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-fruit 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-fruit 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 rockroses (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-fruit 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 road sides may act as stepping stones 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 favour the diversity and the structural complexity of native vegetation while preventing the spread of invasive species.

1. Introduction

Plants are sessile organisms that rely on pollinators 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 endozoochory (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 they ingest 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), wind breaks (Harvey, 2000), perches (Shiels and Walker, 2003) and resting sites (Russo et al., 2006) lead to plant recruitment and establishment (Wenyn, 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 (Wenyn, 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
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 detailed evaluation of seed arrival and seedling recruitment (Hampe, 2011; Sagnard et al., 2007). For example, some studies have found that experimentally clearing off forest can enhance bird-mediated seed dispersal (Leyvraz et al., 2005; Tewksbury et al., 2002) and that this seed corrioreffect improves connectivity, which in turn promotes plant diversity at different scales (Damschen and Brundo, 2012; Damschen et al., 2006). In the same line, an ecotones study in SW Spain (Suárez-Esteban et al., 2013) has suggested that pervasive human–made structures devoid of vegetation, such as trails and fire breaks (called “soft linear developments”; hereafter SLD), can act as seed receptors for native fleshy-fruit shrubs, especially fleshy-fruit seed 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 these 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 crucial 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-fruit 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-fruit species varied in relation to SLD, as a consequence of the feral 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-fruit shrubs dispersed by rabbits and foxes (which defeated 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-fruit shrubs dispersed by ungulates and badgers (Meles meles; which defeated mainly in the scrubland; Suárez-Esteban et al., 2013), and (3) higher rocky substrate 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, drought, herbivory, etc.) could alter these seed templates (Fedrani et al., 2012; Gómez-Aparicio, 2008), we also expected (4) a stronger concordance between seed rain and the density of seedlings of fleshy-fruit shrubs than regarding saplings and adult shrubs. Finally, given that fleshy-fruit 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-fruit 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 (82.5%) and fire breaks (35.5%). The Doñana’s scrubland-harborsadiverse and spatially variable community of native Mediterranean shrubs. To encompass most shrub species present in the area, we chose the 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 ladanifer, Halimium calcicolum, Halimium halimifolium, and gorses (Stauracanthus spp.). It has also a relative high presence of fleshy-fruit species such as Juniperus phoenicea subsp. tuburina, Phyllirea angustifolia and Rubus ulmifolius (overall density is 0.4±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 in dense stands of Cyrtisus grandiflorus, H. halimifolium, and Stauracanthus spp. Fleshy-fruit-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 salviifolius and H. halimifolius, with a variable extension, and a diverse and dense community of fleshy-fruit-plants such as Chamärops humilis, Daphne gignidi, 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 the fleshy-fruit species flower during late winter and spring (February–May) and produce drupes (e.g., P. lentiscus, R. ulmifolius) or berries (e.g., C. communis) throughout the year (Fedrani and Delibes, 2009a; Jordana, 1984). Depending on the species, each fruit contains generally from one to nine seeds (Suárez-Esteban et al., 2013). They are mainly dispersed by birds and mammals (Fedrani and Delibes, 2009b, 2011; Jordana, 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 indisturbed and burned habitats (Guzmán and Vargas, 2009). They are occasionally dispersed by ungulates (Malo and Suárez, 1996).

Suárez-Esteban et al. (2013) found that the seed rain of fleshy-fruit shrubs varied near and away from SLD, depending on the feral marking behavior of the main dispersal vectors. Specifically, 79.49% (N=13,066) of J. phoenicea, P. angustifolia and R. ulmifolius seeds were dispersed along SLD verges, mostly by the European rabbit and the red fox. Contrary, 88.91% (N=451) of A. asparagi spp., C. humilis and P. lentiscus seeds were dispersed in the scrubland (away from SLD), mostly by the Eurasian badger and 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 the four study sites, we set up two 500 m transects along SLD verges and two parallel transects of the same length located 60 m away from SLD in the scrubland. Along each transect, at each of the four study sites, we sampled 12 plots (each 1 m × 1 m) at 12 m intervals. Within each plot, we counted all fleshy-fruited shrubs, as well as rockroses (I. Halimium spp. and Cistus spp.) that were present. We also sampled plants with seedlings or small saplings (plots outside the category of fleshy-fruited shrubs) to assess the influence of habitat on the density of fleshy-fruited shrubs and rockroses. We used the number of fleshy-fruited shrubs 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's glmix procedure; Littell et al., 2006).

We also evaluated the effect of SLD on the structure of the three functional group 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, the site and plot (nested within site) were included as random factors to control 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 the entire population.

To characterize shrub community structure in relation to SLD, we built two models (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 similarity in the plant community between each habitat 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 the absence of any shrub species. ADONIS reports a p-value estimated by permutation 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>
<thead>
<tr>
<th>Plants</th>
<th>SLD Verges</th>
<th>Scrubland</th>
<th>Dispersal vector</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fleshy-fruited shrubs</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Arangus spp.</td>
<td>0.32±0.09</td>
<td>0.67±0.30</td>
<td>Ungulate</td>
<td>Suárez-Esteban et al. (2013)</td>
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<td>Pitaclolentiscus</td>
<td>0.23±0.11</td>
<td>0.20±0.06</td>
<td>Ungulate</td>
<td>Suárez-Esteban et al. (2013)</td>
</tr>
<tr>
<td>Myrtus communis</td>
<td>0.03±0.02</td>
<td>0.18±0.12</td>
<td>Ungulate</td>
<td>Suárez-Esteban et al. (2013)</td>
</tr>
<tr>
<td>Chamaerops humilis</td>
<td>0.17±0.07</td>
<td>0.36±0.18</td>
<td>Badger</td>
<td>Suárez-Esteban et al. (2013), Fedrian and Delibes (2011)</td>
</tr>
<tr>
<td>Pyrus bourgeana</td>
<td>0.10±0.09</td>
<td>0.08±0.06</td>
<td>Badger</td>
<td>Suárez-Esteban et al. (2013), Fedrian and Delibes (2009b)</td>
</tr>
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<td>Rubus spp.</td>
<td>1.01±0.46</td>
<td>0.27±0.25</td>
<td>Birds</td>
<td>Jordano (1984, 1995)</td>
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<td>Osyris alba</td>
<td>0.44±0.32</td>
<td>0.33±0.23</td>
<td>Birds</td>
<td>Jordano (1984, 1995)</td>
</tr>
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<td>Rhamnus oleoides</td>
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<td>0.29±0.09</td>
<td>Birds</td>
<td>Jordano (1984, 1995)</td>
</tr>
<tr>
<td>Daphne gnidium</td>
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<td>0.11±0.06</td>
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<td>Jordano (1984, 1995)</td>
</tr>
<tr>
<td>Olea europaea sylvestris</td>
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<td>0.02±0.02</td>
<td>Birds</td>
<td>Jordano (1984, 1995)</td>
</tr>
<tr>
<td>Tamarix communis</td>
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<td>0.00±0.00</td>
<td>Birds</td>
<td>Jordano (1984, 1995)</td>
</tr>
<tr>
<td>Juniperus phoenicea turbinata</td>
<td>0.60±0.19</td>
<td>0.13±0.07</td>
<td>Rabbit/Fox</td>
<td>Suárez-Esteban et al. (2013)</td>
</tr>
<tr>
<td>Phylirea angustifolia</td>
<td>0.87±0.36</td>
<td>0.43±0.18</td>
<td>Rabbit</td>
<td>Suárez-Esteban et al. (2013)</td>
</tr>
<tr>
<td>Rubus ulmifolius</td>
<td>0.08±0.05</td>
<td>0.01±0.01</td>
<td>Fox</td>
<td>Suárez-Esteban et al. (2013)</td>
</tr>
<tr>
<td>Rockroses</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Halimium calcicola</td>
<td>3.18±0.59</td>
<td>3.44±0.47</td>
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<td>Cistus salvi folius</td>
<td>0.90±0.37</td>
<td>0.87±0.27</td>
<td>None</td>
<td>Bastida and Talavera (2002)</td>
</tr>
<tr>
<td>Cistus ladanifer</td>
<td>0.29±0.10</td>
<td>1.92±0.47</td>
<td>None</td>
<td>Bastida and Talavera (2002)</td>
</tr>
<tr>
<td>Cistus incanus</td>
<td>0.07±0.04</td>
<td>0.00±0.00</td>
<td>None</td>
<td>Bastida and Talavera (2002)</td>
</tr>
</tbody>
</table>
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; $F_{1,1512} = 11.02; P < 0.001$) 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 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-fruiting shrubs reached greater densities along SLD verges than habitats adjacent to 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 more intensive seed rain generated by frugivorous birds selecting as perches fleshy-fruiting 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 lower densities (Fedianni and Delibes, 2009b) and ungulates disperse fewer viable seeds of local fleshy-fruiting shrubs (Pereietal., 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 (Fedianni et al., 2010; Pereietal., 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 within the scrubland (Fig. 2). This can be due to the lower seedling mortality (mainly driven by herbivory, competition and water stress during the Mediterranean summer; Kitajima and Fenner, 2005; Tormoet 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, Rostet al. (2012) found that rabbit predation is a large datum 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 larger 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 responses to SLD.

As expected, we found no differences in the community structure of both fleshy-fruiting species and rockroses between SLD verges and adjacent scrubland. This is likely because rockroses lack of special dispersal mechanisms, and frugivores visit all kinds of habitats with some regularity and thus all of them receive some seeds of every fleshy-fruiting 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-fruiting 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 most terrestrial ecosystems gives our findings potentially wide and important implications 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 select SLD verges for ecological 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 Adiksson, 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.

Shrub that colonizes SLD verges can spread to adjacent habitats, especially those species dispersed by highly mobile animal vectors (Brudvig et al., 2009). Inland farms, such as “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 that the highrates 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-dominant 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-fruiting shrubs found along SLD verges (especially those dispersed by rabbits and foxes), we believe these structures can act as effective corridors for fleshy-fruiting shrubs, serving as movement conduits and 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-fruiting plants vulnerable to climate change (Hampe, 2011; Jump and Peñuelas, 2005). That will improve gene flow and metapopulation dynamics (Leinier and Haddad, 2011), benefiting plant diversity at larger 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 strips of habitat must be cautiously managed. Traditional roadside and hedgerow management practices, including periodic 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 shrub 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 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 the long-term lifecycle, 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 forestation efforts are necessary.

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