

Unpaved road verges as hotspots of fleshy-fruited shrub recruitment and establishment

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A B S T R A C T

Hypothetical low-quality habitats can hold an overlooked conservation value. Some frugivorous mammals such as the red fox (*Vulpes vulpes*) and the European rabbit (*Oryctolagus cuniculus*) disperse many viable seeds of fleshy-fruited shrubs along the verges of soft linear developments (SLD), such as trails and firebreaks. However, seed arrival does not guarantee plant recruitment, since several post-dispersal processes can alter seed rain. To examine whether SLD verges assist shrub recruitment and establishment, we compared the density and the structure of a community of Mediterranean shrubs between SLD verges and the adjacent scrubland.

Both seedlings and adult fleshy-fruited shrubs dispersed by foxes and rabbits reached higher densities along SLD verges than in the scrubland, suggesting SLD verges can be suitable habitats for shrub recruitment and establishment. Bird-dispersed shrubs showed a similar pattern, whereas shrubs dispersed by ungulates and badgers (*Meles meles*) as well as rock roses (*Cistaceae*) showed similar densities in both habitats. Shrub species composition and diversity were similar between habitats.

Due to a marked differential seed arrival, SLD verges housed higher densities of fleshy-fruited shrubs than the adjacent scrubland. Established shrubs may attract seed-dispersing wildlife, and create proper environments for plant recruitment, generating a reforestation feedback. Incipient shrub populations along roadsides may act as steppingstones with potential to connect isolated populations in fragmented landscapes, where SLD are pervasive. We recommend careful management of frugivore populations and SLD verges in order to favor the diversity and the structural complexity of native vegetation while preventing the spread of invasive species.

Keywords:

Colonization
Conservation
Corridors
Hedgerows
Reforestation
Steppingstones

1. Introduction

Plants are sessile organisms that rely on pollen and seed vectors for dispersal. The spatial distribution of seeds (i.e. seed rain) influences the spatial and genetic structures of plant populations and communities, and also determines plant colonization ability (Howe and Miriti, 2000; Nathan and Muller-Landau, 2000; Wang and Smith, 2002). Seed rain often depends on the interaction between seed vectors and landscape structure (Damschen et al., 2008). For example, wind-dispersed species will be further dispersed in open-windy compared to dense-windless habitats (Bacles et al., 2006). Moreover, the presence of certain features (e.g. a forest edge) can promote seed accumulation associated with them (Nathan and Katul, 2005). In the case of endozoochores (plants whose seeds are dispersed in animal interiors), the preferential use of certain structures or habitats by frugivores can also result

in strong seed clustering. For example, birds and monkeys deposit most seeds where they rest underneath perches, roosts and nests (Harvey, 2000; Herrera and García, 2009; Russo et al., 2006; Shiels and Walker, 2003).

However, seed arrival does not guarantee plant recruitment (Gómez-Aparicio, 2008; Hampe et al., 2008). Whether seed dispersal foci such as isolated trees (Herrera and García, 2009), windbreaks (Harvey, 2000), perches (Shiels and Walker, 2003) and resting sites (Russo et al., 2006) lead to plant recruitment and establishment (Wenny, 2001) or, conversely, they become propagule sinks (Hille Ris Lambers and Clark, 2003; Spiegel and Nathan, 2010), has paramount importance for plant diversity (Ozinga et al., 2009), population dynamics (Howe and Miriti, 2000) and ecosystem functioning (Isbell et al., 2011). Wherever seed concentration actually leads to enhanced recruitment, dispersal foci become hotspots of plant colonization (Wenny, 2001), with a huge potential for improving reforestation success (Brederveld et al., 2011) and plant diversity conservation (Ozinga et al., 2009). In particular, pervasive natural or human-made structures

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that receive seeds and also facilitate plant recruitment and establishment should be carefully considered in reforestation and conservation programs worldwide.

Identifying successful places for plant restoration requires a detailed evaluation of seed arrival and seedling recruitment (Hampe, 2011; Sagnard et al., 2007). For example, some studies have found that experimental linear clearings of forest can enhance bird-mediated seed dispersal (Levey et al., 2005; Tewksbury et al., 2002) and that this seed corridor effect improves connectivity, which in turn promotes plant diversity at different scales (Damschen and Brudvig, 2012; Damschen et al., 2006). In the same line, a recent study in SW Spain (Suárez-Esteban et al., 2013) has suggested that pervasive human-made structures devoid of vegetation, such as trails and firebreaks (called “soft linear developments”; hereafter SLD), can act as seed receptors for native fleshy-fruited shrubs, especially for those dispersed by rabbits (*Oryctolagus cuniculus*) and red foxes (*Vulpes vulpes*), which positively select SLD verges for defecation (Suárez-Esteban et al., 2013). However, whether such disproportionate seed arrival along SLD leads to an enhanced local woody species recruitment and establishment is unknown for any study system.

Although SLD can receive a considerable amount of animal-dispersed seeds, they could also represent an ecological trap (sensu Schlaepfer et al., 2002) if most of those seeds fail to establish. Seed accumulation can lead to increased density-dependent mortality (Spiegel and Nathan, 2010), either at the seed (e.g. post-dispersal seed predation; Hulme, 1997) or at the seedling stage (e.g. herbivory, nutrient competition, water stress, trampling; Hille Ris Lambers and Clark, 2003). Therefore, assessing whether pervasive structures such as SLD verges are not only seed dispersal foci but also suitable habitats for woody plant recruitment could be critical to understand the dynamics of natural shrub regeneration and plant diversity in human-dominated landscapes.

In this study, we quantified for the first time the density and diversity of a large community of Mediterranean shrubs composed of both dry-fruit rockroses (*Cistaceae*) and fleshy-fruited shrubs in relation to SLD. Whereas there are no reasons to think that seed rain of rockroses should be modified by the presence of SLD, an earlier study indicated that the seed rain of fleshy-fruited species varied in relation to SLD, as a consequence of the fecal marking behavior of their main dispersal vectors (Suárez-Esteban et al., 2013). Considering the importance of seed rain in shaping spatial patterns of plant recruitment (Howe and Miriti, 2000), we expected to find a concordance between shrub densities and the main habitat used for defecation by their main seed dispersal vectors. This is: (1) higher densities of fleshy-fruited shrubs dispersed by rabbits and foxes (which defecated mainly along SLD verges; Suárez-Esteban et al., 2013) along SLD verges than in the scrubland. Contrary, we expected to find (2) the opposite pattern for fleshy-fruited shrubs dispersed by ungulates and badgers (*Meles meles*; which defecated mainly in the scrubland; Suárez-Esteban et al., 2013), and (3) similar rockrose densities along SLD verges and the scrubland, given their lack of specific dispersal mechanisms (Bastida and Talavera, 2002).

Because post-dispersal processes (i.e. seed predation, droughts, herbivory, etc.) could alter the seed template (Fedriani et al., 2012; Gómez-Aparicio, 2008), we also expected (4) a stronger concordance between seed rain and the density of seedlings of fleshy-fruited shrubs than regarding saplings and adult shrubs. Finally, given that fleshy-fruited shrub seed rain varied in intensity but not in species diversity in relation to SLD (Suárez-Esteban et al., 2013), we expected (5) no differences in the diversity of neither fleshy-fruited shrubs nor rockroses between SLD verges and the scrubland.

This study provides evidence and a basis for assessing the potential of SLD to recruit native shrubs, as well as the influence of

such pervasive landscape features on plant colonization and establishment spatial patterns.

2. Material and methods

2.1. Study area and species

The quantification of shrub abundance and diversity was carried out during the spring (March–April) of 2011 in the Doñana National Park (SW Spain; 37°9'N, 6°26'W; 510 km²; elevation 0–80 m). This area contains several ecosystems (e.g., marshland, scrubland, dunes) and a vast (over 2000 km²) SLD system composed of dirt tracks (62.5%) and firebreaks (35.5%). The Doñana's scrubland harbors a diverse and spatially variable community of native Mediterranean shrubs. To encompass most shrub species present in the area, we chose the same three sites sampled by (Suárez-Esteban et al., 2013), which are separated from each other by 2.5–14 km and are called “Reserva”, “Rocina” and “Matasgordas”. “Reserva” is covered by pine woods and a dense Mediterranean scrubland dominated by dry-fruit rockroses (*Cistaceae*), such as *Cistus libanotis*, *Halimium calicinum*, *Halimium halimifolium*, and gorses (*Stauracanthus* spp.). It has also a relative high presence of fleshy-fruited species such as *Juniperus phoenicea* subsp. *turbinata*, *Phillyrea angustifolia* and *Rubus ulmifolius* (overall density is 0.14 ± 0.03 shrub/m²; mean ± SE). “Rocina” is a riparian woodland zone surrounded by Mediterranean scrubland and croplands. The scrubland area comprises scattered *Pinus pinea* with a dense understory of *Cytisus grandiflorus*, *H. halimifolium*, and *Stauracanthus* spp. Fleshy-fruited plants such as *Asparagus* spp., *Olea europaea* var. *sylvestris*, *Osyris alba*, and *R. ulmifolius* are present but scarce (overall density 0.07 ± 0.02 shrub/m²). “Matasgordas” is characterized by an open Mediterranean woodland dominated by scattered *Fraxinus angustifolia*, *Quercus suber*, with patches of rockroses such as *Cistus salvifolius* and *H. halimifolium* with a variable extension, and a diverse and dense community of fleshy-fruited plants such as *Chamaerops humilis*, *Daphne gnidium*, *Myrtus communis*, *P. angustifolia*, *Pistacia lentiscus*, *Pyrus bourgaeana*, *Rhamnus oleoides* and *Rubia* spp. (overall density 0.42 ± 0.08 shrub/m²; for further details concerning the study area see (Suárez-Esteban et al., 2013)).

In Doñana most of these fleshy-fruited species flower during late winter and spring (February–May) and produce drupes (e.g., *P. lentiscus*, *R. ulmifolius*) or berries (e.g., *M. communis*) that ripen during August–December (Fedriani and Delibes, 2009a; Jordano, 1984). Depending on the species, each fruit contains generally from one to eight seeds, though *R. ulmifolius* fruits can contain more than 20 seeds (Jordano, 1995). They are mainly dispersed by birds and mammals (Fedriani and Delibes, 2009b, 2011; Jordano, 1984). Rockroses flower in April–June and their seed release mechanism consists basically in the dehiscence and fragmentation of the capsules containing many small seeds (Bastida and Talavera, 2002). Though these plants have no long-distance dispersal adaptations, they have considerable colonization ability, especially in disturbed and burned habitats (Guzmán and Vargas, 2009). They are occasionally dispersed by ungulates (Malo and Suarez, 1996).

Suárez-Esteban et al. (2013) found that the seed rain of fleshy-fruited shrubs varied near and away from SLD, depending on the fecal marking behavior of their main dispersal vectors. Specifically, 79.49% ($N=13,066$) of *J. phoenicea*, *P. angustifolia* and *R. ulmifolius* seeds was dispersed along SLD verges, mostly by the European rabbit and the red fox. Contrary, 88.91% ($N=451$) of *Asparagus* spp., *C. humilis* and *P. lentiscus* seeds was dispersed in the scrubland (away from SLD), mostly by the Eurasian badger, the red deer *Cervus elaphus*, the fallow deer *Dama dama* and the wild boar *Sus scrofa* (boar and both deer species will be subsequently referred to as “ungulates”).

2.2. Sampling design

In each of our three study sites, we set up two 500m transects along SLD verges and two parallel transects of the same length located 60m away from SLD, in the scrubland. Along each transect in Matagorda and Reserva, we sampled fifteen (12m²) plots placed equidistantly (around 27m apart), where we counted all fleshy-fruited shrubs as well as all rockroses (i.e. *Halimium* spp. and *Cistus* spp.). In the Rocina site, we proceeded in the same way except that we surveyed double-sized plots (24m²) to offset the local low densities of fleshy-fruited shrubs. We controlled for plot size in all analyses to enable meaningful among-sites comparisons.

We classified fleshy-fruited shrub species into three functional groups according to their main dispersal vectors in our study sites (Table 1): (1) species whose seeds are mostly dispersed by rabbit and fox, (2) species whose seeds are mostly dispersed by ungulates and badger, and (3) species that in Doñana are mostly dispersed by birds (according to Jordano 1984, 1995). Rockroses were used as control species because they have not any dispersal mechanism (Bastida and Talavera, 2002).

Furthermore, we measured the height, and the maximum and minimum diameter (their product estimates the volume occupied by each individual) of every fleshy-fruited shrub within the sampling plots. Shrubs were then classified into three size classes: seedlings (plants with cotyledons and/or with a volume lower than 100cm³), adults (plants with flowers, fruits or their remains and/or with a volume higher than 8.5m³), and saplings (plants outside the other categories). Due to logistic limitations, rockroses could not be measured and thus were excluded from some analyses (see below).

2.3. Statistical analyses

To assess whether recruitment and establishment in relation to SLD varied according to shrub dispersal vector, we determined the combined influence of habitat (SLD verges vs. scrubland) and dispersal vectors in the density of both fleshy-fruited shrubs and rockroses. We used the number of shrubs found per plot (standardized by using the plot area as offset variable) as the response variable with habitat, dispersal vector and their interaction as fixed factors in a generalized linear mixed model (GLMM) with negative binomial distribution (which was more appropriate than Poisson

distribution for our zero-inflated count data; Quinn and Keough, 2002) and log-link function (by means of SAS 9.2 glimmix procedure; Littell et al., 2006).

We also evaluated the effect of SLD on the size structure of the three functional groups of fleshy-fruited shrubs. To do so, we fitted a GLMM with negative binomial distribution and log-link function with the number of fleshy-fruited shrubs found per plot (standardized by plot area as above) as the response variable, and habitat, dispersal vector, size class and their second- and third-order interactions as fixed factors.

In our mixed models, site and plot (nested within site) were included as random factors to control for environmental heterogeneity. For interactions, we tested the effect of one factor on the different levels of the other factor ("tests of simple main effects") using the SLICE option in the LSMEANS statement (Littell et al., 2006). Adjusted means and standard errors were calculated using the LSMEANS statement, which estimates the marginal means over a balanced population.

To characterize shrub community structure in relation to SLD, we built two matrices (one for fleshy-fruited shrubs and one for rockroses) with the number of shrubs found per plot of each species considering all size classes within each habitat. We evaluated the similarities in the plant community between the habitats using the ADONIS procedure (permutational multivariate analysis of variance using distance matrices) in the VEGAN package (Oksanen et al., 2012). It was performed in R 2.15.0 (R development core team, 2012) with 9999 permutations and the pairwise Bray-Curtis approximation (Bray and Curtis, 1957). In the fleshy-fruited shrub matrix we removed three plots from the analysis due to absence of any shrub species. ADONIS reports a *P*-value estimated by repeated permutations of the data (Oksanen et al., 2012) that indicates potential differences in shrub species composition and diversity between habitats.

3. Results

3.1. Influence of dispersal vectors on shrub density and community structure in relation to SLD

We found fleshy-fruited shrubs and rockroses in 49.4% and 93.89% of the sampled plots (*n* = 180), respectively. Overall, we

Table 1
Mean (±SE) density of each shrub taxa per plot (12m²) along SLD verges and 60m away in the scrubland. The major dispersal vector of each taxa – selected based on the references provided below – is shown.

Plants	SLD verges	Scrubland	Dispersal vector	References
<i>Fleshy-fruited shrubs</i>				
<i>Asparagus</i> spp.	0.32±0.09	0.67±0.30	Ungulate	Suárez-Esteban et al. (2013)
<i>Pistacia lentiscus</i>	0.23±0.11	0.20±0.06	Ungulate	Suárez-Esteban et al. (2013)
<i>Myrtus communis</i>	0.03±0.02	0.18±0.12	Ungulate	Suárez-Esteban et al. (2013)
<i>Chamaerops humilis</i>	0.17±0.07	0.36±0.18	Badger	Suárez-Esteban et al. (2013), Fedriani and Delibes (2011)
<i>Pyrus bourgaeana</i>	0.10±0.09	0.08±0.06	Badger	Suárez-Esteban et al. (2013), Fedriani and Delibes (2009b)
<i>Rubia</i> spp.	1.01±0.46	0.27±0.25	Birds	Jordano (1984, 1995)
<i>Osyris alba</i>	0.44±0.32	0.33±0.23	Birds	Jordano (1984, 1995)
<i>Rhamnus oleoides</i>	0.30±0.10	0.29±0.09	Birds	Jordano (1984, 1995)
<i>Daphne gnidium</i>	0.27±0.10	0.11±0.06	Birds	Jordano (1984, 1995)
<i>Olea europaea sylvestris</i>	0.02±0.02	0.02±0.02	Birds	Jordano (1984, 1995)
<i>Tamus communis</i>	0.01±0.01	0.00±0.00	Birds	Jordano (1984, 1995)
<i>Juniperus phoenicea turbinata</i>	0.60±0.19	0.13±0.07	Rabbit/Fox	Suárez-Esteban et al. (2013)
<i>Phillyrea angustifolia</i>	0.87±0.36	0.43±0.18	Rabbit	Suárez-Esteban et al. (2013)
<i>Rubus ulmifolius</i>	0.08±0.05	0.01±0.01	Fox	Suárez-Esteban et al. (2013)
<i>Rockroses</i>				
<i>Halimium halimifolium</i>	10.14±1.33	9.79±1.13	None	Bastida and Talavera (2002)
<i>Halimium calycinum</i>	3.18±0.59	3.44±0.47	None	Bastida and Talavera (2002)
<i>Cistus salvifolius</i>	0.90±0.37	0.87±0.27	None	Bastida and Talavera (2002)
<i>Cistus libanotis</i>	0.29±0.10	1.92±0.47	None	Bastida and Talavera (2002)
<i>Cistus crispus</i>	0.07±0.04	0.00±0.00	None	Bastida and Talavera (2002)

located 678 fleshy-fruited shrubs belonging to 14 species (Table 1), with 59.14% and 40.86% of individuals found within SLD and scrubland plots, respectively. Rockroses were more abundant but less diverse than fleshy-fruited shrubs. Overall, we found 2754 individuals belonging to only five rockrose species (Table 1), with 47.64% located within SLD plots and 52.36% within scrubland plots.

As predicted, the dispersal vector affected the distribution of shrubs in relation to SLD (interaction Habitat*Dispersal vector; $F_{3,623} = 4.70$; $P < 0.01$). Whereas the density of rockroses and ungulate/badger-dispersed fleshy-fruited shrubs was similar between habitats, rabbit/fox- and bird-dispersed species reached 2.7 and 2.0 times higher densities along SLD verges, respectively (Fig. 1).

As we expected, matrix analyses performed with the ADONIS procedure showed that the community structure (species composition and diversity) of both fleshy-fruited shrubs ($F_{1,56} = 1.66$; $P = 0.09$) and rockroses ($F_{1,59} = 1.94$; $P = 0.11$) did not significantly differ between SLD verges and the scrubland.

3.2. Size distribution of fleshy-fruited functional groups in relation to SLD

Considering seedling, saplings and adults altogether, the overall density of fleshy-fruited shrubs was 2.2 times greater along SLD verges than in the scrubland ($F_{1,1513} = 15.13$; $P < 0.001$). However, the relative density of each size class varied between habitats (interaction Habitat*Size class; $F_{2,1513} = 3.73$; $P < 0.05$). The density of seedlings and adults was 5.2 (test of slices; $F_{1,1513} = 11.02$; $P < 0.001$) and 1.7 ($F_{1,1513} = 3.59$; $P = 0.058$) times higher along SLD verges than in the scrubland, respectively, whereas the density of saplings was very similar between both habitats ($F_{1,1513} = 0.90$; $P = 0.342$; Fig. 2).

Nonetheless, while the density of saplings was similar between habitats for every plant functional group (Fig. 2), the differences in the density of seedlings and adults between habitats varied among different plant functional groups. Regarding bird-dispersed species, we found 29.9 times greater seedling density along SLD verges as compared with the scrubland, and a similar density of adult shrubs in both habitats (Fig. 2A). In the case of rabbit/fox-dispersed species, we found 3.2 times and 4.2 times greater seedling and adult densities along SLD verges than in the scrubland, respectively (Fig. 2B). Despite the lack of significant differences for some size classes, the trend of shrub densities was positively related with

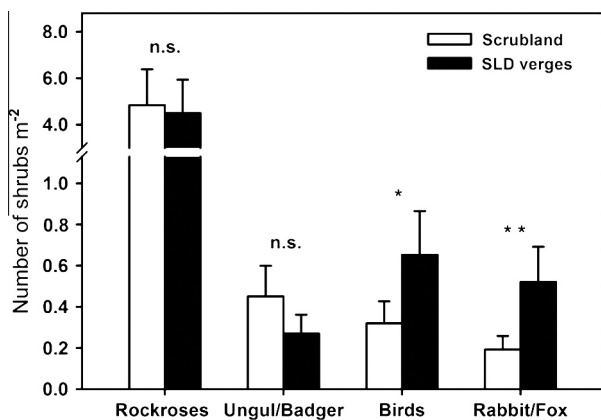


Fig. 1. Differences in the adjusted mean density (\pm SE) of rockroses and fleshy-fruited shrubs between habitats. Whereas the density of rockroses and ungulate/badger-dispersed fleshy-fruited shrubs did not differ between habitats, the density of both bird- and rabbit/fox-dispersed fleshy-fruited shrubs were higher along SLD than in the scrubland. P-values of the corresponding test of slices are shown, indicating whether the differences between habitats were significant (n.s., non-significant; * $P < 0.05$, ** $P < 0.01$).

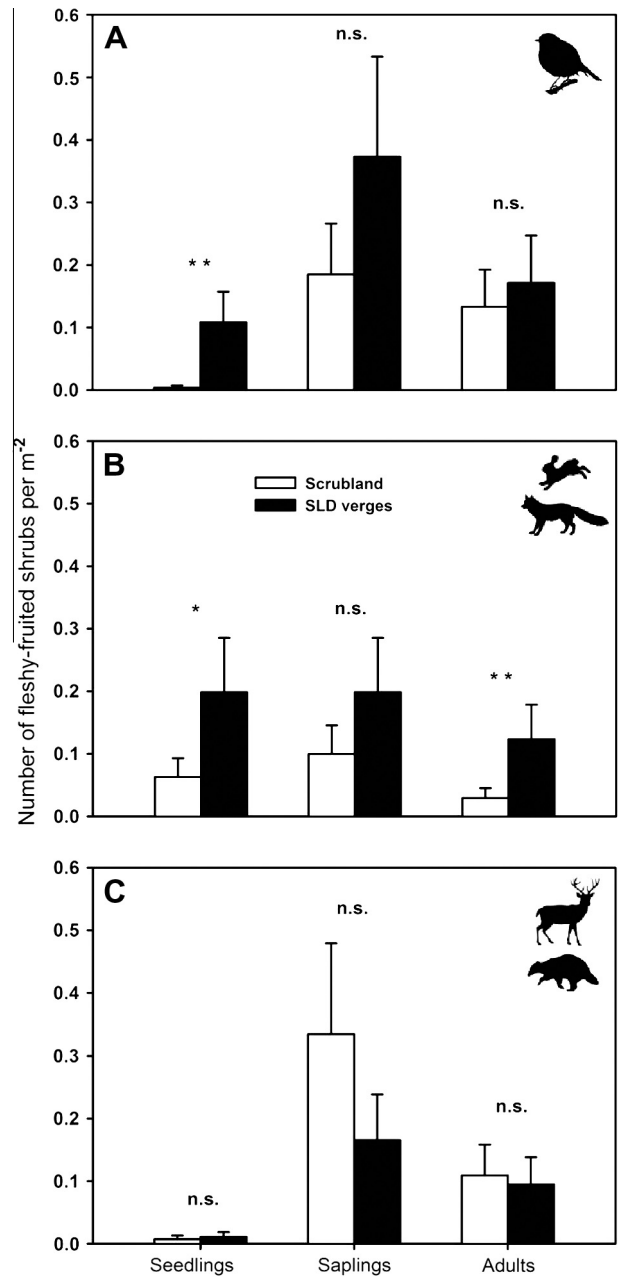


Fig. 2. Differences in the mean density (\pm SE) of shrub size classes between habitats in the three functional groups of fleshy-fruited shrubs (bird-dispersed, above; rabbit/fox-dispersed, middle; ungulate/badger, below). P-values of the differences of least square means are shown, indicating whether the differences between habitats were significant in each case (n.s., non-significant; ** $P < 0.01$; **** $P < 0.0001$). Interestingly, rabbit/fox-dispersed fleshy-fruited species appeared in higher densities along SLD verges than in the scrubland either at seedling or adult stage. Thus the presence of SLD is likely promoting their recruitment and establishment.

SLD in both plant functional groups (Fig. 2A and B). However, the absence of differences between habitats in the density of ungulate/badger-dispersed species was consistent for all size classes (Fig. 2C).

4. Discussion

Although seed arrival does not guarantee plant recruitment and establishment, it seems to play an important role in determining

shrub recruitment in relation to SLD in the Doñana area. As expected based on the observed seed rain (Suárez-Esteban et al., 2013), rabbit/fox-dispersed fleshy-fruited shrubs reached greater densities along SLD verges than in the adjacent scrubland, whereas rockroses showed similar densities in both habitats. These results add support to the hypothesis that plant community responses to habitat structure are strongly influenced by seed dispersal vectors, corroborating evidence from other studies (Damschen et al., 2008; Higgins et al., 2003).

Unexpectedly, we found also higher densities bird-dispersed species along SLD verges than in the scrubland. We suspect this is probably related to a more intensive seed rain generated by frugivorous birds selecting as perches fleshy-fruited shrubs already established along SLD verges, which provide birds with shelter and food resources (Hinsley and Bellamy, 2000). A similar seed reception of bird-dispersed species has been documented in other linear plant formations such as windbreaks (Harvey, 2000) and hedgerows (Pulido-Santacruz and Renjifo, 2011). Contrary to our prediction, ungulate/badger-dispersed shrub densities were similar between habitats, perhaps because badger occurs in low densities (Fedriani and Delibes, 2009b) and ungulates disperse few viable seeds of local fleshy-fruited shrubs (Perea et al., 2013; Suárez-Esteban et al., 2013).

Because mammalian and avian frugivores disperse different shrub species, they probably have a complementary and synergic effect on plant recruitment and establishment along SLD verges rather than being functionally redundant (Loiselle et al., 2007). Furthermore, different species within the local mammal community disperse seeds of different shrubs into different habitats (Fedriani et al., 2010; Perea et al., 2013; Suárez-Esteban et al., 2013), promoting plant spatial heterogeneity. Therefore, the maintenance of diverse communities of frugivores is necessary to ensure plant diversity conservation (McConkey et al., 2012; Ozinga et al., 2009) and ecosystem resilience (Loiselle et al., 2007), especially in fragmented landscapes where long-distance dispersal of plants relies on seed rather than on pollen movement (Damschen et al., 2008).

The greater density of seedlings found along SLD verges suggests that these structures can be suitable places for shrub recruitment. However, the overall density of saplings suggests that the proportion of seedlings that reached the sapling stage was greater in the scrubland (Fig. 2). This can be due either to a lower seedling conspicuousness for herbivores in the scrubland or to higher seedling mortality (mainly driven by herbivory, competition and water stress during the Mediterranean summer; Kitajima and Fenner, 2005; Tormo et al., 2006), along SLD verges. For example, the positive selection of SLD by rabbits (Suárez-Esteban et al., 2013) can lead to higher local herbivory pressure on seedlings and thereby higher mortality. Indeed, Rost et al. (2012) found that rabbits predate large amounts of Mediterranean hackberry (*Celtis australis*) seedlings in habitats similar to our study sites.

On the other hand, considering the density of adult plants, the proportion of saplings that reached the adult stage seemed to be higher along SLD verges. That could be due to a stronger herbivory pressure on saplings by large herbivores such as deer, which avoid SLD (Suárez-Esteban et al., 2013). This hypothesis is consistent with the results of (Cadenasso and Pickett, 2000), showing that meadow voles (*Microtus pennsylvanicus*) predate greater amounts of seedlings along forest edges than in forest interiors, whereas white-tailed deer (*Odocoileus virginianus*) feed mainly on saplings within the forest. The relative importance of seedling and sapling predators is known to differ among communities and microhabitats (Kitajima and Fenner, 2005). Thus, beyond seed arrival, the suitability of SLD verges as recruitment and establishment habitats will depend also on the identity and the abundance of herbivores, and their response to SLD.

As expected, we found no differences in the community structure of both fleshy-fruited species and rockroses between SLD verges and the adjacent scrubland. This is likely because rockroses lack of special dispersal mechanisms, and frugivores visit all kind of habitats with some regularity and thus all of them receive some seeds of every fleshy-fruited shrub species. Such similarity in species composition and diversity suggest that SLD verges recruit a species pool equivalent to that found in the scrubland, contrary to the patterns detected both along some paved roads (Arévalo et al., 2010) and forest edges (Harper et al., 2005).

Given the higher density and comparable species diversity of fleshy-fruited shrubs along SLD verges as compared with the scrubland, SLD verges (usually considered to be marginal, low-quality habitats) could yield poorly understood conservation benefits. Furthermore, the pervasiveness of SLD in almost every terrestrial ecosystem gives our findings potentially wide and important applicability in vegetation restoration and conservation programs.

4.1. Implications for plant conservation and landscape management

Planting narrow tree strips is a proper method to favor the maintenance of plant diversity in fragmented landscapes, as well as to control erosion and to soften local microclimate conditions (e.g. wind, temperature, humidity; Harvey, 2000). Conserving highly mobile frugivores that positively selected SLD verges for fecal marking (such as rabbits and foxes), and by promoting the growth of native plant recruits, stakeholders can reforest SLD verges without any cost, creating natural hedgerows (i.e. shrub strips). Hedgerows will likely attract seed-dispersing wildlife (Hinsley and Bellamy, 2000; Johnson and Adkisson, 1985) and create favorable microclimate conditions for the establishment of new recruits (Harvey, 2000), which boost both seed arrival and plant recruitment (Pulido-Santacruz and Renjifo, 2011), leading to a reforestation feedback.

Shrubs that colonize SLD verges can spread to adjacent habitats, especially those species dispersed by highly mobile animal vectors (Brudvig et al., 2009). In farmlands, such "spillover" effect of plants established along SLD hedgerows, which often act as reservoirs and corridors for native plants (Freemark et al., 2002; Wehling and Diekmann, 2009), can accelerate the reforestation of abandoned fields by native species, probably hindering the colonization success of exotics (Standish et al., 2008). This could be particularly important in southern Europe, considering the high rates of farmland abandonment and consequent risk of exotic plant invasion (Lenda et al., 2012). Furthermore, the diversity of plants in SLD hedgerows may offer habitat and resources for beneficial insects (Mwangi et al., 2012), bats (Fuentes-Montemayor et al., 2011) and birds (Hinsley and Bellamy, 2000) that in turn provide ecosystem services such as pollination (Blake et al., 2012) and pest control (Boyles et al., 2011) in agricultural lands.

In human-dominated landscapes, habitat patches are usually separated by long distances, so plants may be unable to disperse between them, requiring establishment, growth and reproduction within intermediate habitats (Damschen et al., 2008). Given the high density of reproductive fleshy-fruited shrubs found along SLD verges (especially those dispersed by rabbits and foxes), we believe these structures can act as effective corridors for fleshy-fruited shrubs, serving both as movement conduits and as stepping stone habitats for the establishment of new plant populations. In the long term, such intermediate populations can connect otherwise isolated fragments, even boosting the migration of fleshy-fruited plants vulnerable to climate change (Hampe, 2011; Jump and Peñuelas, 2005). That will improve gene flow and metapopulation dynamics (Leidner and Haddad, 2011), benefiting plant diversity at large scales, such as documented for linear, narrow clear-cuts (Damschen and Brudvig, 2012; Damschen et al., 2006).

To take advantage of all the described potential benefits of SLD verges holding shrubs, which certainly deserve further research (Haddad and Tewksbury, 2005; Ries et al., 2001), these stripes of habitat must be cautiously managed. Traditional roadside and hedgerow management practices, including periodical mowing and the use of herbicides, are highly unadvisable (Avon et al., 2013). In order to increase shrub abundance, diversity and structural complexity along SLD verges, we suggest selectively removing undesirable species and to cut only potentially dangerous branches/shrubs rather than using destructive and unselective methods that remove any shrubby cover.

This is the first study documenting the potential role of SLD verges as pervasive hotspots not only for the reception of seeds, but also for the recruitment and the establishment of many Mediterranean fleshy-fruited shrubs. Although SLD verges occur in high densities worldwide and hold a high potential as plant conservation habitats, the extension of these results to larger scales and ecosystems are complicated by lack of data and must proceed with caution. Beyond seed dispersal, processes influencing the dynamics of shrub colonization (e.g. germination, seedling emergence and survival, growth) along SLD verges remain largely unexplored. Long-term comprehensive studies are therefore necessary to understand SLD effects on each step of the plant life cycle, helping us to close the seed dispersal loop (Wang and Smith, 2002) in human-dominated ecosystems. Such essential information would bring stakeholders the opportunity to design and manage SLD more efficiently whenever plant conservation and landscape restoration efforts are necessary.

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