014 here, Zhou personal observation). With the expectations of the predator satiation hypothesis and the animal-mediated seed dispersal hypothesis which are gernerally well supported in recent studies (e.g. Kelly and Sork, 2002; Vander Wall, 2002; Zwolak et al., 2016), massive seed crops in a bumper year (i.e. mast seeding years, the synchronous intermittent production of large seed, and a very common phenomenon in many oak species) can satiate seed predators and promote seed dispersal. Our results showing a higher SDE and longer dispersal distance in 2014 supported these hypotheses about the mast seeding recruitment. Although seed removal is considerably

slower in mast than in non-mast years (Lichti et al., 2017), in the long term, rodents still remove a large proportion of the seeds in mast seeding years (as revealed by our field experiments), where rodents are allowed to forage on seeds throughout fall, winter, and spring. Notably, no tagged acorns were dispersed across the road, implying that the negative effects of roads will be further intensified due to the barrier effects on animal-mediated seed dispersal and plant recruitment (Lambert et al., 2014). As it is widely evidenced that small mammals avoid roads (Grilo et al., 2018), future studies should consider the reciprocal translocation of the rodent population to provide information for comprehensive assessments of the influence of the barrier effects.

Depressed seed dispersal processes have several important implications for plant regeneration success. First, although it remains equivocal as to whether a lower SDE necessarily translates directly into a decline in plant regeneration because of many influential factors (e.g., seed production, disperser community and abundance, and seedling survival) (Kellner et al., 2016), a higher SDE is typically regarded to facilitate tree recruitment (Schupp et al., 2010). Second, dispersal distance was shorter in closer proximity to the road, causing acorns to remain closer to their parent trees. As the predictions of the Janzen-Connell model (Connell, 1971; Janzen, 1970), the mortality of offspring increases in the proximity of conspecific adults because host-specific natural enemies are attracted by parents (Caughlin et al., 2015). Furthermore, although we found that rodents scatter-hoarded acorns, acorns still ended up with a clumped (rather than homogeneous) distribution which entails the structure alteration and/or loss of genetic diversity (Pérez-Méndez et al., 2018), because the dispersal distances involved were so short (typically < 5 m, Fig. 2d). Ultimately this caused the number of acorns we found translocated to suitable germination sites to be low (Jansen et al., 2014). Collectively, these depressed seed dispersal processes are associated with a disproportionately high mortality and thus have wider implications for the recruitment success for tree species due to negative density dependence across life stages (Caughlin et al., 2015). Specifically, although, with small home range (Table 3), rodents disperse typically seeds within 100 m (Lichti et al., 2017), the deterioration of the dispersal process may still impair seed-mediated gene flow and eventually collapse among-plant population connectivity, especially in complex heterogeneous landscapes, which ultimately impacts the regional distribution of genetic variation (Pérez-Méndez et al., 2018).

5. Conclusions

Our study not only highlighted the negative impact of roads on seed dispersal effectiveness, but also revealed the 'road-effect' gradient to influence seed dispersal service provided by rodents. Although our results obtained from only four sites may present site-level bias, our 8 transects with 40 replicate acorn provisioning stations and statistical procedures with random effect could reduce this bias. Oak forest is one of keystone and widespread vegetation in Asia (including China) (Chen, 2004), and thus our findings should have important implications for informing forest management strategies. Low seed dispersal effectiveness can cause decreased seedling establishment (Schupp et al., 2010), which can cascade upward to trigger recruitment limitation and/or failure of forests proximity to the road (Levine and Murrell, 2003). In the disturbed habitat (especially in the road effect zone), despite decreased population abundance, rodents are still dominate and primary remnant seed dispersers due to their strong resistance to anthropogenic disturbance (Chen et al., 2017a). Thus, the maintenance of rodent mediated seed dispersal is becoming more important in the road effect zone. As most of rodents are nocturnal, limitation of traffic volume, access, and speed at night, especially in fruiting seasons of mast seeding years, would be effective and critical for retaining their seed dispersal service and thus can potentially facilitate forest regeneration. With road infrastructure development so closely tied to human population growth (Leonard and Hochuli, 2017; Watts et al., 2007), it is important to better understand the full extent of how roads alter seed dispersal, plant regeneration and ultimately the complete dynamics of ecological communities (Ibisch et al., 2016), informing a global road planning scheme for forest management and conservation.

Declarations of interest

None.

Acknowledgments

We thank K. Tian, W. Xu for statistical support, and W.X. Zou, M. Wang for the assistance during field survey. We are grateful to the National Observation and Research Station for Forest Ecosystem in Shennongjia for field support. This work was supported by the National Natural Science Foundation of China (No. 31500359, 31470491) and the Youth Innovation Promotion Association CAS (2016078).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.11.029.

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