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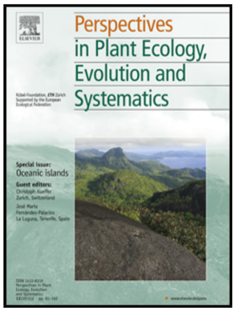

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Roads disrupt rodent scatter-hoarding seed-dispersal services: implication for forest regeneration

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Highlights

- Road developments have pervasive effects on seed dispersal and plant recruitment.
- Seed (nut) dispersal effectiveness was greater nearer the road.
- Consequently, high densities of trees and regeneration occurred closer to roads.
- Contrary to these benefits, nut dispersal distances were shorter closer to roads.
- Ever-expanding effect of roads may cause profound changes in plant communities.

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ABSTRACT

Currently, 43% of the world's terrestrial surface is within five kilometres of a road, and therefore understanding how road networks impact species and ecosystem processes is highly relevant to applied conservation ecology. Among various effects on wildlife, roads can disrupt the interaction between plants and their animal-mediated seed dispersers, compromising plant community composition and regeneration. Here, using the Chinese beech (*Fagus engleriana*) nut-rodent system, we quantified the extent to which rodent functions on seed dispersal were modified in habitats adjacent to roads. Compared to transects 200 m from the road, we observed approximately nine times greater seed dispersal effectiveness at transects 10 m proximity to the road and six times greater at 100 m from the road. Associated with this, high densities of seedlings, saplings and mature trees occurred closer to the road, suggesting that the road effect zone may facilitate plant recruitment. However, road proximity resulted in shorter nut dispersal distances, which did not support a benefit to plant recruitment. These counteractive effects may be caused by modified rodent behaviour in the vicinity of the road, and also by effects on rodent distribution and activity in relation to road-side habitat structure and environmental pressure. Crucially, no tagged seeds were dispersed across the road, implying that it imposed a barrier effect on animal-mediated seed dispersal and plant recruitment. We conclude that the ever-expanding effect of roads on zoochorous seed dispersal may ultimately cause profound changes in the structure of plant communities across diverse ecosystems, on a global scale.

Keywords**:** Barrier effects; *Fagus engleriana*; Forest regeneration; Human-modified landscapes; Road disturbance; Seed dispersal.

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1. Introduction

Within the framework of Human-Induced Rapid Environmental Change (HIREC; Sih et al., 2011), road networks present one of the most widespread human-mediated habitat transformations. They act as barriers to dispersal and population connectivity and cause modification to wide strips of road-side habitat that can fragment populations and alter ecological community composition at the landscape level (Ascensão et al., 2015; Laurance et al., 2009). A minimum of 25 million kilometres of new roads are projected to be built globally by 2050 (Laurance et al., 2014), and thus understanding these effects is highly relevant to conservation ecology.

Here we develop the road-effect paradigm beyond effects due to traffic collisions with wildlife (Ascensão et al., 2015; Laurance et al., 2015), or how roads simply act as barriers to dispersal (Ascensão et al., 2017; Forman and Alexander, 1998), fragmenting ecological communities (Hosaka et al., 2014; Lambert et al., 2014). Rather we investigate whether and how seed dispersal function is altered in the 'road-effect zone' (Forman and Alexander, 1998; Laurance et al., 2015). Zoochorous seed dispersal is a critical ecological process that determines the plant recruitment template and shapes subsequent seedling establishment and regeneration success; thus, it plays a vital role in ecosystem functionality and the persistence of biodiversity (Jansen et al., 2014; Rey and Alcántara, 2014). It can facilitate recruitment success by allowing offspring (i.e., seeds) to avoid distance- and density-dependent mortality and colonise favourable sites (Connell, 1971; Janzen, 1970), supporting the establishment of individual offspring (Jansen et al., 2014).

Zoochorous seed dispersal is, however, being disrupted by development worldwide (Fontúrbel et al., 2017; McConkey and O'Farrill, 2016; Suárez-Esteban et al., 2016). Although in certain circumstances, unpaved roads may act as corridors aiding the dispersal of fleshy-fruited shrub seeds by frugivorous carnivores and

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rabbits, thus facilitating recruitment and establishment (Suárez-Esteban et al., 2013a, 2013b), and roads may contribute to retaining water or enhancing nutrient availability (Auerbach et al., 1997), previous studies have revealed that more major roads often have negative impacts on seed dispersal. This arises due to roads: (1) imposing barrier effects on the species enacting dispersal (Lambert et al., 2014; Niu et al., 2018), and (2) decreasing seed dispersal function near roadsides compared with forest interior sites (Hosaka et al., 2014; Niu et al., 2018; Suhonen et al., 2017). Furthermore, plants in these road-side zones typically produce less fruit (Suárez-Esteban et al., 2014). Several factors, such as habitat alteration (e.g., canopy gap) during road construction, noise, chemical and light pollution from vehicles and road use, can have impacts near roadsides (Ascensão et al., 2015; Laurance et al., 2009; Leonard and Hochuli, 2017), where the magnitude of these influences tends to decline along a gradient towards adjacent forest interior. Consequently, road sides are prone to the establishment of pioneer plant communities involving colonisation by invasive/ exotic species at the cost of regeneration of former dominant species (Suárez-Esteban et al., 2016). Nevertheless, to date, these seed dispersal ecology aspects of the road-effect paradigm have been under-studied.

Rodents are important vectors for seed dispersal (Chen et al., 2017a; Lichti et al., 2017); particularly so in the road-effect zone, where their populations are more tolerant of road disturbances than larger mammalian seed dispersers (e.g. deer) due to high reproductive rates, small home ranges, and their avoidance of road surfaces irrespective of traffic volume (Ascensão et al., 2015; Laurance et al., 2015; Suárez-Esteban et al., 2014). In terms of the mechanism of seed dispersal by rodents, disturbance caused by road encroachment into forest ecosystems can impact food availability, and thus the energetic intake by primary consumers (a ‘bottom-up’ ecological process: Hunter and Price, 1992) in the road-effect zone. This risks three important (and possibly counteractive) effects on the interaction between rodents

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and seed dispersal, potentially influential on seed fate: (1) more open canopy adjacent to roads may have positive (edge-effect: Storch et al., 2005) or negative (predation release hypothesis: Downing et al., 2015) effects on predator abundance and/ or on perceived predation risk (‘top-down’ processes: Carthew et al., 2013; Downing et al., 2015), causing changes in rodent activity, vigilance and seed caching behaviour (Kellner et al., 2016; Sunyer et al., 2013); (2) more light reaching the forest floor may increase the density of understorey vegetation, providing better ground-level cover for rodents, causing more seeds to be removed from this zone (Kellner et al., 2016), linked to enhanced seed caching (Perea et al., 2011); and (3) residual impacts of road construction, such as gravel piles resulting from blasting, or filling material used to build up road foundations over marshy ground, may provide rodents with artificial refugia and skew their distribution (Ascensão et al., 2015) and/ or seed caching behaviour (Perea et al., 2011).

We quantify how these effects interact to disrupt seed dispersal in proximity to a major road bisecting Shennongjia World Natural Heritage Site in Central China. We apply the “Seed dispersal effectiveness (SDE)” framework, developed by Schupp et al. (2010, 2017), which provides an informative ecological metric for evaluating seed predation and dispersal, calculated as the product of the probability of seed removal and seed survival given removal. Greater SDE for any given tree implies more seedling recruitment (Schupp et al., 2017), working under the assumption that seeds left un-dispersed under the parent tree are unlikely to recruit successfully (Kellner et al., 2016). We focus here on the Chinese beech (*Fagus engleriana*) nut-rodent system, where rodents act as conditional mutualists because they both predate and disperse nuts (Chen et al., 2017c). Some nuts encountered by rodents are eaten immediately, whereas others are dispersed and cached, which potentially promotes germination and survival compared with un-dispersed nuts, if the cached nuts are not recovered (Lichti et al., 2017). By tracking seed (henceforth

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nut) fate in three transects at distances to the road (10 m, 100 m and 200 m), we test the prediction that road disturbance could (i) promote nut dispersal and SDE due to greater rodent presence caused by either ‘bottom-up’ and/ or ‘top-down’ ecological processes (Carthew et al., 2013; Downing et al., 2015; Hunter and Price, 1992), and/ or (ii) depress nut dispersal distance due to the response of animal nut dispersers to disturbance (Ascensão et al., 2015); conditions that would lead to high *F. engleriana* recruitment (Suárez-Esteban et al., 2013a, 2013b). Finally, given the critical role of rodents in seed dispersal (Chen et al., 2017b; Lichti et al., 2017; Perea et al., 2011), we consider the implications of our findings in terms of ecological engineering and the sustainable development of transport infrastructures to accommodate and mitigate this novel road-side anthropogenic ecosystem (Ibisch et al., 2016).

2. Materials and methods

2.1. Study area and study species

Shennongjia World Natural Heritage Site (SNWHS, 31°19′4″ N，110°29′44″ E) is a globally significant biodiversity hotspot (Myers et al., 2000; Zhou et al., 2017), characterized by montane evergreen and deciduous broad-leaved mixed climax forest vegetation, dominated by *Quercus* spp., *Castanea* spp., *Cyclobalanopsis* spp. and *Fagus* spp (Chen et al., 2017c). With rugged terrain and topography, elevation ranges from 420 m in the deepest gorges to 3,106 m at Shennong Peak, the highest mountain in central China. National Road 209 bisects SNWHS, impeding species movement, habitat connectivity and ecosystem functions (Zhou et al., 2017). When first constructed in 1966, this was a 4.5-7.5 m wide gravel road, but it was upgraded to a paved (bitumen) standard road (Grade II of the Chinese National Road classification) in 1990, and then re-paved with bitumen-based asphalt in 2001 due to a substantial increase in traffic (Zhou et al., 2017; Zhu, 2011). There is only a single

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lane of traffic in each direction, with no barrier dividing opposing lanes. During our study period, traffic volume averaged ca. 42 vehicles (mainly trucks and cars) per hour (Zhou Y., unpublished data).

For our experiments, we selected three replicated sites, 3-5 km apart along stretches of National Road 209 that comprised homogeneous patches of Chinese beech forest, reaching heights of up to 25 m (Cui et al., 2016), which were subject to little non-road related human disturbance (Zhou et al., 2017; Zhu, 2011). The Chinese beech is monoecious and flowers from mid-April to mid-May. Nuts develop within bristly involucres (i.e., mature fruits; Fig. A.1), which grow from wind-pollinated catkins. Mature nuts are shed during the autumn, from late September to late October. Similar to other member of the genus *Fagus* (Jensen, 1985; Zwolak et al., 2016), scatter-hoarding rodents are key nut predators and dispersers of *F. engleriana* (Cui et al., 2016). Nuts typically have a high germination rate (65%; Zhou Y., unpublished data), although seedlings undergo high mortality; for example, Guo (2003) reported that almost all seedlings were dead within 12 weeks in a forest site in southwestern China.

In our study area, 31 species of Rodentia have been recorded, of which many rely on tree seeds and nuts as important food sources (Chen et al., 2017c). Of these, at least five species from genera *Apodemus*, *Niviventer*, and *Leopoldamys* disperse beech nuts (Chen et al., 2017c; Cui et al., 2016). Informed by previous research on rodent distributions in habitat adjacent to roads (Zhang, 2014), in each of the three replicated sampling sites we delineated three transects at 10 m, 100 m and 200 m from the road edge, along which we conducted surveys of beech nut fate. All transects were 150 m long and parallel to the road edge.

2.2. Seed dispersal and predation

During the first week of October 2014, we collected beech nuts from 40 fruiting trees, and then discarded empty and insect-damaged seeds using water

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floatation and visual inspection (Chen et al., 2017b, 2017c). In the second week of October, we used 50 of these nuts to provision each of three stations positioned 50 m apart along each transect line, replicating this experimental set-up at all three sampling sites. In total, 1350 seeds were offered (3 sites × 3 transects × 3 stations × 50 seeds). Each nut was labelled with a numbered white plastic tag (length × width: 3.6 × 2.5 cm) attached by a 100 mm long and 0.3 mm wide stainless-steel wire, which allowed us to track the exact fate and spatial dispersal pattern of each nut (Chen et al., 2017c; Cui et al., 2016).

Beech nuts are known to typically be removed by rodents within a distance range of 5 m, with very few nuts dispersed farther than 10 m (up to 15 m) at our site (Cui et al., 2016) and other study sites (Jensen, 1985; Zwolak et al., 2016). To cover this search radius area amply, we therefore tracked the fate of tagged nuts daily within a 25 m radius surrounding each provisioning station, over the four weeks after provisioning. We then repeated this protocol once per week over the following four week period. We marked cache sites with wooden sticks (50 cm × 0.5 cm) to allow easy re-identification, and recorded the hoarding category involved (i.e., scatter- or larder-hoarding: Chen et al., 2017c; Cui et al., 2016; Vander Wall and Jenkins, 2003). When a rodent subsequently removed a nut from a marked cache, the search radius was increased to 40–50 m until we had searched ~25 m beyond all nuts discovered. In the following summer (July, 2015), we re-checked all cache sites to determine whether remaining nuts had survived and germinated. In the summer of the third year (July, 2016), we re-checked germinating seeds to determine whether seedlings had established from tagged nuts. For all provisioning sites along transects within 10 m from the road, we also searched for nuts potentially transported across the road, repeating the same protocol as described above. In total, we found 97.42% of tags originally tethered to nuts, and all nuts and nut fragments distributed within 11 m of the provisioning stations (see *Results*).

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Based on previous studies (Chen et al., 2017c; Cui et al., 2016; Wang et al., 2013), nut fate was first categorized in terms of survival (left intact *in situ*), eaten *in situ* (nut fragments with dental marks found; tag remained), or removed (Fig. 1). Removed nuts were further categorized as cached (i.e., buried in the surface soil or covered with leaf litter), eaten elsewhere (ex situ), or missing (tag not found). We recorded the tag number of each recovered nut and measured the distance (in centimetres) to the provisioning station of origin.

2.3. Consequences for Fagus engleriana *population density*

To assess *F. engleriana* population density, we identified, mapped and measured all *F. engleriana* individuals through 20 × 20 m plots centred on each nut provisioning station in each of the three replicated sampling sites along transects at 10 m, 100 m and 200 m from the road edge. We defined seedlings as individuals less than 50 cm tall, including individuals that had retained cotyledons and older individuals. Saplings were defined as individuals up to 10 cm diameter at breast height (DBH), and adults as trees larger than 10 cm DBH (Jansen et al., 2014).

2.4. Data variables and analysis

Based on the nut fate data, we analysed the effects of transect distance from the road using five metrics: (i) the proportion of nuts removed from each provisioning station (including nuts that were cached and eaten after removal), (ii) the proportion of nuts cached among removed nuts, (iii) time (days) after which nuts were removed, along with the number of nuts cached after removal (i.e. primary caches), (iv) seed (nut) dispersal effectiveness (SDE) (see below), and (v) the dispersal distance of nuts removed and cached. These parameters indicated the probability of nuts being dispersed from the source to other sites, with the potential for nut germination and further seedling establishment (Chen et al., 2017c; Kellner et al., 2016).

Metrics (i) and (ii) were recorded as binary data, and fitted to the generalized

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linear mixed models (GLMM) with a binomial distribution (the ‘*lme4*’ package in R). The timing of nut transportation (i.e. metric iii) was analysed using survival analysis with a Weibull distribution (the *survreg* function in the ‘*survival*’ package in R), which allows for the inclusion of censored cases, i.e., those in which nut fate was not recorded during the monitored timeframe (Kleinbaum and Klein, 2006). Distance parameters (log-10 transformed to meet assumptions of the statistical models) were analysed using the linear mixed models (LMM).

For metric (iv), SDE was estimated as the product of the probability of nut removal (ρ) and the probability of nut caching (ψ_ρ) (Chen et al., 2017c; Kellner et al., 2016; Schupp et al., 2010). With seed dispersal by scatter-hoarding rodents, SDE relating to the qualitative probability of being cached, rather than consumed immediately, can be substituted by the ‘quality of seed treatment in mouth and gut’ (Gómez et al., 2008; Schupp et al., 2010). We simulated 1000 posterior estimates of ρ and ψ_ρ from the fitted models for each stratum (i.e., distance to the road). We then calculated the product of each pair of simulated probabilities to yield a posterior distribution for SDE. Significant differences in SDE among different distances to the road and between years were tested by bootstrapping a 95% confidence interval (CI) for the difference between strata means, and then determining if these intervals overlapped zero (Kellner et al., 2016).

F. engleriana population density in relation to transect distance from road was tested using GLMMs, applying a Poisson distribution with the number of adults, saplings and seedlings found per 20 × 20 m plot (standardized by plot area, as above) as the response variable.

The use of the mixed models allowed us to model non-normal variables as well as to introduce random factors in order to account for spatial and environmental heterogeneity, in addition to potential individual effects that might influence our results (Suárez-Esteban et al., 2013b, 2014). Specifically, we included the

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provisioning stations and the plots (nested within the sampling site) as random factors for seed dispersal and recruitment models, respectively. Transect proximity to the road was included as a fixed factor in these models. Multiple comparisons among transects were made using the Tukey's HSD multiple comparison tests for GLMMs, LMMs and survival analysis. All statistical analyses were performed in *R* version 3.3.1 (R Development Core Team, 2016).

3. Results

3.1. Nut dispersal and fate

Of the 1350 nuts provisioned in the field experiments, wild boar (*Sus scrofa*) ate almost all nuts at 3 of the 27 feeding stations (one station on a transect at 100 m from the road edge and two stations on the transect at 200 m); this supports that more nuts may be eaten by wild boar (and potentially by other ungulates) away from roads than in close proximity, and thus more nuts could be dispersed close to roads. Our analyses therefore apply to the dispersal of the remaining 1200 nuts from 24 feeding-stations. We retrieved 97.42% (1169/ 1200) tags originally tethered to nuts, of which 1043 tags remained in situ, but the nut each was attached to had been eaten by rodents. Only 154 (12.83%) nuts were removed from provisioning stations, among which 96 (62.34%) nuts had been eaten and 31 (20.13%) nuts had gone missing, with just 27 (17.53%) nuts remaining at primary caches, illustrating the extremely high rate of nut predation involved in forest systems. Of these, two nuts subsequently remained at secondary caches (one from a transect at 10 m from the road, the other from a transect 100 m away) (see Fig. A.2 for details).

Road proximity had significant effects on both ρ, the probability of nuts removed ($p < 0.001$; Table 1, Fig. 2a), and $\psi_{\rho,}$ the probability of nuts cached ($p = 0.016$; Table 1, Fig. 2b). More nuts were removed by rodents from transects at 10 m

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from the road compared to transects 100 and 200 m away (Tukey's HSD, $p < 0.001$ in both cases). For nuts that were removed, there was a higher cache detection probability (i.e., more found) at transects 10 m (marginally significant Tukey's HSD, $p = 0.042$) and 100 m ($p = 0.093$) from the road compared with transects 200 m away (Table 1). 83.12 % (128) of nuts removed and 77.78 % (21) of nuts cached were dispersed during the first two weeks. Time to nut removal, but not time to nut caching, differed significantly among transects (Table 1). Nuts were removed more quickly from transects at 10 m from the road than from transects 100 m away (but not transects 200 m away; Table 1) (Fig. 3).

Mean SDE (mean ± se) was 0.028 ± 0.017 across all transects within the three sampling sites. However, SDE was significantly higher in transects at 10 m (8.607 times greater) and 100 m (5.609 times greater; Fig. 4) from the road compared to transects 200 m away (mean differences [D]: 0.042, CI: 0.019 - 0.068, and 0.026, CI: 0.011 - 0.042, respectively); although no statistical significance was detected between transects at 10 and 100 m from the road (D: 0.016, CI: -0.011 - 0.045; i.e., the 95% bootstrap CI did not overlap zero in all cases). These findings suggest that nut dispersal was promoted by proximity to the road effect zone in the study system.

In the following summer (July), only one nut remained at a provisioning station along any of the transect types, which finally deteriorated due to pathogens. Six nuts survived and germinated; five in primary cache sites (3 at transects at 10 m from the road, and 2 at transects 100 m from the road) and one in a secondary cache sites at a transect 10 m from the road. However, none of these survived and established as seedlings in the summer (July) of the third year (Fig. A.2). These findings support our contention that road proximity may facilitate seedling recruitment.

Dispersal distances ranged from 0.50 to 11.00 m for nuts removed (mean ± se: 2.04 ± 0.16 m), and 0.90 to 4.90 m for nuts cached (2.02 ± 0.21 m). There was also a significant effect of transect distance from road on removal distances ($p = 0.002$)

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and cached distances ($p = 0.028$; Table 1). At transects 10 m and 100 m from the road, nuts were removed over shorter distances (Tukey's HSD, $p < 0.013$ in both cases; Table 1 and Fig. 5) compared with transects 200 m away; i.e., 46.62% and 32.15% respectively. The effect on the distance of nuts cached was, however, only significant when comparing transects 10 m from the road with transects 200 m away (Tukey's HSD, $p = 0.012$; Table 1 and Fig. 5).

3.2. Consequences for Fagus engleriana *population density*

We counted a total of 703 *F. engleriana* individuals (405 adults, 261 saplings and 37 seedlings) across 27 400-m^2 plots. Significant differences in densities of adult trees and saplings were evident among the three transects ($p < 0.024$ for both stages of development); with marginal differences ($p = 0.071$) in seedling density (Table 1). The densities of adult trees and saplings along transects 10 m from the road were higher than those along transects 100 and 200 m away, while seedling densities along transects at 10 m were higher than those at transects 200 m away (Fig. 6). This suggests that road proximity-related factors promote *F. engleriana* population density in the road-effect zone.

4. Discussion

Only 154/1350 nuts provisioned were dispersed, highlighting the scale on which this type of investigation must be undertaken, where seed/ nut caching, germination and seedling establishment rates are typically extremely low in natural forests (Lichti et al., 2017; Nathan and Muller-Landau, 2000). Our experiments revealed that more nuts were dispersed from transects in closer proximity to the road, but over shorter distances (supporting hypothesis ii), leading to a significant positive effect of road proximity on seed (nut) dispersal effectiveness (SDE) (supporting hypothesis i). Corroborating this, we found higher densities of adult trees, sapling and seedlings closer the road, indicating that the road-effect zone supported greater

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F. engleriana population density.

High SDE for a plant species typically implies greater recruitment success (Kellner et al., 2016; Schupp et al., 2010). Within this framework, however, we identified two contrasting (and possibly counteractive) effects of road proximity on plant reproductive performance. On the one hand, we found that a greater numbers of nuts were dispersed from the transect 10 m from the road. This largely obviated any other limitations on dispersal (Jansen et al., 2014) with more nuts arriving at potentially suitable germination sites away from the shade of parent trees (Hirsch et al., 2012; Wenny and Levey, 1998). Conversely, however, short nut dispersal distances along transects closer to the road did not support a benefit to plant recruitment. This contravenes the Janzen-Connell model (Connell, 1971; Janzen, 1970), where short dispersal distances result in nuts remaining closer to their parent tress, which is posited to lead to higher seed mortality rates due to host-specific natural enemies, such as granivorous insects, rodents and pathogenic fungi, being attracted (Swamy and Terborgh, 2010). This effect can, however, be counteracted somewhat when more rapid dispersal tends to enhance seed (nut) survival probability (Jansen et al., 2014). Furthermore, although we found that rodents scatter-hoarded nuts, nuts still ended up with a clumped (rather than homogeneous) distribution, because the dispersal distances involved were so short (typically < 10m). Ultimately, therefore, the number of nuts we found translocated to suitable germination sites was small (Jansen et al., 2014).

Large ungulate seed dispersing species tend to avoid activity in road effect zone areas altogether, thus taking seed away from the road-edge zone (Suárez-Esteban et al., 2013a). Interestingly, we noted that no tagged nut were eaten by wild boar at provisioning stations along transects 10 m from the road, whereas nuts were eaten by boar at one station on a 100 m distant transect and at two stations along 200 m distant transects; this suggests that ungulates may avoid road proximity, leaving seed

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dispersal primarily to rodents.

In our study, the cutting in which the road was constructed imposed a 5.5-8.5 m wide break in canopy cover. It was built through Shennongjia by blasting away rock, resulting in numerous rock piles extending up to 150 m into roadside habitat (Zhou et al., 2017; Zhu, 2011). Such habitat is known to provide shelter for rodents (Garden et al., 2007); indeed disturbed road-side habitats generally seem to promote the clustering of zoochorous seed dispersing rodents (Bagchi et al., 2018; Harrison et al., 2013; Pérez-Méndez et al., 2018). As evidenced by our survey showing higher nut and seedling recruitment closer to road, rodents living in such conditions appear to disperse nuts disproportionately back toward their burrows along the road edge (Fig. 6). Maintaining rodent mediated seed dispersal may therefore be of under-realised importance in such disturbed sites, where restrictions on traffic speed and signage to promote vigilance among motorists may prove beneficial. Importantly, any road disturbance effect on the seed disperser community may ultimately influence plant population dynamics over large spatial scales, where greater clustering could hinder seed-mediated gene flow among plant populations and cause reduced population connectivity by imposing substantial limitation on nut dispersal distance (Bagchi et al., 2018; Pérez-Méndez et al., 2018). A finer scale experiment would be needed to corroborate this link, although this would not capture the vegetation effect gradients seen in this study.

Vegetation cover may also be relevant because over the 30 years since initial road construction, canopy cover has re-established at Shennongjia over transect replicates at 10 m from the road edge. We observed a typical response, where rodent seed dispersal function was greater under denser vegetation cover, closer to the road edge (10 m transects), which we infer to be due to a lower real and perceived predation risk (Perea et al., 2011; Cao et al. 2017), tending to cause more rapid seed removal (Fig. 1). The risk of nuts being eaten is, however, proportional to the

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activity of granivorous rodents (Vander Wall and Jenkins, 2003; Wróbel and Zwolak, 2017). Consequently, the likelihood that a proportion of nuts will be cached, to protect them from pilfering by conspecifics (Gu et al. 2017), also tends to increase with the urgency with which nuts are cached under conditions of high competitive pressure, termed the "search time relocation hypothesis" (Macdonald, 1976; Sunyer et al., 2013). This would explain the observed shorter dispersal distances with proximity to the road (Fig. 3). Collectively, to better understand the rodents' decisions and their responses to conspecific competitive pressures and environmental predation risks, it would be interesting (but difficult) to measure the rates at which dispersed seeds are pilfered or recovered by the original cacher.

In summary, our study revealed two contrasting (and possibly counteractive) effects of road proximity on plant reproductive performance. Road proximity promoted seed (nut) dispersal effectiveness, and our surveys also indicated that there was higher *F. engleriana* population density closer to the road. Conversely, short nut dispersal distances closer to the road resulted in nuts remaining closer to their parent trees, potentially inducing more clustering of animal-dispersed seeds that could hinder seed-mediated gene flow within / between plant populations (Bagchi et al., 2018; Harrison et al., 2013; Pérez-Méndez et al., 2018). In disturbed habitats, here represented by the road effect zone, rodents tend to dominate the primary remnant seed disperser community, due to their resilience to anthropogenic disturbance (Chen et al., 2017a, 2017c). Therefore, we propose that roads may have the potential to promote plant recruitment, by hosting incipient plant populations that can act as 'stepping stones' providing a seed source at an intermediate distance between primary habitat areas (Suárez-Esteban et al., 2013a, 2013b). As such, roads may provide plant migration routes in response to accelerated anthropogenic climate change, enhance connectivity between otherwise isolated populations, and promote plant species richness at large spatial scales (Suárez-Esteban et al., 2016). With road

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infrastructure development so closely tied to human population growth (Ibisch et al., 2016; Laurance et al., 2014), long-term comprehensive studies are therefore necessary 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 (Balmford et al., 2016; Laurance et al., 2015).

Conflict of interest

None.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version.

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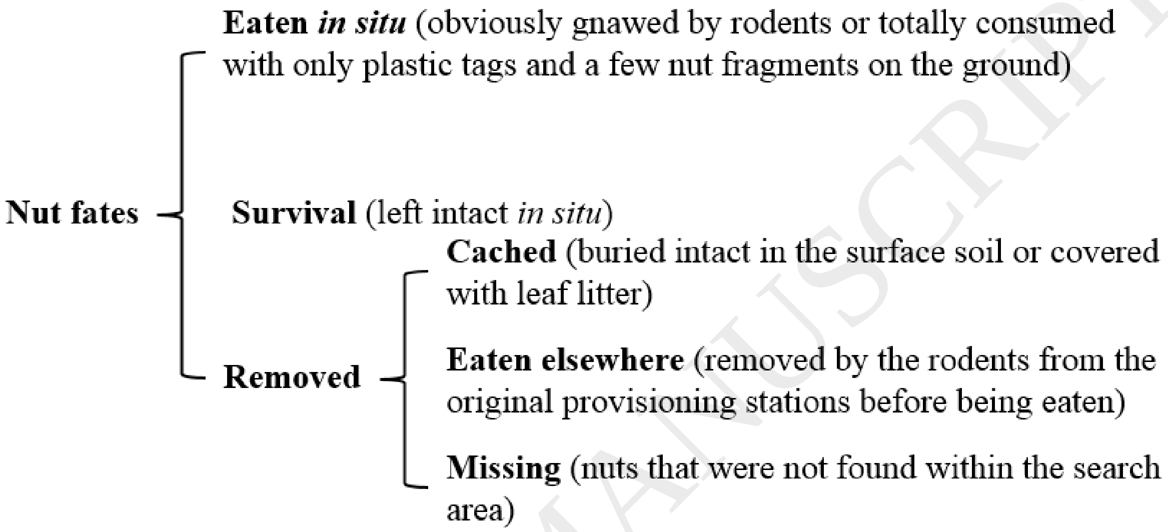
Figure legends

Fig. 1. Definitions of different nut fates during the scatter-hoarding nut-dispersal process.



Nut fates

Eaten *in situ* (obviously gnawed by rodents or totally consumed with only plastic tags and a few nut fragments on the ground)

Survival (left intact *in situ*)

Removed

Cached (buried intact in the surface soil or covered with leaf litter)

Eaten elsewhere (removed by the rodents from the original provisioning stations before being eaten)

Missing (nuts that were not found within the search area)

Fig. 2. The probability of nuts that were removed from provisioning stations (a) and those hoarded at primary caches (b) as a function of distance to road. Error bars show the standard error of the mean.

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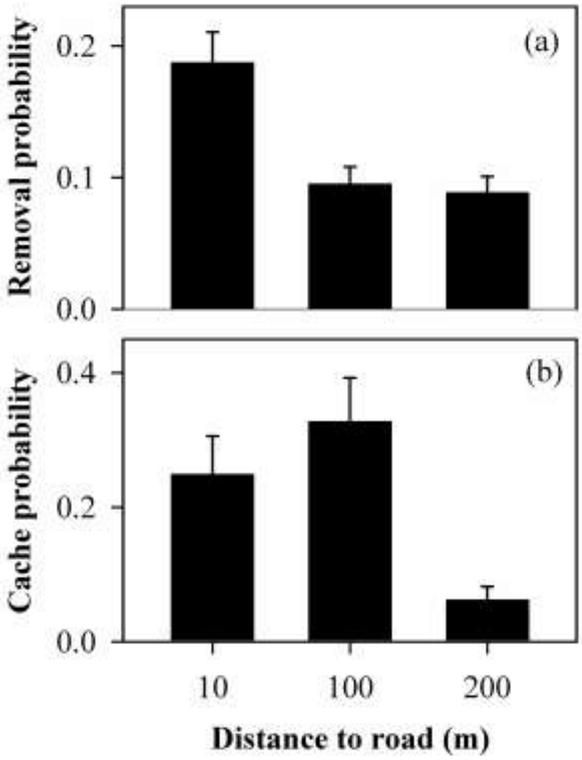

Fig. 3. Survival analysis curves with Weibull distribution, of nuts remaining at seed provision stations as a function of distance to road.

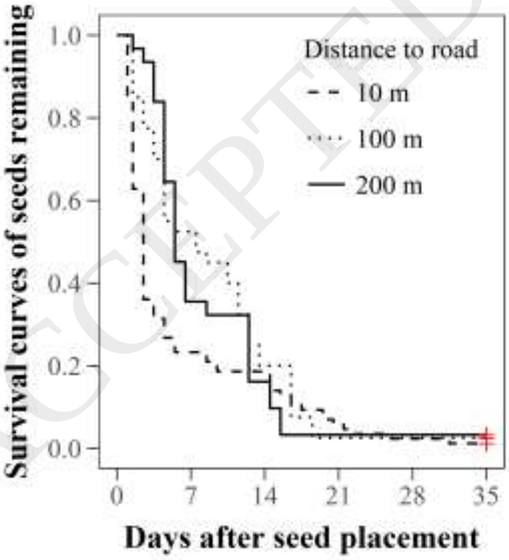

Fig. 4. Seed dispersal effectiveness (SDE, the product of the quantitative component [the probability of nut removal] and qualitative component [the probability of nut

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caching] of seed dispersal, Schupp et al., 2010; 2017) as a function of distance to road. Error bars show the standard deviation of the mean.

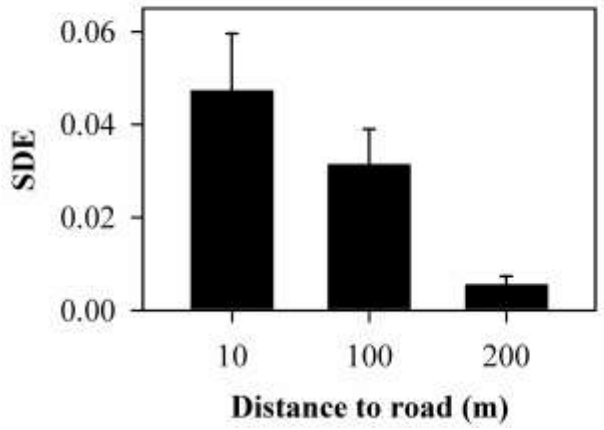

Fig. 5. Dispersal distance for nuts that were (a) removed from provisioning stations and (b) cached at primary caches as a function of distance to road.

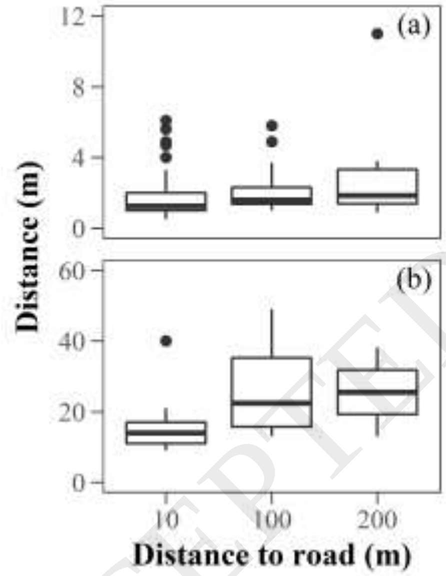

Fig. 6. Adults, saplings and seedlings density of the Chinese beech (*Fagus engleriana*) as a function of distance to road.

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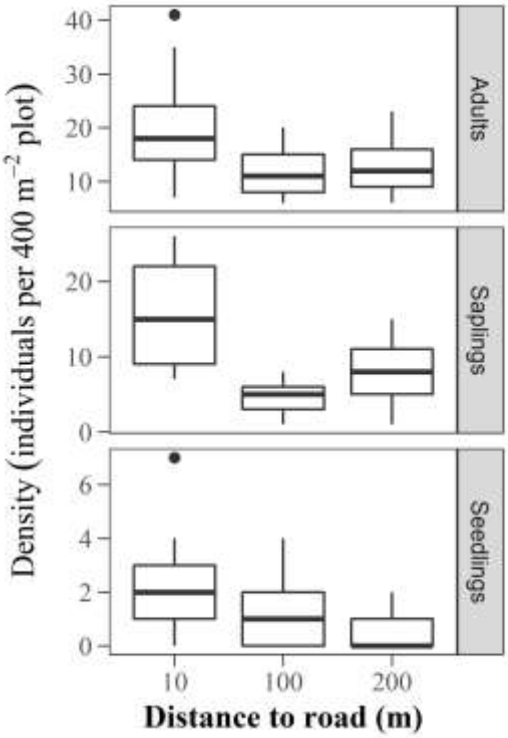

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Table 1

Statistical results from GLMMs, LMMs and survival analysis with Tukey's HSD multiple comparisons testing the effects of road disturbance on the metrics of nuts dispersal and density of the Chinese beech (*Fagus engleriana*) individuals. Fixed factors in bold indicate significant differences ($p < 0.05$).

Fixed factors	Distance to road		Tukey's HSD multiple comparison (*p*-values)		
	χ^2	p	10 - 100 m	10 - 200 m	100 - 200 m
Probability of nuts dispersed					
Nuts removed	**22.280**	**< 0.001**	**< 0.001**	**< 0.001**	0.952
Nuts cached	**8.328**	**0.016**	0.681	0.093	**0.042**
Time to nut dispersal					
Nuts removed	**7.527**	**0.023**	**0.050**	0.109	0.994
Nuts cached	2.317	0.314			
Nuts dispersal distance					
Nuts removed	**12.306**	**0.002**	0.556	**< 0.001**	**0.012**
Nuts cached	**7.125**	**0.028**	**0.012**	0.896	0.611
Density of *Fagus engleriana* individuals					
Adults	**8.821**	**0.012**	**< 0.001**	**< 0.001**	0.936
Saplings	**7.514**	**0.023**	**< 0.001**	**0.010**	0.308
Seedlings	5.291	0.071	0.177	**0.005**	0.286

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