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Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles

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ABSTRACT

Aim To determine seed retention rates on vehicles as a function of distance driven, road surface, weather condition and seed location on the vehicle undercarriage.

Location Montana, United States.

Methods Metal plates were covered with a seed-soil slurry, dried and attached to different locations underneath a vehicle. The vehicle was then driven on paved and unpaved roads under both wet and dry conditions. Plates were removed from the vehicle at seven distances between 4 and 256 km. The number of seeds remaining was determined. Four general models were assessed to explain observed seed retention.

Results Under dry conditions, seed retention rates were high on both unpaved and paved roads, with 86–99% of the seeds remaining at 256 km. Under wet conditions, lower rates of seed retention were observed for both road surfaces: 0.3–80% of seeds were retained at 256 km on paved wet roads and 50–96% of seeds were retained at 256 km on unpaved wet roads. Plate location had a significant effect on seed retention under certain road surfaces and conditions, with loss generally being highest from the wheel wells. Of the statistical models compared, a double exponential model explained the most variation in seed retention.

Main conclusions Vehicles act as vectors of long-distance dispersal. Seed adhered to vehicles can be retained for hundreds of kilometres under dry conditions. When wet conditions occur, a greater proportion of seeds will be dispersed shorter distances. Consequently, vehicle seed dispersal has implications for plant invasions and species migration rates, and those concerned with prevention and control of non-native plant invasions should consider vehicle seed transport when developing management strategies and plans.

Keywords
Human-mediated dispersal, long-distance dispersal, non-native plant invasions, seed dispersal, seed retention curves, vehicle dispersal.

INTRODUCTION

Seed dispersal is a complex process that crucially influences species migration rates, metapopulation dynamics, plant invasions and community assembly (Puth & Post, 2005). Although difficult to quantify, long-distance dispersal (LDD) is important (Nathan, 2006), spreading the fewest seeds but distributing seeds, and their genetic material, the most widely (Portnoy & Willson, 1993), thus contributing to genetic connectivity (Trakhtenbrot *et al.*, 2005). LDD occurs through a variety of vectors including humans, wind and animals. LDD has been found to contribute to plant invasions and influence species distributions (Shigesada *et al.*, 1995; Higgins & Richardson, 1999; Trakhtenbrot *et al.*, 2005; Engler & Guisan, 2009) by accelerating range expansion (Shigesada *et al.*, 1995). When even a small proportion of available seeds

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(0.001) experience LDD (1–10 km), the predicted plant migration rate can increase by an order of magnitude (Higgins & Richardson, 1999). Major threats to global biodiversity include excessive LDD of non-native species and inadequate LDD of certain native species, demonstrating the importance of considering LDD for conservation purposes (Trakhtenbrot *et al.*, 2005).

Introduction events and pathways greatly influence plant invasions (Wilson *et al.*, 2009; Essl *et al.*, 2010; McDougall *et al.*, 2011) and the non-native species composition in a region will reflect the dominant introduction pathway (McDougall *et al.*, 2011). Human-mediated introduction pathways often cause more rapid dispersal in the new range than natural pathways because they generally initiate multiple introductions to multiple locations across a large area; post-introduction anthropogenic activities such as transportation along roads, railways and waterways then ensure high spread rates (Wilson *et al.*, 2009). Studies have found that in mountain ecosystems, the non-native species at higher elevations are a subset of the same species found at lower elevations, suggesting that non-native plants are spreading upwards from anthropogenic centres in valleys as road construction and human activity in mountain areas increase (Pauchard *et al.*, 2009; Alexander *et al.*, 2011; McDougall *et al.*, 2011). These results also imply that certain non-native species have large ecological amplitude and the only factor preventing their invasions into mountain ecosystems is dispersal limitation (Alexander *et al.*, 2011). To protect areas with high conservation value, it is necessary to understand and quantify how humans and other vectors are spreading seeds into less-invaded areas.

While hikers and their clothing or equipment can directly cause significant seed dispersal, their vehicles have been recorded to transport even more species (Pickering & Mount, 2010). Seeds of many different species (33–88 species, Lonsdale & Lane, 1994; Zwaenepoel *et al.*, 2006) have been found on passenger vehicles in varying quantities (1–135 per vehicle, Lonsdale & Lane, 1994; Zwaenepoel *et al.*, 2006; Veldman & Putz, 2010). In addition, seed traps placed in highway tunnels collected seeds from 204 species: of which, 50% were non-native and 32% came from species not found within 100 m of the tunnel entrances; however, exact distances travelled by the seeds were not quantified (von der Lippe & Kowarik, 2007). Seed spread has been measured specifically for combine harvesters with dispersal distances of up to 130 m recorded (Ballare *et al.*, 1987; McCanny & Cavers, 1988; Rew *et al.*, 1996; Blanco-Moreno *et al.*, 2004). Thus, these studies suggest that vehicle dispersal plays an integral role in the invasion of many plant species.

Roads are becoming increasingly pervasive around the world, with seven nations each containing more than one million kilometres of roads and other nations nearing that mark (Anon., 2009). While a range of statistical models have been used to describe seed dispersal and retention (for review see Cousens *et al.*, 2008; Pickering & Mount, 2010; Bullock *et al.*, 2011), no study has addressed seed dispersal distances by passenger vehicles. Dispersal distances have only been measured for agricultural equipment (Ballare *et al.*, 1987; McCanny & Cavers, 1988; Rew *et al.*, 1996; Blanco-Moreno *et al.*, 2004), which have different patterns of movement and are used in different habitats than most other vehicles. Therefore, the aim of this study was to evaluate the distances seeds were retained on a passenger vehicle and determine which factors have the greatest influence on this distance. Here, we (1) evaluated four general curves to empirically model these LDD data and (2) determined the effect of road surface (paved vs. unpaved), weather condition (wet vs. dry) and location of seeds on a four-wheel drive vehicle, on seed retention distances.

METHODS

Study sites

Sections of paved and unpaved roads (henceforth referred to as transects) were driven to assess seed retention over distance between May and October, 2010 and May 2011 when the appropriate weather conditions existed. The paved transects were driven on a 143 km section of road from Bozeman, MT (45°40′N, 111°03′W) to Alder, MT (45°19′N, 112°06′W). The unpaved transects were driven on a 35 km section of improved gravel road on Dry Creek and Sixteen Mile Creek Roads beginning 13 km north of Belgrade, MT (45°46′N, 111°10′W). Sections of unpaved roads particularly tend to be relatively short, and it was not possible to find longer suitable transects of continuous paved or unpaved road surfaces in our area, consequently, to achieve the desired distances, some sections of each transect were driven more than once.

Seed retention plates

To facilitate homogenous application of seeds and accurate quantification of seed loss, removable plates were used. A retention frame was constructed and mounted to the chassis of a 2004 Ford Ranger 4 × 4 truck. Aluminium plates were fabricated and spray painted with the same textured rust-resistant paint used on passenger vehicles. Plates were made to attach to the undersides, front and rear bumpers, and wheel wells of the truck. For the undersides and bumpers, 16 smooth featureless plates and 16 featured plates (all 0.1 m^2, with featured plates containing grooves and an overhanging lip) were fabricated to represent the underside of passenger vehicles (see Fig. 1). The plates were bolted to the frame underneath the truck. Wheel well plates were smaller (0.05 m^2) and had a smooth surface to mimic mud flaps and to fit within the space available. There were eight smooth wheel well plates, to provide two sets. These plates were also bolted to the vehicle but vertically (Fig. 1).

Figure 1 The plate retention system showing the (a) rear bumper with a featured plate on the left, and a smooth plate on the right, and, (b) driver side of the truck. The three plate locations were (i) bumper, (ii) wheel well and (iii) underside.

Field trials

A slurry containing a known amount of soil (55% sand, 26% silt and 19% clay), water and seed was applied to the aluminium plates. The slurry mixture contained: 850 g of soil and 340 ml of water for featured plates, 750 g soil and 300 ml water for smooth plates, and 375 g soil and 150 ml water for wheel well plates. It was necessary to alter the amount of soil added to the plates to keep the depth of soil (0.5 cm) on the plate constant because of differences in plate size and texture. The slurry for each plate contained 90 seeds/caryopses (hereafter termed seed) total, 30 each of *Triticum aestivum* L., *Brassica napus* L. and *Elymus trachycaulus* (Link) Gould ex Shinners. These species were chosen to provide a representative range of seed sizes, weights and morphologies found on vehicles, and owing to the low potential landscape impact associated with their experimental dispersal. *T. aestivum* seeds were large, heavy (38, SD 2.0 mg) and oblong; *B. napus* seeds were small, light (4.7, SD 0.26 mg), smooth and round; and *E. trachycaulus* seeds were light (2.7, SD 0.14 mg), long and thin. All seeds were sprayed with waterproof, fluorescent orange paint ('Glo Spray Fluorescent' by Ace, Oak Brook, IL, USA; Wichmann *et al.*, 2009), which aided in identification during the sample processing phase because the seeds were easy to distinguish from similarly sized pebbles. The seed and soil-substrate was applied evenly to plates laid horizontally with a spatula, and these plates were air-dried for 40 h or until a constant weight was achieved. Plates were then transported to the beginning of the study transects in plastic boxes with lids and wooden frames attached inside to prevent plate movement and minimize seed loss during transportation.

At the start of each transect, 20 plates were attached to the frame underneath the vehicle. Two plates were mounted below the front bumper, two below the rear bumper, six on each side of the vehicle between the wheel wells and one in each wheel well; the type of plate (featured or smooth) was randomized. To quantify the effect of distance driven, road surface and weather condition on seed retention, four transects were driven for each road surface/weather condition combination (paved dry, paved wet, unpaved dry and unpaved wet). Initially, we drove one transect of each type to 128 km, but owing to large data variability at longer distances, we increased the transect length to 256 km for all future transect replicates. On each transect, plates (two undersides, one bumper and one wheel well) were removed from the truck at seven distances (4, 8, 16, 32, 64, 128 and 256 km) and placed in a plastic bag and box for transportation back to the laboratory. The exact location of the plates removed at each distance was randomized within general plate locations. As the number of slots on the frame was limited, some plates were attached after others were removed to achieve all distances. Owing to logistic constraints, the number of replications in each treatment varied and this was accounted for in the analysis. The truck was driven at a constant speed, to the extent possible, on the different road surfaces averaging 65.97 km h^{-1} on paved transects and 42.73 km h^{-1} on unpaved transects. Once in the laboratory, the plates were dried and weighed. The substrate was then scraped off the plates and run through a set of sieves to separate seeds from the soil mixture. Seeds were then counted.

Three control measures were completed to quantify the experimental bias and variability attributed to these procedures. Control 1 measured seed loss due directly to soil and seed application and removal from the plates. This control was performed for each plate type (smooth, featured, wheel well) and replicated three times. A mean of 88.9 (SD 1.3) seeds were recovered. Control 2 determined how many seeds were lost during the plate mounting process. This control was repeated 12 times for each type of plate. A mean of 89.2 (SD 1.1) seeds were recovered. Control 3 tested for seed loss owing to transportation of plates and boxes to and from the transect start. There were three replicates of each type of plate. A mean of 89.6 (SD 0.79) seeds were recovered. Thus, seed loss for the different steps of the experimental protocol was low and did not differ by plate type (smooth or featured for underside and bumper plates) or by species. Thus, we pooled data for plate type and also species for all further analyses.

Seed retention modelling

A review of the seed dispersal and retention literature provided models that described animal (Manzano & Malo, 2006; Bullock *et al.*, 2011), human (Wichmann *et al.*, 2009) and wind (Clark *et al.*, 1999) seed dispersal and retention patterns. We observed that the seven seed retention and dispersal models used in these studies are special cases of three general models. The first general model incorporated simple exponential and power exponential functions (*sensu* Taylor, 1978; Wichmann *et al.*, 2009) to take the form:

$$\mathrm{sd}(d) = e^{b \times d^{g}} \qquad \text{(Model 1)}$$

where sr indicates the proportion of seeds retained, d is distance for all models, and b, c and g are parameters controlling the shape and scale of the models. The second was a double exponential (*sensu* Wichmann *et al.*, 2009; Bullock *et al.*, 2011) of the form:

$$\mathrm{sr}(d) = e^{b \times e^{c \times d^{g}}} \qquad \text{(Model 2)}$$

The third model encompassed both wind dispersal (Clark *et al.*, 1999) and animal retention (Manzano & Malo, 2006) models and took the form:

$$\mathrm{sr}(d) = (b \times d^{g+1})^{c} \qquad \text{(Model 3)}$$

We also tested a linear model as visualizations of the data only partially supported curvilinear relationships. The linear model took the form:

$$\mathrm{sr}(d) = 1 + (b \times d) \qquad \text{(Model 4)}$$

To test for the effects of road surface (two levels), road condition (two levels), and plate location (four levels) on seed retention, we varied the b parameter in all four models to estimate a unique b for each of the 16 possible treatments. The other parameters (c and g) were estimated from the data but not allowed to vary between treatments within a model. All models were optimized using nonlinear least squares via the nls function in the statistical package R (R Development Core Team, 2010). The model that best described the mean structure of the data was determined by comparing Akaike Information Criterion (AIC) values and the model with the lowest AIC score was selected (*sensu* Venables & Ripley, 2002). The best model was then used for subsequent analysis.

There was evident heteroscedasticity in the data: variance tended to increase with distance for some treatments. This precluded making inferences assuming errors were Normal $(0, \sigma^2)$. Thus, we adopted a nonparametric bootstrapping procedure to characterize the sample distribution to then look for differences between treatments. Simple random samples with replacement to the original sample size were taken 1000 times, and the model optimized to the resample data at each run of the bootstrap (Davison & Hinkley, 1997). The regression coefficients were recorded at each run and empirical 95% confidence intervals for the mean regression lines for the 16 treatments were constructed from these data.

P-values for all pairwise comparisons of the b coefficients were estimated between the 16 treatments using an inverted hypothesis test (Pawitan, 2001) at decreasing alpha significance levels (1 to 0.000 by increments of 0.001). These were based on empirical data quantiles of the 1000 replicate bootstrap distributions of the test statistics. The alpha-level at which 0 was first included in the confidence interval was defined as the probability that the difference in b coefficients between two treatments was equal to 0.

RESULTS

Evaluation of seed retention models

Four general seed retention models were tested for their ability to approximate mean seed retention for the 16 treatments (two road surface types by two road conditions by four plate locations under the vehicle). Comparison of the four different models found that Model 4 (linear form) was the worst performing, while Model 1 and Model 3 performed much better with the difference in AIC (ΔAIC) between Model 4 and the other two models equal to 253. Model 2 (double exponential) best approximated mean seed retention for the 16 treatments (ΔAIC 262 compared with Model 4; Fig. 2; Table 1). Model 2 allowed for non-plausible values to be attained in some bootstrap replicates (proportion of seed retention >1.0, Fig. 3) and, although this represented a limitation in the model, it did best describe the shape of the retention curves for most of the 16 treatments. The double exponential model was a substantial improvement over Models 1 and 3 (ΔAIC 9) due primarily to the four paved wet treatments. The double exponential allows seed retention rate to vary with distance. In paved wet conditions, seed loss was fast initially but then slowed with greater distances. There were differences in decay function with plate location. Both dry treatments retained near 100% of seeds at 256 km while unpaved wet conditions showed almost linear declines in seed retention with a constant seed dropping rate. Model 2 was subsequently used to test for treatment effects as it best approximated the mean structure of the entire data set.

Effect of road surface, weather condition and seed location on the vehicle

The number of seeds retained across the different plate locations, road surfaces and weather conditions varied from 0 to 90 seeds at 256 km. Much higher rates of seed retention were observed under dry than wet conditions for all plate locations on both paved and unpaved roads (Fig. 2). The most seeds were lost under paved wet conditions and the fewest under paved dry conditions.

The full seed retention model including road surface, weather condition, plate location and all interactions explained 74.5% of the total variation. Road surface and weather condition independently explained similar amounts of the total variation and more variation than plate location alone.

Seed retention was significantly lower under wet than dry conditions on both paved and unpaved roads for underside plates ($P < 0.001$; see Table S1 in Supporting Information for all *P*-values mentioned in the later section). Plates in the wheel wells and front and rear bumpers had significantly lower seed retention under wet conditions on paved roads only ($P = 0.000$–0.006).

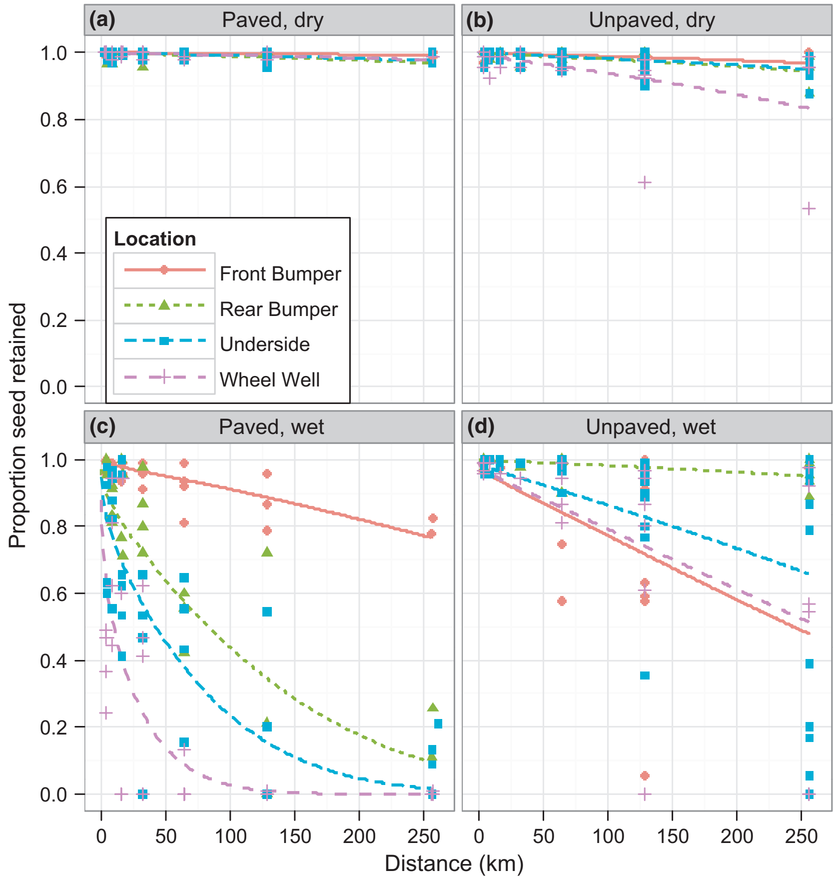

Figure 2 Mean regression lines for seed retention as a function of distance using a double exponential model (Model 2) for paved, dry (a; n = 90); unpaved, dry (b; n = 100); paved, wet (c; n = 109); and unpaved, wet (d; n = 96) road conditions. Plate locations are denoted as: rear bumpers (··▲··), undersides (··■··), wheel wells (+) and front bumpers (–●–). The double exponential model had main effects of road surface, road condition and plate location, with all possible interactions to allow for a unique curve in each of the 16 treatments.

Seed retention was lower on paved roads than unpaved roads under wet conditions for underside, wheel well and rear bumper plates (P < 0.001). Road surface did not have a significant effect on seed retention for front bumpers under any weather condition or for all other plate locations under dry conditions (P = 0.05–0.53).

Under dry conditions on the paved and unpaved roads, plate location did not affect seed retention (P = 0.102–0.968 for all comparisons between locations), which was very high for all locations. On paved dry roads, 99% of seed was retained at 256 km in all locations (Figs 2a and 3a), while on unpaved dry roads, 96% of seed was retained at 256 km in all locations except for the wheel wells, which only retained 86% (Figs 2b and 3b).

Plate location had the greatest effect on seed retention in the paved wet treatment (Figs 2c and 3c). Front bumpers retained the most seeds (80% at 256 km; P = 0.002 for comparisons with rear bumpers, undersides and wheel wells) of the four plate locations with rear bumpers (P = 0.020, 0.002 and P < 0.001 for comparisons with undersides, front bumpers and wheel wells, respectively), undersides (P < 0.001 for comparison with wheel wells) and wheel wells (0.3% at 256 km) retaining progressively less seed with distance (Fig. 3c).

Plate location was also important in explaining seed retention for the unpaved wet treatment, with rear bumpers retaining more seed (95% at 256 km) than front bumpers (P = 0.014), undersides (P < 0.001) and the least in wheel wells (50% at 256 km; P < 0.001; Figs 2d and 3d). Wheel wells exhibited a trend of lower retention with distance compared with undersides; however, there was no statistical evidence for a difference in the mean response (P = 0.358).

Interestingly, the relationship between seed retention and distance at the two bumper locations reversed between the paved wet and unpaved wet treatments. Front bumpers retained more seeds with distance than rear bumpers in the paved wet treatment (P = 0.002; Fig. 3c), whereas rear bumpers retained more seeds with distance than front bumpers in the unpaved wet treatment (P = 0.014; Fig. 3d), although the front bumper data were highly variable under unpaved conditions.

DISCUSSION

Vehicles as vectors of LDD

Vehicles carried seeds over 250 km under dry conditions on both paved and unpaved roads, but under wet conditions, seed loss increased dramatically. These results suggest that seeds could travel very long distances on vehicles along roads until wet conditions are encountered, at which time they will likely be dispersed.

A previous review suggested that 99% of seeds dispersed unintentionally by humans, including vehicles, will travel no more than 5 km (Vittoz & Engler, 2007), although the authors highlighted the lack of data available for human-mediated seed

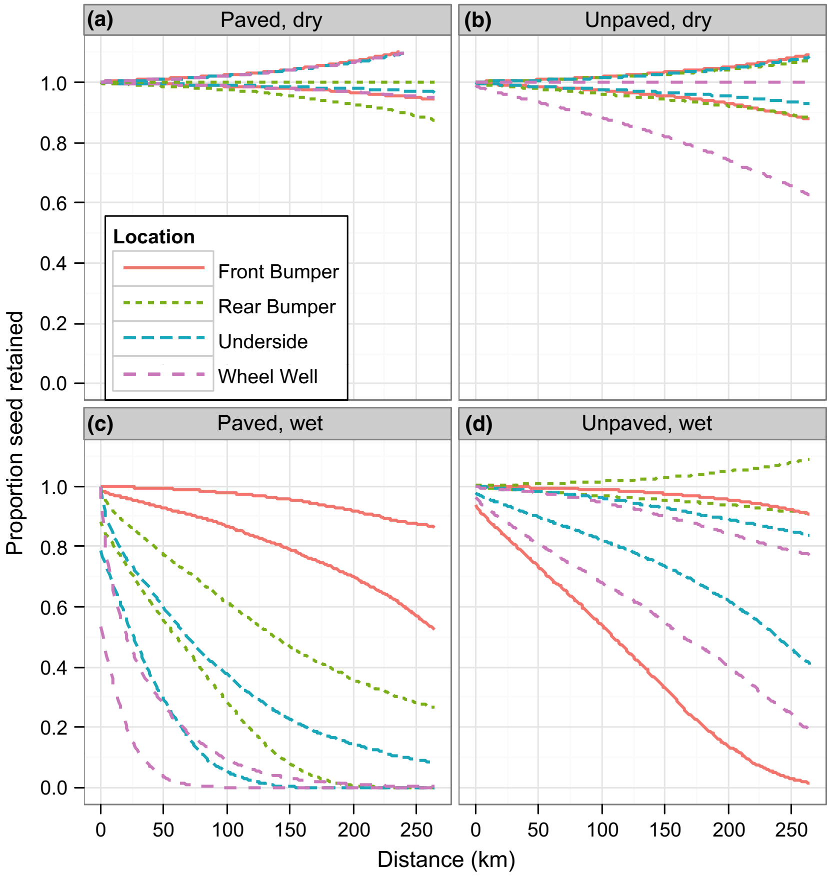

Figure 3 Ninety-five percent bootstrap confidence intervals (n = 1000) for seed retention as a function of distance for: paved, dry (a); unpaved, dry (b); paved, wet (c); and unpaved, wet (d) road conditions. Confidence interval boundaries are delineated for each treatment combination, with red solid (front bumper), green small dash (rear bumper), blue medium dash (underside) and purple long dash (wheel well). The model used to describe these data was a double exponential form (Model 2) with main effects (road surface, road condition and plate location) and all possible interactions to allow for a unique curve in each of the 16 treatments.

Table 1 Coefficient estimates and associated 95% empirical bootstrap confidence intervals from the double exponential model (Model 2) for the 16 treatments. Estimates of b were summarized from a linear combination of dummy coded variables. The other two model parameters were estimated globally for the double exponential model. They were estimated as c = 0.6556 and g = 0.3311.

Surface	Condition	Location	b	Lower	Upper
Paved	Dry	Rear Bumper	−0.000396	−6.05791E−14	−0.0041688
Paved	Dry	Undersides	−0.000305	−8.25884E−13	−0.0010981
Paved	Dry	Wheel Wells	−0.000284	−9.21386E−13	−0.0015458
Paved	Dry	Front Bumpers	−0.000110	6.53538E−14	−0.0012968
Unpaved	Dry	Rear Bumper	−0.000963	−3.08587E−12	−0.0036795
Unpaved	Dry	Undersides	−0.000849	−1.12069E−12	−0.0054627
Unpaved	Dry	Wheel Wells	−0.003027	−1.21977E−12	−0.0124249
Unpaved	Dry	Front Bumpers	−0.000530	2.31312E−04	−0.0057557
Paved	Wet	Rear Bumper	−0.040386	−1.06526E−10	−0.1344666
Paved	Wet	Undersides	−0.071215	−2.57733E−10	−0.2445022
Paved	Wet	Wheel Wells	−0.176874	−4.97052E−10	−0.6069654
Paved	Wet	Front Bumpers	−0.004430	−1.59239E−11	−0.0154153
Unpaved	Wet	Rear Bumper	−0.000853	−2.85481E−12	−0.0025797
Unpaved	Wet	Undersides	−0.006999	−2.36765E−11	−0.0230122
Unpaved	Wet	Wheel Wells	−0.011017	−3.97715E−11	−0.0358334
Unpaved	Wet	Front Bumpers	−0.012390	−4.00427E−11	−0.0662570

dispersal. Our finding that under dry conditions, seeds can travel hundreds of kilometres on vehicles, combined with the results of previous studies that found seeds on vehicles driven unknown distances (Lonsdale & Lane, 1994; Zwaenepoel *et al.*, 2006; Veldman & Putz, 2010), suggest that more than 1% of human dispersed seeds are likely to travel distances >5 km.

The pervasiveness of roads and vehicles around the world, combined with vehicles' potential to carry seeds long distances, indicates that vehicle dispersal is an important mechanism of plant propagule redistribution, even if the number of seeds per vehicle is small. The United States of America (USA) has 6.5 million km of roads (Anon., 2009), on which a quarter of a billion vehicles travel 37 trillion km per year (Forman, 2004) for an average of 59.36 km per vehicle per day (Hu & Reuscher, 2004). These numbers highlight the potential magnitude of the vehicle seed dispersal in just the USA. Additionally, 80% of the USA's roads are rural and 10% are on USDA Forest Service land (Forman, 2004), suggesting that vehicles have the ability to transport seeds to relatively remote areas. Outside the USA, road networks are expanding in many countries [e.g. China and India (Anon, 2009)], increasing the chance of homogenizing current vegetation (von der Lippe & Kowarik, 2008). Therefore, the growing quantity of roads around the world and the potential of vehicles to transport seeds may have detrimental consequences on biodiversity at both the local and global scales.

The ability of vehicles to disperse a diversity of seed morphologies (Zwaenepoel *et al.*, 2006; von der Lippe & Kowarik, 2007; Veldman & Putz, 2010; Lisa J. Rew, unpublished data) is compounded by the fact that there is often a large diversity of plant species, especially non-native species, along roadsides. Total plant species richness has been found to increase with proximity to paved (Cui *et al.*, 2009) and unpaved roads (Buckley *et al.*, 2003; O'Farrell & Milton, 2006), and many studies have found increases in non-native species richness and abundance along roadsides (Gelbard & Belnap, 2003; Pickering & Hill, 2007; Christen & Matlack, 2008; Veldman & Putz, 2010; Seipel *et al.*, 2011). These findings imply that seeds transported by vehicles will likely include non-native species.

Invasive species are initially limited by dispersal rather than by growing conditions or habitat suitability (Veldman & Putz, 2010; Alexander *et al.*, 2011; McDougall *et al.*, 2011). Therefore, increased propagule pressure, as a result of vehicle dispersal, may intensify invasion rates and amplify directional ecological filtering. We documented seed transport for 256 km, with strong evidence that the seeds could travel much farther under dry conditions. This scale is large enough to suggest that vehicles are capable of spreading plant invasions along roads into new ecosystems and regions. Areas of high conservation value, such as mountainous and wildland regions, may experience species introduction by vehicles. While vehicle dispersal may not represent a large proportion of the total seeds dispersed for a plant, it is the rare LDD events that often accelerate plant invasions (Shigesada *et al.*, 1995; Higgins & Richardson, 1999). Migration rates can also depend on disturbance and habitat availability (Higgins & Richardson, 1999); given that roadsides are often disturbed and provide better habitat and growing conditions for some plants, particularly non-native ruderal species (Christen & Matlack, 2008; Flory & Clay, 2009), seeds of vehicle dispersed invasive species may have a high probability of establishment.

Evaluation of seed retention models

The selection of the double exponential form (Model 2) as the best model to describe passenger vehicle seed retention highlights the differences between seed retention on vehicles and other LDD vectors. Seed retention on animals was best described over a short time period (minutes to 48 h) by a simple exponential model, while over longer time periods, seed retention was best described by the power exponential model (Bullock *et al.*, 2011). The power exponential model also best described seed retention on hiking boots, socks and pants (Wichmann *et al.*, 2009; Pickering *et al.*, 2011). The model that incorporated both the power exponential and simple exponential functions (Model 1) did not fit our data as well as the double exponential model (Model 2), suggesting that the pattern of seed retention on vehicles differs from that of animals and hikers. However, both the power exponential and the double exponential functions allow the seed dropping rate to decrease over time or distance, which appears to be important for seed retention on animals, hikers and passenger vehicles alike. In contrast to dispersal on other vectors (Couvreur *et al.*, 2005), vehicles showed minimal dispersal in dry conditions and relatively constant rates of seed loss in unpaved wet conditions.

Effect of road surface, weather condition and plate location on seed retention

Weather condition, road surface and their interaction had the largest effect on seed retention, while plate location was slightly less important. Seed retention was extremely high on paved and unpaved dry roads and was unaffected by road surface. Wheel wells on the dry unpaved roads showed slightly higher variability, likely due to gravel thrown by the wheels knocking seeds off the plates. Under wet conditions on both road surfaces seeds were rapidly lost, although seed retention was lower on paved roads. It is possible that retention rates were underestimated if seeds moved from the plates to other parts of the undercarriage, although no seeds were ever observed remaining on the vehicle. Low seed retention on paved roads was likely due to the water that wheels splash behind them, especially in the wheel wells. Seed retention on wet unpaved roads may have been more variable than on wet paved roads because in some cases, new mud covered the plates preventing seed loss, while in others, water cleaned the plates before they accumulated new mud. On wet unpaved roads, seeds from a range of new species were collected from the road, indicating the potential for seed turnover under wet conditions. The results for wet conditions corroborate the results of Zwaenepoel *et al.* (2006) who found that seed accumulation on car undersides driven in suburban areas (and thus mostly paved roads) was negatively correlated with precipitation, presumably because the wet driving conditions detached seeds from vehicle undersides.

Different road surfaces and conditions interacted to change the effect of plate location on seed retention. We saw the opposite trend in bumpers on the paved and unpaved wet roads. Splashing from wheels may explain the high level of seed loss from rear but not front bumpers on paved wet roads. On unpaved wet roads the larger quantity of deep puddles that soaked the front bumper as the suspension compressed with initial impact likely caused the decrease in seed retention on front bumpers in comparison with the rear bumpers.

Other factors such as vehicle speed or vehicle clearance height could affect seed retention; however, we were unable to evaluate the effect of these additional factors. Our study provides a first assessment of seed retention on a representative passenger vehicle (the Ford Ranger is intermediate between passenger vehicles and larger trucks), driven at representative speeds for paved and unpaved roads. Future studies could address these and other nuances.

Our results show variable seed loss from different locations under the vehicle under wet conditions, which would suggest that it may be difficult to fit a single dispersal model to an entire vehicle without accounting for differential seed loss by location. The amount of variation in the seed retention data demonstrates the stochasticity of vehicle dispersal, which makes predicting seed redistribution rates on the landscape difficult. Furthermore, the differential seed retention by certain plate locations under wet conditions demonstrates that while a majority of seeds may be lost on wet road surfaces, reservoirs of seeds are likely to remain and contribute to rare, LDD events. While these differences are important and could be further investigated, our data provide the first known quantitative evaluation of seed retention on a passenger vehicle and provide data and a model form that could be used for seed dispersal predictions.

Management implications

Dispersal is the most important, although least studied, aspect of invasion because all other stages are dependent upon it (Puth & Post, 2005). Management efforts to reduce LDD can prevent the establishment of, and damage caused by, invasive species (Puth & Post, 2005). As a result, it has been found to be more cost effective to spend money on prevention than on eradication or control once an invasion occurs (Leung *et al.*, 2002). In particular, when there may be excessive LDD of non-native species occurring, quantifying LDD can improve conservation management efforts (Trakhtenbrot *et al.*, 2005). Our results show that vehicles can carry seeds for hundreds of kilometres under dry conditions and then rapidly lose seeds as soon as wet conditions occur. These findings suggest that managers charged with limiting invasion by non-native species should target vehicle dispersal as a means of prevention and consider the potential for LDD along roads. Most seed will be lost under wet conditions, and in areas of high conservation interest, it may be appropriate to restrict access when wet conditions occur or are likely. Alternatively, it may be easier to clean vehicles prior to entering such sensitive areas (Taylor *et al.*, 2011). Some countries such as Australia and New Zealand already require cars entering the country to be cleaned or inspected for seeds. Given our results, it is recommended that more countries, regions and parks require vehicles to be cleaned and inspected before entering.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 P-values for all pairwise comparisons for the *b* values for the 16 treatment groups.

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