



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



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ABSTRACT

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 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-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 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 favor the diversity and the structural complexity of native vegetation while preventing the spread of invasive species.

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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 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), 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 (Brederfeld 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 km) 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 later 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”).

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