

Barriers or corridors? The overlooked role of unpaved roads in endozoochorous seed dispersal

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Summary

1. Ubiquitous linear developments, such as dirt tracks and firebreaks, termed ‘soft’ linear developments (SLD), represent weaker landscape modifications than paved roads and highways but still could strongly affect populations and communities. Many animals avoid SLD, but some terrestrial mammals seem to select them for faecal marking. Faeces often contain many viable seeds; therefore, SLD may receive a substantial amount and diversity of seeds, which could have important overlooked consequences for plant recruitment.

2. To evaluate the potential role of SLD as seed attractors, we surveyed transects along SLD verges and along the adjacent scrubland in three patches of Mediterranean scrubland. On each transect, we collected ungulate, carnivore and rabbit faeces during two fruiting seasons (2009 and 2010). We quantified all seeds from fleshy-fruit shrubs within faeces and compared their abundance and diversity at SLD verges vs. adjacent scrubland.

3. The frequency of defecation along SLD varied greatly among dispersers, but ungulates avoided SLD for defecation, and carnivores and rabbits positively selected them. Seed prevalence was higher in faeces of carnivores, and seed damage low compared with faeces of rabbits and especially ungulates.

4. The role of SLD as seed attractors was species-dependent. We found from 2.7 to 124 times more viable seeds of carnivore- and rabbit-dispersed plants along SLD than in the scrubland, while ungulate-dispersed plants were more abundant in the scrubland. Of 13 mammal-dispersed shrubs, 4 species were exclusively found along SLD verges, two were found only in the scrubland, and seven were found in both habitats.

5. *Synthesis and applications.* By promoting mammal-mediated seed dispersal, soft linear developments (SLD) may act as seed corridors. Given the extremely high density of SLD world-wide, SLD hold a significant overlooked role for management and plant conservation actions. Dispersers selecting SLD can promote roadside restoration, potentially saving financial resources. These feasible benefits must be weighed up against potential spread of alien or undesirable plant species, but we demonstrate the SLD represent a valuable management tool.

Key-words: biodiversity, connectivity, dirt tracks, endozoochory, firebreaks, fragmentation, human structures, linear developments, Mediterranean scrubland, reforestation

Introduction

Land-use change is one of the main components of global change (Foley *et al.* 2005) and one of the most important drivers of biodiversity loss (Vitousek *et al.* 1997). This involves the transformation of natural or semi-natural

habitats into croplands, pastures and urban land (Lambin & Geist 2006). Such modifications are almost invariably associated with linear developments such as roads, highways, tracks, railways and firebreaks. These structures have reached an extremely high density world-wide (Forman 1998). Some linear developments such as paved roads and highways are usually wide, noisy (due to high traffic levels) and even fenced. Because their effects extent

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beyond their boundaries, habitat loss, fragmentation and limited animal and plant dispersal are among their known effects (Forman & Alexander 1998; Trombulak & Frissell 2000). However, other types of linear developments such as dirt tracks, logging roads and firebreaks, hereafter described as ‘Soft’ Linear Developments (SLD), represent much lighter landscape alterations, having probably subtle and unknown ecological effects. Given that SLD represent a form of clearing, the lack of vegetation means that they can facilitate the movement of terrestrial animals (Kuefler *et al.* 2010), acting as corridors (Haddad *et al.* 2003; Haddad & Tewksbury 2005). Moreover, some studies suggested that experimental linear clearings immerse in a forest matrix may enhance ecosystem services such as seed dispersal (Tewksbury *et al.* 2002; Levey *et al.* 2005), which is essential for plant populations (Levin *et al.* 2003), and boosts biodiversity conservation (Damschen *et al.* 2006; Ozinga *et al.* 2009). Could other similar linear clearings such as SLD also promote seed dispersal?

Although linear developments are known to assist the spread of some alien species (Gelbard & Belnap 2003; Christen & Matlack 2006), very little is known about their potential effects on native populations (but see Tikka, Högmänder & Koski 2001; Karim & Mallik 2008). This lack of knowledge is especially surprising in the case of plants, since their mobility is limited and relies on dispersal vectors that are likely to interact with prominent landscape elements (Damschen *et al.* 2008) such as linear developments. Indeed, whereas some vertebrates avoid them (Forman & Alexander 1998; James & Stuart-Smith 2000), many seed-dispersing mammals all over the world, such as the red fox *Vulpes vulpes* L. (Rost, Pons & Bas 2012), the coyote *Canis latrans* Say (Fedriani & Kohn 2001), the martens *Martes* spp (López-Bao & González-Varo 2011) and the European rabbit *Oryctolagus cuniculus* L. (Authors unpublished data), seem to positively select SLD verges for defecation.

Frugivorous mammals ingest and disperse viable seeds of a huge variety of both native and exotic fleshy-fruit plant species world-wide (Myers, Vellend & Gardescu 2004; Stoner *et al.* 2007; Matias *et al.* 2010). Many of these terrestrial dispersers may deposit viable seeds along SLD verges (see references above), presumably with consequences for the dynamic and the spatial and genetic structures of plant populations (Howe & Miriti 2000; Nathan & Muller-Landau 2000; Levin *et al.* 2003). Furthermore, mammals are highly mobile and disperse seeds through long distances (Jordano *et al.* 2007). Such long-distance seed dispersal events usually imply plant fitness advantages (Levin *et al.* 2003; Nathan 2006). Despite their potential for fragmenting the landscape for some dispersers, SLD may also connect isolated plant populations by enhancing long-distance seed dispersal by other species.

Dispersed seeds often lead to established plants (Howe & Miriti 2000); therefore, SLD verges could be reforested by some mammal-dispersed plants (Karim & Mallik 2008). By promoting plant dispersion, SLD would be

acting as corridors connecting the landscape at large. Even though these potential effects are likely to occur and could have important ecological and applied consequences, these intriguing possibilities had not been considered to date. In this study, we examine whether SLD influence mammal-generated seed rains (i.e. spatial distribution of dispersed seeds).

Although from a plant ‘perspective’ the absolute number of seeds effectively dispersed is the important factor, dissecting seed dispersal qualitative and quantitative components is important to understand such complex processes (Schupp, Jordano & Gómez 2010). In the case of endozoochorous plants (plants dispersed through ingestion by animal), the abundance and the spatial distribution of dispersed seeds are determined by the abundance and distribution of faeces containing viable seeds. This in turn is a function of (i) the spatial pattern of defecation of frugivores, (ii) their fruit consumption (i.e. proportion of faeces with fruit remains) and (iii) whether they damage the seeds they ingest. To assess in detail whether such mammal-generated seed rain components are influenced by SLD, we chose several patches of Mediterranean scrubland in south-western Spain characterized by a diverse community of fleshy-fruit shrubs and frugivorous mammals, as well as a vast SLD system.

Previous studies and observations suggest that carnivores and rabbits often defecate along SLD verges (Fedriani, Palomares & Delibes 1999), while ungulates generally avoid these structures (James & Stuart-Smith 2000). Furthermore, carnivores are recognized as legitimate seed dispersers (Herrera 1989; López-Bao & González-Varo 2011), whereas ungulates and rabbits often act as seed predators rather than dispersers (Fedriani & Delibes 2009b; Perea *et al.* 2012). Consequently, the potential role of SLD as seed attractors was expected to depend on the species-specific defecation places and dispersal effectiveness (*sensu* Schupp, Jordano & Gómez 2010) of dispersal vectors.

Materials and methods

STUDY SITES, PLANTS AND THEIR DISPERSERS

This study was carried out during the fruiting seasons (August–December) in 2009 and 2010 in the Doñana National Park (510 km²; 37°9′ N, 6°26′ W; elevation 0–80 m), located on the west bank of the Guadalquivir River mouth, south-western Spain. The climate is Mediterranean subhumid, characterized by dry, hot summers (June–September) and mild, wet winters (November–March). Annual rainfall is very irregular, averaging 577 mm ± 39 SE, with 88.4% of rain falling between October and April (data from Natural Processes Monitoring Group, Doñana Biological Station, <http://www-rbd.ebd.csic.es/Seguimiento/seguiamiento.htm>).

The Doñana area includes seasonally flooded marshes on a clay substrate (marshland) and pine *Pinus pinea* L. plantations and scrubs with other scattered trees on a sandy substrate (scrubland). We focused on the scrubland, which occurs in several patches varying in size and structure and which are isolated from

each other by natural (e.g. marshes) and human (e.g. cultivations) barriers. Furthermore, Doñana has more than 2000 km of dirt tracks (62.5%) and firebreaks (35.5%), most of which were established c. 50 years ago.

To enable assessment of the whole fleshy-fruit shrub community of Doñana, we chose three study sites (called Reserva, Rocina and Matasgordas, respectively) separated by distances between 2.5 and 14 km. Reserva is covered by pine woods and a dense Mediterranean scrubland (covering 11.6 km²) dominated by *Halimium halimifolium* L., *Rosmarinus officinalis* L. and *Stauracanthus* spp. It has a relatively high presence of fleshy-fruit species such as *Juniperus phoenicea* subsp. *turbinata* (Guss) Nyman, *Juniperus macrocarpa* Sibth & Sm., *Corema album* L., *Rubus ulmifolius* Schott, *Pistacia lentiscus* L. and *Phillyrea angustifolia* L. (overall 0.14 ± 0.03 shrub m⁻²; mean ± SE). The scrubland area at Reserva has about 48 km of SLD. Rocina is a riparian woodland zone along a stream and surrounded by Mediterranean scrubland and croplands. Its scrubland area (3.5 km²) comprises scattered *P. pinea* with a dense understorey of *Stauracanthus* spp. *Cytisus grandiflorus* (Brot.) DC., and *H. halimifolium*. Here, fleshy-fruit plants such as *Myrtus communis* L., *Asparagus* spp, *Arbutus unedo* L., *Vitis* spp, *R. ulmifolius*, *Chamaerops humilis* L. and *Olea europaea* L. var. *sylvestris* are scarce (overall 0.07 ± 0.02 shrub m⁻²; mean ± SE). The local SLD system is 36 km long. Matasgordas is characterized by open Mediterranean scrubland (4.2 km²) dominated by scattered *Quercus suber* L., *Fraxinus angustifolia* Vahl and patches of *H. halimifolium* with a variable density, and a great amount of fleshy-fruit plants such as *P. lentiscus*, *Pyrus bourgaeana* Decne., *C. humilis*, *P. angustifolia*, *R. ulmifolius*, *M. communis* and *O. europaea* (overall 0.42 ± 0.08 shrub m⁻²; mean ± SE). This site contains 21 km of SLD.

In the Mediterranean basin, fleshy-fruit shrub species generally flower during later winter and spring (February–May) and produce drupes (e.g. *P. lentiscus*, *R. ulmifolius*, *P. angustifolia*) or berries (e.g. *C. album*, *M. communis*) that ripen between August and December (Jordano 1984a; Fedriani & Delibes 2009a). Depending on the species, each fruit contains generally from one to eight seeds, although *R. ulmifolius* frequently contain more than 20 seeds per fruit (Jordano 1995).

In Doñana, most of those plants are dispersed by mammals (Herrera 1989; Fedriani & Delibes 2009a,b), although some of them are also dispersed by birds (Jordano 1984b; Herrera 1995). Specifically, six frugivorous mammals are known to be local important seed dispersers: wild boar *Sus scrofa* L. (Matias *et al.* 2010), red deer *Cervus elaphus* L. (Perea *et al.* 2012), fallow deer *Dama dama* L. (Eycott *et al.* 2007), red fox (Fedriani & Delibes 2009a), Eurasian badger *Meles meles* L. (Fedriani & Delibes 2009b) and European rabbit (Delibes-Mateos *et al.* 2008). Genets *Genetta genetta* L. and Egyptian mongooses *Herpestes ichneumon* L. also occur in Doñana, but were not recorded in our surveys. Radiotracking studies (Fedriani, Palomares & Delibes 1999) and sign censuses (data from Natural Processes Monitoring Group, Doñana Biological Station) suggested that carnivores and rabbits tended to positively select SLD, whereas ungulates (boar and red/fallow deer) seem to avoid them. Furthermore, recent studies in the same area suggested that they also differ in the proportion of seeds they damage (Fedriani & Delibes 2009b; Perea *et al.* 2012). Therefore, and for the sake of simplicity, we classified these potential seed dispersers into three groups: ungulates (boar and red/fallow deer), carnivores (fox and badger) and rabbits.

COLLECTION AND ANALYSIS OF FAECAL SAMPLES

To assess the potential effect of SLD on different aspects of mammal-generated seed rains (i.e. faeces abundance and distribution, fruit consumption and seed damage), we surveyed four transects (500 × 2 m) for mammal faeces once a week, during both fruiting seasons in each study site (overall 12 transects, 6 km). At each site, two transects were established along SLD verges and two parallel to the SLD but at a distance of 60 m into the scrubland. The distance was selected to ensure the collection of ungulate faeces (a preliminary study suggested that ungulates avoided a buffer of around 30 m from SLD) and also that sampled transects fall within the same shrub community. Along each transect, we recorded the location and removed all faeces of target mammals. We assigned each mammal faecal sample to species on the basis on their shape, size and smell. For wild boar and carnivores, we assumed that all faecal samples were found. Deer and rabbit faecal pellets are scattered and therefore difficult to sample, we used the 'pellet group' as the sampling unit, defined as ≥ 30 pellets for deer and ≥ 50 pellets for rabbits, within a circular 50-cm diameter plot.

To attain a relative estimate of the number of seeds delivered in each habitat (SLD vs. adjacent scrubland) as well as the group-specific fruit consumption and seed damage, we analysed up to three faecal samples per disperser and survey (i.e. each transect sampled per week), depending on availability. Overall, we analysed 62.3% of collected faeces ($n = 987$). Faeces were dried and stored in paper bags. For their processing, they were soaked, carefully broken and cleaned. Then, we successfully identified and counted all seeds from fleshy-fruit plants, either damaged or intact. The number of damaged seeds was estimated by assessing the minimum number of pieces that made up a seed, considering the size of the whole seed and of each damaged piece and using a broad seed reference collection (Herrera 1989; Fedriani & Delibes 2009b; Perea *et al.* 2012). Although it is possible that mammals digested a fraction of ingested seeds, such fraction is likely to be small (Traveset 1998) and similar between habitats, hence this should not have a major effect on our results.

STATISTICAL ANALYSES

To examine whether SLD influence mammal-generated seed rains, we first examined for potential differences between habitats in the number of mammal faeces found per survey. To determine mammal fruit consumption and seed damage, we considered the proportion of analysed faeces containing fruit remains (i.e. seeds, pulp, skin or their fragments) and the proportion of damaged seeds regarding the overall number of seeds within the faeces, respectively. To assess the intensity of mammal-generated seed rain in both habitats, we considered the estimated number of unbroken seeds (mostly viable; Fedriani & Delibes 2009a) dispersed per survey as response variable. Finally, we also looked for potential differences between habitats in the richness and the diversity (estimated by the Shannon index) of dispersed plant species.

We evaluated potential differences among habitats and dispersers in our response variables by fitting generalized linear mixed models (by means of SAS 9.2 GLIMMIX procedure; Littell *et al.* 2006). Negative binomial distribution and log-link function were assumed in all models, except for fruit consumption, which was fitted to a binomial distribution. For seed damage estimation, binomial distribution led to strong over-dispersion. Thus, we

adjusted the model to a negative binomial distribution considering the number of damaged seeds per survey as response variable and introducing the total number of seeds found per survey as a random factor, to control for sample size variation.

In all mixed models, we considered the habitat (scrubland and SLD verges), the disperser group and their second-order interaction as fixed factors. When this interaction was significant, we performed tests for the effect of a factor at the different levels of the other factor ('tests of simple main effects') using the SLICE option in the LSMEANS statement (Littell *et al.* 2006). Year, the month of sampling (nested within year) and the transect (nested within site) were included as random factors to control for temporal and spatial heterogeneity. Adjusted means and standard errors were calculated using the LSMEANS statement, which estimate the marginal means over a balanced population (Littell *et al.* 2006). Whereas in a balanced sampling observed and adjusted means are usually similar, in unbalanced samplings (as it was the case of this study) observed and adjusted means may differ considerably.

Results

FAECAL DEPOSITION PATTERN

Overall, we carried out 264 surveys (a total of 132 km) and found mammal faeces in 78.0%. A total of 987 mammal faeces were found, 70.2% in the scrubland and 29.8% along SLD verges.

Once corrected for the effects of random factors, the overall mean number of faeces found per survey did not differ between habitats ($F_{1,774} = 2.98$; $P = 0.08$). The overall number of faeces deposited by each disperser group was rather heterogeneous. From 987 faeces, 59.4% belonged to ungulates, 32.9% to rabbits and only 7.7% to carnivores. However, most ungulate faeces (83.1%; $n = 586$) were recorded in Matasgordas, where these species are particularly abundant (Fedriani & Delibes 2009b). Once corrected by site effect, we found 0.59 ± 0.17 (mean \pm SE) ungulate, 1.15 ± 0.30 rabbit and 0.21 ± 0.06 carnivore faecal

samples per survey, being such differences highly significant ($F_{2,774} = 40.05$; $P < 0.0001$). Disperser groups differed in their habitat preferences for defecation (interaction Habitat*Disperser; $F_{2,774} = 91.61$; $P < 0.0001$). Specifically, ungulates deposited 27.08 times more faeces in the scrubland compared with SLD verges (Table 1a). Conversely, rabbits and carnivores deposited 2.17 and 5.47 times more faeces along SLD verges than in the scrubland, respectively (Table 1a; Fig. 1a).

Faecal samples collected per survey for each disperser group could be not independent of each other (they might belong to the same individual disperser); therefore, we performed a similar analysis considering the same explicative variables and their interaction but using the presence/absence of faeces of each disperser group per survey as response variable and reached essentially the same results as above (see Table S1, Supporting information).

FRUIT CONSUMPTION AND SEED DAMAGE

Around 66.0% ($n = 615$) of analysed faeces contained fruit remains. Although all three disperser groups consumed fruits, there were significant differences among them in the frequency of occurrence of fruit remains within the faeces ($F_{2,268} = 3.70$; $P < 0.05$). Specifically, fruits were more prevalent in carnivore faeces ($88.9 \pm 26.8\%$ of them contained fruit remains; $n = 76$), whereas fruit prevalence was similar in faeces of rabbits and ungulates ($66.7 \pm 34.1\%$, $n = 325$, and $62.8 \pm 41.4\%$, $n = 586$, respectively; Table 1b).

Overall, we found 21037 seeds (either damaged or not) within the faecal samples. Mammal groups varied significantly in seed damage ($F_{2,190} = 36.45$; $P < 0.0001$). Specifically, ungulates, rabbits and carnivores damaged $73.9 \pm 25.4\%$ ($n = 4215$), $59.8 \pm 18.3\%$ ($n = 6300$) and $1.8 \pm 0.7\%$ ($n = 10522$) of ingested seeds, respectively (Table 1c). Interestingly, rabbit and ungulate seed damage

Table 1. Coefficients of the generalized linear mixed models fitted for testing the effects of the habitat and the disperser group over the number of faeces found (a), the proportion of faeces containing fruit remains (b), the proportion of damaged seeds (c) and the estimated number of unbroken seeds found per survey

Factor	(a) Faeces			(b) Fruit consumption			(c) Seed damage*			(d) Seed rain		
	β	SE	P	β	SE	P	β	SE	P	β	SE	P
Habitat												
Scrubland	3.30	0.28	<0.0001	-0.64	0.97	0.51	0.30	0.46	0.51	3.60	0.68	<0.0001
SLD	0	-	-	0	-	-	0	-	-	0	-	-
Disperser												
Carnivores	1.45	0.31	<0.0001	0.89	1.05	0.39	-3.67	0.59	<0.0001	4.79	0.67	<0.0001
Rabbits	2.70	0.29	<0.0001	-0.14	1.00	0.89	0.53	0.51	0.30	5.37	0.76	<0.0001
Ungulates	0	-	-	0	-	-	0	-	-	0	-	-
Habitat*Disperser												
Scrubland-Carnivores	-5.00	0.44	<0.0001	1.33	1.35	0.32	1.13	0.80	0.16	-6.67	0.86	<0.0001
Scrubland-Rabbits	-4.07	0.33	<0.0001	0.63	1.04	0.55	-0.70	0.55	0.21	-4.86	0.99	<0.0001

For the interaction, only the combinations different from zero are shown. SLD, soft linear developments. *To achieving model convergence, we did not include month of sampling as random factor in this analysis.

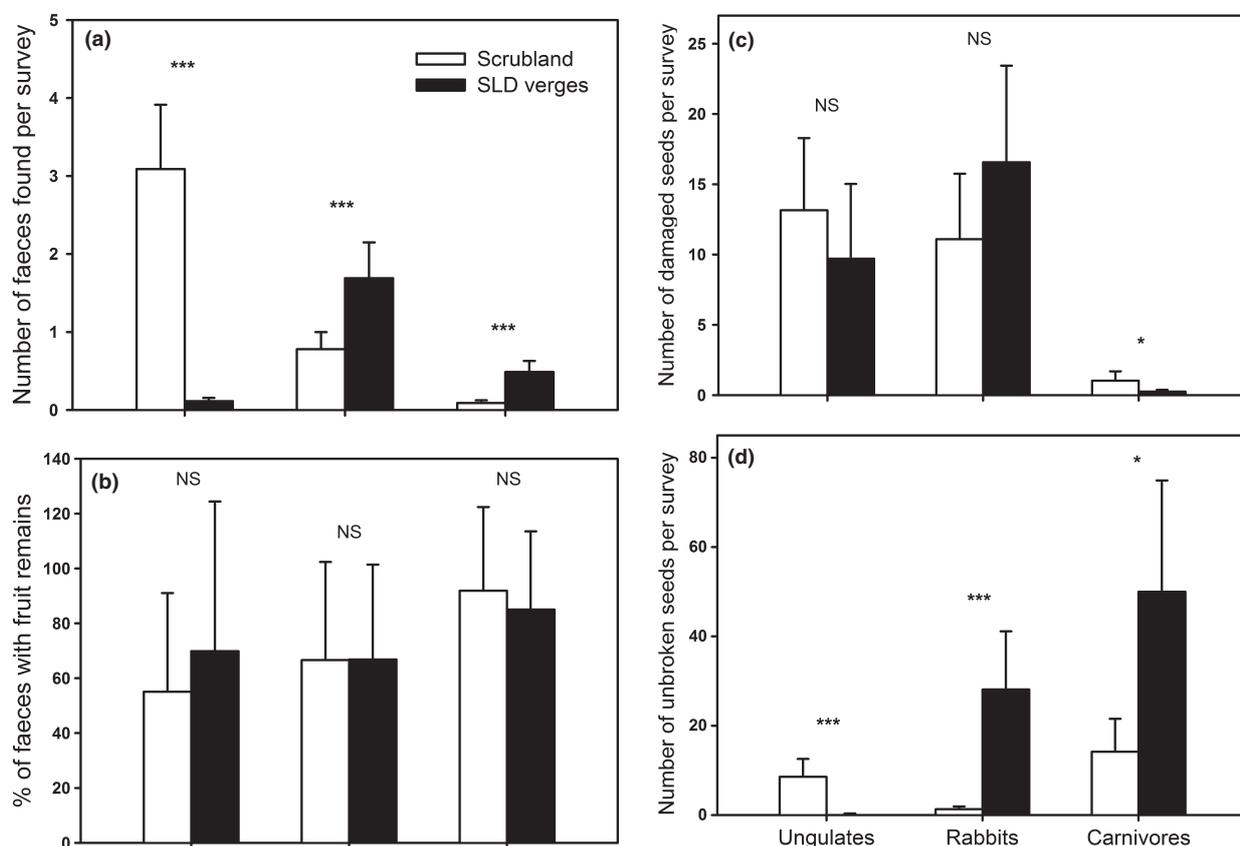


Fig. 1. Model-adjusted means (\pm SE) of number of faeces (a), the proportion of faeces containing fruit remains (b), the number of damaged seeds (c) and the estimated number of unbroken seeds (d) found per survey delivered by each disperser group between the scrubland and soft linear developments verges. *P* values resulted from the test of slices are shown (**P* < 0.05; ****P* < 0.0001). The influence of the fruit consumption and the seed damage leads to high and low contributions to the overall seed rains by carnivores and ungulates, respectively (compare Fig. 1a and d). The slightly significant differences in seed damaged by carnivores between habitats disappeared ($F_{2,189} = 1.22$; *P* = 0.30) when we removed one faecal sample from the analysis.

were plant species-specific. For instance, whereas seeds of *O. europaea* and *P. lentiscus* were severely damaged (overall, more than 90% were damaged), seeds of species such as *M. communis* and *P. angustifolia* were less than 60% damaged (Table S2, Supporting information).

SEED RAIN

Overall, we collected 13931 unbroken seeds from 13 plant species (77.2% along SLD verges and 22.8% in the scrubland; Table S2, Supporting information). Once corrected for random effects, the overall number of unbroken seeds found per survey did not significantly differ between habitats ($F_{1,774} = 0.44$; *P* = 0.51), probably due to great heterogeneity among surveys.

There were significant differences in the estimated number of seeds dispersed by each mammal group ($F_{2,774} = 19.30$; *P* < 0.0001). Ungulates dispersed the fewest unbroken seeds per survey (1.41 ± 0.50 ; mean \pm SE), while carnivores dispersed the most (26.62 ± 10.94), even though they delivered the fewest faeces. Meanwhile, rabbits dispersed 6.08 seeds on average (± 2.12 SE) per survey (Table 1d). According to the faecal deposition pattern, the number of seeds dispersed by each mammal

group varied between habitats (Habitat*Disperser; $F_{2,774} = 30.05$; *P* < 0.0001). Whereas ungulates dispersed 36.75 times more seeds in the scrubland as compared with SLD verges, rabbits and carnivores dispersed 21.39 and 3.53 times more seeds along SLD verges than in the scrubland, respectively (Table 1d; Fig. 1d).

Consequently, despite the overall number of seeds did not differ between habitats, we found strong significant differences in the number of seeds found between habitats for many plant species. Specifically, the number of *C. album*, *R. ulmifolius* (mainly dispersed by carnivores) and *P. angustifolia* (mainly dispersed by rabbits) seeds was 124, 2.76 and 6.26 greater along SLD verges than in the scrubland ($\chi^2 > 242$; *P* < 0.0001), while for *P. lentiscus* (typically dispersed by ungulates), the reverse pattern was found ($\chi^2 = 237.07$; *P* < 0.0001). In contrast, the abundance of *M. communis* and *P. bourgaeana* (dispersed by all frugivores) seeds showed no significant difference between habitats ($\chi^2 < 3.13$; *P* > 0.05).

Of 13 fleshy-fruit shrub species found within the faeces, unbroken seeds from four (*J. phoenicea*, *J. macrocarpa*, *Vitis* spp and *A. unedo*) were exclusively found along SLD verges. Whereas seven species were found in both habitats (*C. humilis*, *P. bourgaeana*, *C. album*, *R. ulmifolius*, *P. len-*

tiscus, *P. angustifolia* and *M. communis*) and only two were exclusively found in the scrubland (*Asparagus* spp and *O. europea* var. *sylvestris*; Table S2, Supporting information). Thus, neither species richness nor diversity significantly differed between habitats (Richness: $F_1 = 0.16$; $P = 0.69$; Diversity: $F_1 = 3.80$; $P = 0.053$).

Discussion

SLD AS SEED CORRIDORS

Forest linear clearings can improve seed dispersal, thereby benefiting biodiversity (Tewksbury *et al.* 2002; Levey *et al.* 2005; Damschen *et al.* 2006; Ozinga *et al.* 2009). However, no previous study had assessed the possibility that some ubiquitous linear developments such as dirt tracks and firebreaks, also devoid of vegetation and generally considered as barriers (Forman & Alexander 1998; Trombulak & Frissell 2000), can also promote native seed dispersal, even over long distances.

Our results strongly suggest that, by influencing the defecation patterns of non-flying mammals, SLD are landscape features that receive seeds of many native fleshy-fruit shrubs. Indeed, SLD received much greater number of seeds of most species of the focal plant community than the adjacent scrubland. Thus, in contrast to patterns found in Canary Islands along paved roads (Arévalo *et al.* 2010), we would not expect a plant community homogenization along SLD in Doñana. Both seed rain intensity and diversity are key factors in predicting colonization success (Brederveld *et al.* 2011). If SLD receive a greater amount and at least the same diversity of seeds than the adjacent scrubland, they may play a role as dispersal corridors. Furthermore, this role could be amplified by a 'spillover effect' (*sensu* Brudvig *et al.* 2009) that additionally promotes species spread in surrounding habitats. However, strong local seed accumulation may enhance post-dispersal seed and seedling mortality (Spiegel & Nathan 2010). Further research on the potential effects of SLD on pre-dispersal and post-dispersal stages of the plant recruitment cycle (e.g. fruit and seed production, seed survival, germination, seedling emergence and survival) is needed for closing the seed dispersal loop (Wang & Smith 2002) to better understand the effects of SLD on plant populations and communities.

The strength and direction of SLD effect on seed rains are likely to be strongly context-dependent. For example, a sizeable positive effect would require the presence of seed dispersers that positively select SLD for defecation (such as rabbits and carnivores in Doñana). Likewise, SLD perturbation levels and the characteristics of the surrounding landscape are likely conditioning mammal SLD use. For instance, when the cost of moving through the habitat matrix is similar to moving along SLD, we would expect weak mammal selection for SLD (Kuefler *et al.* 2010). Furthermore, we would not expect such a 'corridor effect' for other pervasive linear developments such as highways and

paved roads, which are most likely to act as barriers for many vertebrates (Forman & Alexander 1998), hence negatively affecting the potential of dispersal of the seeds they ingest (Ozinga *et al.* 2009).

CARNIVORES AS GARDENERS IN HUMANIZED LANDSCAPES

Our results suggest that SLD are positively selected by some mammals that deliver viable seeds in faeces. This positive selection was especially accentuated in the red fox. Although some human perturbations such as traffic or hunting could reduce fox SLD selection, there are several examples of other canids that also positively select these structures (Fedriani, Fuller & Sauvajot 2001; Vieira & Port 2007). These are generalist carnivores, highly mobile, widely distributed and strongly resilient to human activity. Therefore, these mammals are likely to be interacting with a huge diversity of fleshy-fruit shrubs in humanized landscapes world-wide (D'Hondt *et al.* 2011). Moreover, the benefits for plant populations in their interaction with mammalian carnivores go usually further. For instance, they can improve germination and seedling survival of many fleshy-fruit shrubs (Juan *et al.* 2006). Thus, through long-distance seed dispersal and other sort of benefits, carnivores are likely to provide a diverse pool of seeds for natural revegetation in strongly humanized landscapes. Therefore, we encourage cautious management of these efficient dispersers (Stoner *et al.* 2007).

CONCLUSIONS AND APPLICATIONS

We found that SLD may receive many mammal-dispersed seeds similar to the way that remnant trees usually receive bird-dispersed seeds (Herrera & García 2009). If seeds dispersed along SLD enhance local recruitment, these structures could improve the colonization of native species and genotypes, boosting revegetation success (Brederveld *et al.* 2011). This in turn could assist connectivity among shrub populations. In that case, SLD would be acting as corridors for those endozoochorous species dispersed by mammals which positively select SLD for defecation. Over the long term, the establishment of some native species along SLD verges (e.g. *J. phoenicea*; Fig. 2) may create hedgerows that would provide habitat for some organisms (Lugo & Gucinski 2000; Pulido-Santacruz & Renjifo 2011), stop erosion, reduce invasion risk (Lugo & Gucinski 2000; Grant *et al.* 2011) and improve the settlement of other plant species by promoting seed arrival (e.g. acting as perches for frugivorous birds; Herrera & García 2009) or by creating a proper environment (e.g. acting as nurse plants; Armas & Pugnaire 2009). Therefore, the interaction between SLD and frugivorous mammals could be used in natural restoration.

Undesirable outcomes of SLD such as the potential barrier effect for several plant and animal species (Forman & Alexander 1998) and the increase in human



Fig. 2. Example of soft' linear developments (SLD) effect on fleshy-fruit plant recruitment. Individuals belonging to several size classes of *J. phoenicea* subsp. *turbinata* seem to make 'living fences' along SLD verges in the Reserva study site.

disturbances (Laurance, Goosem & Laurance 2009) often lean managers towards SLD removal. By doing so, they could also hinder some other negative consequences directly derived from the SLD corridor effect, such as the spread of alien plants (Gelbard & Belnap 2003; Christen & Matlack 2006; Rost, Pons & Bas 2012) and the hybridization between cultivated varieties and wild sibling species (Ellstrand 2005). When considering whether SLD removal is desirable, managers must take into account that reforestation success and speed as well as the connectivity between isolated shrub populations are likely improved by seed dispersers along SLD, a service that will be lost or much reduced. To improve reforestation and connectivity between isolated fragments without SLD may require substantially more financial and personal human resources (Watkins *et al.* 2003).

Whenever connecting isolated shrub populations is a management aim, we recommend the use of SLD as corridors to connect them, as long as the community includes seed dispersers that positively select these structures for defecation (a pattern that can be readily quantified following our protocol; see Materials and methods). We demonstrated that such pervasive human-made structures can act as seed receptors and avenues for some mammal-dispersed plant species. This overlooked role represents a new and practical application to manage shrub populations in fragmented landscapes, equally important as the use of SLD to identify invasion pathways of mammal-dispersed alien plants.

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Supporting Information

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

Table S1. Coefficients of the generalized linear mixed model fitted for testing the effects of the habitat and the disperser group over the presence/absence of feces found per survey.

Table S2. Relation of damaged and unbroken seeds dispersed by ungulates, rabbits and carnivores along soft' linear developments verges and in the scrubland.