

UNIVERSIDAD DE OVIEDO

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**"Ingenieros del paisaje en Doñana: Efecto combinado de las estructuras lineales
y las interacciones planta-animal sobre el matorral mediterráneo"**

"Ecological engineers in Doñana: combined effect of linear structures and plant-
animal interactions on the Mediterranean scrubland"

TESIS DOCTORAL

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Ingenieros del paisaje en Doñana

Efecto combinado de las estructuras lineales y las interacciones planta-animal sobre el matorral mediterráneo.

Ecological engineers in Doñana

*Combined effect of linear structures and plant-animal interactions
on the Mediterranean scrubland*



Doctorado en Recursos Biológicos y Biodiversidad

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A mi familia

A los amantes de la naturaleza

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Introducción general

La biodiversidad es equivalente a un motor, en el que multitud de piezas (e.g. genes, individuos, especies, poblaciones) con una determinada organización espacial, interaccionan funcionalmente entre sí y con el ambiente, proporcionando bienes y servicios ecosistémicos (e.g. alimentos, agua, oxígeno, fibras, energía, medicamentos, control de plagas, regulación climática, reciclado de residuos, valor terapéutico, estético y cultural, recreo, etc.; Schröter et al., 2005). La alteración de los hábitats naturales, la sobreexplotación de recursos, el cambio climático, la invasión de especies exóticas, y otros componentes del cambio global están deteriorando la biodiversidad a una velocidad vertiginosa (Vitousek et al., 1997), poniendo en jaque el abastecimiento de bienes y servicios necesarios para el bienestar humano (Schröter et al., 2005, Barnosky et al., 2012).

Incrementar nuestro conocimiento sobre el funcionamiento de los ecosistemas es fundamental para garantizar su conservación y un uso sostenible de los bienes y servicios que nos proveen (Kremen, 2005, MacDougall et al., 2013, Willis et al., 2007, Tomimatsu et al., 2013). La capacidad de soportar perturbaciones (*resiliencia*) y de proveer servicios de los ecosistemas está fuertemente ligada a las interacciones biológicas (i.e. las conexiones dentro del motor; Tylianakis et al., 2008, Bastolla et al., 2009, Bascompte et al., 2006). Son especialmente importantes las interacciones en las que están implicadas las plantas, ya que constituyen la base sobre la que se asientan la mayor parte de los sistemas vivos, y por tanto definen de forma decisiva la estructura y la diversidad de los ecosistemas terrestres (Isbell et al., 2011).

Muchas plantas dependen de su interacción con animales para completar su ciclo vital. Plantas y animales interactúan de múltiples formas mediadas por el paisaje, al que a su vez condicionan y modelan. Por ello, algunos de éstos organismos son considerados *ingenieros del paisaje* (Jones et al., 1994). La influencia humana, muy intensa en la mayor parte de los ecosistemas (Vitousek et al., 1997), añade una nueva e importante

variable a la relación entre plantas, animales y paisaje (Tylianakis et al., 2008). Por ejemplo, las alteraciones de los hábitats naturales conllevan a menudo cambios comportamentales o la extinción local de algunos animales, lo que a su vez conllevaría la extinción local de las plantas que dependen de ellos para polinizar sus flores o dispersar sus semillas (McConkey et al., 2012).

Esta tesis trata de interacciones entre plantas y animales, y de un caso particular de alteración del hábitat: las infraestructuras lineales humanas, concretamente caminos y cortafuegos. Ambos temas han sido ampliamente abordados en la literatura científica, como veremos. Sin embargo, y pese a sus potenciales consecuencias sobre la dinámica de las poblaciones de plantas, prácticamente no habían sido considerados conjuntamente hasta ahora.

Antecedentes

Basados en sus observaciones de campo en el Parque Nacional de Doñana, José M^a Fedriani y Miguel Delibes de Castro, sospecharon que las altas densidades de arbustos que se observaban en los bordes de caminos y cortafuegos de Doñana (Fig. 1) podrían deberse al efecto combinado de las estructuras lineales y las interacciones planta-animal (fundamentalmente la dispersión de semillas).

Este proyecto de tesis surgió precisamente de su interés por averiguar los mecanismos ecológicos que explicaban la sorprendente alta densidad de arbustos en las lindes de estructuras lineales humanas.

Puesto que cada uno de los capítulos de esta tesis incluye una introducción detallada y orientada al tema específico tratado en el mismo, remito a dichas introducciones, y me limitaré a exponer aquí brevemente las líneas generales de la ecología de carreteras, por un lado, y de las interacciones planta-animal, por otro, ubicando los distintos capítulos en el contexto del efecto potencial de las primeras sobre las segundas, y sus consecuencias sobre la vegetación.



Figura 1: Seto de sabinas (*Juniperus phoenicea* subsp. *turbinata*) en el *camino del control*, que conecta la carretera A-483 (Almonte-Matalascañas) con el Palacio de Doñana.

Ecología de carreteras

Como consecuencia del crecimiento de la población humana y las necesidades de transporte y accesibilidad, estructuras lineales como carreteras, autopistas, caminos, pistas, cortafuegos, etc. han alcanzado densidades extremadamente altas en prácticamente todos los ecosistemas terrestres (Forman et al., 2003, Forman, 1998). Además, su construcción suele implicar la apertura de otras estructuras lineales accesorias (Forman, 2004), y su efecto sobre los hábitats que atraviesan suele extenderse más allá de los límites de la superficie que ocupan (Forman, 2000, Avon et al., 2010, Fuentes-Montemayor et al., 2009). Por todo ello, cabe suponer que cualquier efecto de estas estructuras lineales en los ecosistemas, sea positivo o negativo, puede ser enorme. Precisamente para entender y solventar los impactos de algunas de esas estructuras, surgió como disciplina científica la ecología de las carreteras, o «*Road Ecology*» (Forman et al., 2003).

Desde el nacimiento de esta rama de conocimiento se han descrito un sinnúmero de efectos perjudiciales de las carreteras para los ecosistemas, tanto terrestres como

acuáticos. Entre ellos destacan: destrucción y fragmentación del hábitat (Reed, 1996), aislamiento entre poblaciones (efecto barrera; Forman and Alexander, 1998, Mader, 1984), muerte de organismos sésiles o poco móviles durante la fase de construcción (Trombulak and Frissell, 2000), muerte de organismos por colisión con vehículos (Alisa W, 2007, Bennett, 1991, Taylor and Goldingay, 2004, Fahrig and Rytwinski, 2009), alteración del comportamiento animal (Sage Jr et al., 1983, Develey and Stouffer, 2001, Kerley et al., 2002, McLellan and Shackleton, 1988), alteración del medio físico y químico (Legret and Pagotto, 2006, Trombulak and Frissell, 2000), mejora del acceso humano y posterior incremento de la presión sobre los recursos naturales (Laurance et al., 2008, Laurance et al., 2006, Laurance et al., 2009), y propagación de especies invasoras (Arteaga et al., 2009, Brown et al., 2006, Chen et al., 2012, Christen and Matlack, 2009, Craig et al., 2010, Gelbard and Belnap, 2003).

Casi todos estos efectos negativos han sido descritos para carreteras pavimentadas de mayor o menor extensión. Sin embargo, existen otras estructuras lineales como caminos, pistas forestales y cortafuegos, con unas características que hacen prever que sus potenciales efectos han de ser mucho más suaves (Lugo and Gucinski, 2000). Por ejemplo, estas estructuras suelen tener una anchura mucho menor que las autopistas o las carreteras pavimentadas, lo que reduce la superficie directa e indirectamente afectada por la estructura y también la probabilidad de atropello de fauna (Lugo and Gucinski, 2000). Además, suelen ser mucho menos transitadas, lo que probablemente atenúe los posibles cambios comportamentales derivados del tráfico y las perturbaciones humanas en general (ruido, contaminación, caza, deforestación, invasión de especies, etc.; Ramp et al., 2006, Lugo and Gucinski, 2000). Todo esto sugiere que el potencial efecto barrera de caminos, pistas y cortafuegos probablemente sea mucho menor que el esperable para autopistas y carreteras. Por ello, cabe considerar a caminos, pistas y cortafuegos como estructuras lineales “suaves” (en adelante «*Soft Linear Developments*»; **SLD**; Fig. 2).



Figura 2: Ejemplos de SLD en distintos lugares de la Península Ibérica. Pese a ser estructuras lineales dedicadas a mejorar la accesibilidad humana a distintos lugares, su construcción no implica una transformación del medio tan aparente como la asociada a carreteras pavimentadas y autopistas.

Pese a que su impacto sobre los ecosistemas puede ser menor, la densidad de SLD a escala global es realmente elevada, incluso en zonas protegidas. Por ejemplo, en el Parque Nacional de Doñana (Huelva), la densidad de caminos y cortafuegos es tal que más del 80 % de la superficie del Parque se encuentra a menos de 200 metros de una de éstas estructuras (Román et al., 2010). Dada su omnipresencia, conocer sus potenciales efectos ecológicos es una cuestión clave para la conservación de la biodiversidad.

Ingeniería ecológica: las interacciones planta-animal condicionan el paisaje

En ecosistemas terrestres, la mayor parte de los servicios ecosistémicos dependen directa o indirectamente de las plantas (Isbell et al., 2011), organismos sin capacidad de movimiento autónomo y por tanto particularmente sensibles a cualquier alteración ambiental.

Aunque las plantas adultas prácticamente no pueden desplazarse, sus estructuras reproductoras, el polen y las semillas, pueden servirse de diversos vectores para hacerlo. Algunas plantas han desarrollado adaptaciones como, por ejemplo, estructuras que permiten su transporte por el viento (e.g. semillas aladas, como las sámaras de los arces), por el agua (e.g. semillas flotantes, como los cocos de las palmeras) o adheridas a

animales (e.g. semillas con ganchos, como las de muchas herbáceas). Otras han establecido relaciones con multitud de animales, a quienes atraen gracias a la producción de ciertas recompensas. Por ejemplo, a cambio de ofrecer polen y/o néctar, las plantas con flores consiguen atraer animales polinizadores (e.g. insectos, aves, murciélagos) que transportan polen de unas flores a otras, favoreciendo su fecundación y la producción de frutos y semillas (Klein et al., 2007, Ashman et al., 2004).

Una de las estrategias de dispersión de semillas más generalizada entre las plantas es la producción de frutos (Jordano et al., 2011, Fleming and Estrada, 1993). A cambio de proveer de alimento a animales frugívoros, las semillas de las plantas son ingeridas y transportadas fuera del entorno materno, lo que suele implicar ciertas ventajas como escapar de predadores y parásitos asociados a las plantas madre, evitar la competencia con congéneres, y aumentar la probabilidad de encontrar un lugar favorable en el que asentarse (Janzen, 1970, Howe and Smallwood, 1982, Wenny, 2001). Además, los procesos de ingestión y digestión pueden afectar, a menudo mejorándola, a la capacidad de germinación de las semillas (Traveset, 1998, Traba et al., 2006, Delibes et al., 2012), siendo incluso imprescindibles para la germinación de algunas especies.

Una vez las semillas son depositadas sobre el terreno, si sobreviven al ataque de depredadores y patógenos, y las condiciones ambientales son propicias, pueden germinar dando lugar a plántulas. Si esas plántulas consiguen sobrevivir, a su vez, asentándose y creciendo, darán lugar a una nueva planta reproductora, cerrando el ciclo (Wang and Smith, 2002). Las interacciones con animales, que también pueden ser negativas (e.g. los depredadores de semillas y los herbívoros limitan fuertemente el número de plántulas y plantones que alcanzan la edad reproductora (Hulme, 1997, Olofsson et al., 2004), condicionan de forma decisiva la transición de un estadio de desarrollo al siguiente en el ciclo vital de las plantas (Fig. 3). Por ello, algunos animales son capaces de definir el paisaje vegetal, actuando como *ingenieros del paisaje*.

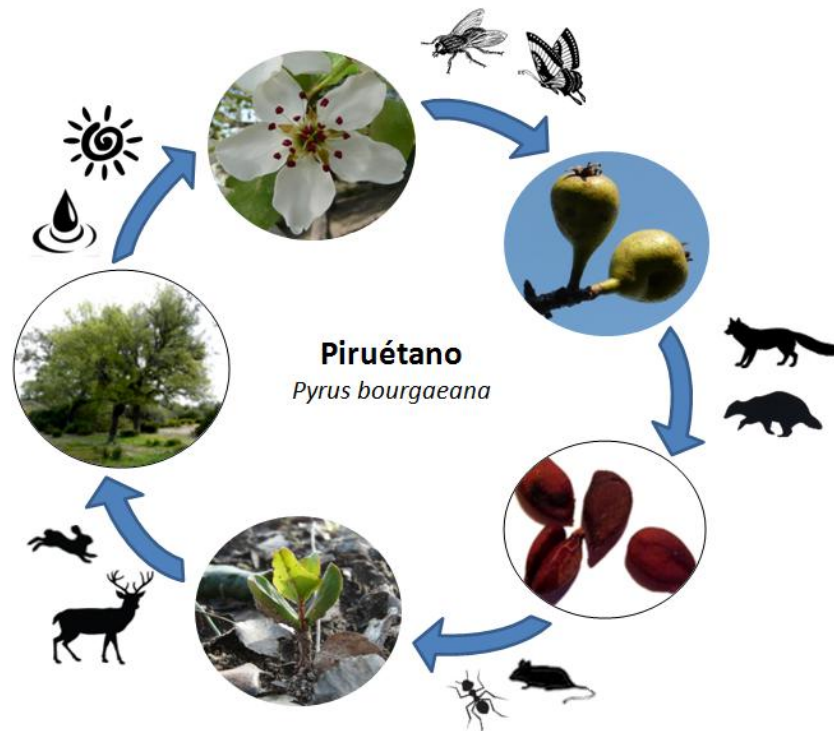


Figura 3: Esquema del ciclo vital del piruétano (*Pyrus bourgaeana*), con 5 fases (adulto, flor, fruto, semilla y plántula) y las interacciones con animales (polinización por insectos, dispersión de semillas por mamíferos, depredación de semillas por ratones y hormigas, herbivoría por ungulados y lagomorfos) y las condiciones ambientales (importantes en todo el ciclo), que intervienen en la transición de una fase a otra.

Los patrones, mecanismos y consecuencias de las interacciones entre plantas y animales están caracterizados por una acusada variación espacial y temporal (Thompson, 2005). La presencia de SLD añade una nueva fuente de variación, ya que éstas estructuras son capaces de alterar profundamente las poblaciones de plantas, animales y sus interacciones (e.g. modificando localmente las condiciones ambientales, la abundancia de animales y plantas, el comportamiento de los animales, etc.; Magrach et al., 2011, Ness and Morin, 2008, Cadenasso and Pickett, 2000). Pese a la omnipresencia y abundancia de SLD, no se conocen sus potenciales efectos sobre las interacciones planta-animal, y las consecuencias que tales efectos pueden conllevar para las comunidades de plantas y, por tanto, para la estructura y la funcionalidad de los ecosistemas terrestres. Esta carencia de conocimiento científico básico nos limita a la hora de minimizar los efectos ecológicos negativos de las SLD y de potenciar los positivos. Solamente a través de la investigación de los efectos de las SLD sobre las comunidades vegetales lograremos gestionar ambos de forma eficaz.

Objetivos

El objetivo de esta tesis doctoral es evaluar en detalle los efectos de las SLD sobre las interacciones entre plantas y animales y, en consecuencia, sobre la configuración espacial, la abundancia y la diversidad del matorral mediterráneo. Para abordar este amplio objetivo, lo desgranamos en varios objetivos concretos siguiendo el ciclo vital de los arbustos y sus interacciones con animales, expuestos en la figura 3.

En el Capítulo 1 se analiza el efecto de las SLD sobre la polinización por escarabajos y la depredación de flores y frutos por ungulados, y sus consecuencias para la producción de frutos y semillas del jaguarzo (*Halimium halimifolium*). Mediante un experimento de campo se responderá a preguntas tales como: ¿Afecta la proximidad de SLD a la eficiencia de la polinización? ¿Y a la tasa de herbivoría sobre las flores?

En el Capítulo 2 se evalúa cómo las SLD afectan a la dispersión de semillas de arbustos de frutos carnosos. Concretamente, se comparará la cantidad de semillas que llegan a los bordes de SLD y al matorral adyacente, dispersadas por distintos mamíferos terrestres que difieren en el uso del espacio.

En el Capítulo 3 se estudiará experimentalmente el efecto de las SLD sobre la supervivencia post-dispersiva de semillas de arbustos de frutos carnosos. Para ello se comparará el número de semillas depredadas por roedores, aves y hormigas granívoros tanto en los bordes de SLD como en el matorral adyacente.

En el Capítulo 4 se examinará mediante una siembra experimental cómo condicionan las SLD la emergencia y supervivencia temprana de plántulas.

En el Capítulo 5 se cuantificarán la abundancia y la diversidad de arbustos en relación a las SLD, lo que aportará una visión indirecta del efecto acumulado de las SLD sobre el conjunto de fases del ciclo vital de los arbustos (analizadas en los objetivos anteriores), junto con la supervivencia tardía, es decir, la transición del estadio juvenil al de adulto. Finalmente se discutirán las implicaciones de los resultados encontrados para el manejo de las SLD y el matorral mediterráneo.

Área de estudio

La investigación del efecto de las SLD sobre las interacciones planta-animal y sus consecuencias en el matorral mediterráneo tuvo lugar entre octubre de 2009 y junio de 2013 en el Parque Nacional de Doñana (542,5 km²; 37° 9' N, 6° 26' W; altura 0–80 m), localizado en la margen oeste del río Guadalquivir, en la provincia de Huelva (suroeste de España; Fig. 4).

El clima de Doñana es mediterráneo sub-húmedo, caracterizado por veranos secos y calurosos, e inviernos suaves y húmedos. La precipitación anual es muy variable, con una media de 577 mm (\pm 39 error estándar; SE) en los últimos 30 años. La distribución de las lluvias a lo largo del año es irregular, con el 88.4% de la pluviosidad concentrado entre octubre y abril (datos del Programa de Seguimiento de Procesos Naturales de la Estación Biológica de Doñana; <http://www-rbd.ebd.csic.es/Seguimiento/seguimiento.htm>)

El área de Doñana alberga dos principales sustratos edáficos:

- Sustrato arcilloso, que permite la formación de extensas marismas de inundación estacional.
- Sustrato arenoso, sobre el que se asientan multitud de ecosistemas como: dunas móviles, dunas fijas, matorral mediterráneo, y bosques de repoblación de pino piñonero (*Pinus pinea*) y eucalipto (*Eucalyptus* spp.).

Esta tesis se centra en el matorral mediterráneo, que a su vez está compuesto por distintas comunidades vegetales. Dos de las más características y abundantes son:

- Monte blanco: compuesto por arbustos pirófitos como jaras (*Cistus crispus*, *C. libanotis*, *C. salvifolius*, etc.), jaguarzos (*Halimium calicinum*, *H. halimifolium*), aulagas (*Genista* spp., *Stauracanthus* spp., *Ulex minor*), romeros (*Rosmarinus officinalis*) y tomillos (*Thymus mastichina*), y también de arbustos de frutos carnosos con una amplia tolerancia a la escasez de agua, como la esparraguera (*Asparagus* spp.), la camarina

(*Corema álbum*), el enebro marítimo (*Juniperus macrocarpa*) y la sabina mediterránea (*Juniperus phoenicea* subsp. *turbinata*), entre otros.

- **Monte negro:** ubicado en zonas de mayor humedad, compuesto por arbustos como brezos (*Calluna vulgaris*, *Erica scoparia*), madresevas (*Lonicera* spp), zarzamoras (*Rubus ulmifolius*), sauces (*Salix* spp.), zarzaparrillas (*Smilax aspera*), y también por helechos (*Pteridium aquilinum*) y arbustos de mayor porte como madroños (*Arbutus unedo*) y mirtos (*Myrtus communis*).

El Parque Nacional de Doñana es un lugar ideal para evaluar el efecto de las SLD sobre el matorral mediterráneo ya que, además de la gran diversidad de especies arbustivas (y de animales que interaccionan con ellas) que alberga, presenta un sistema de más de 2.000 km de SLD, concretamente caminos de tierra (62.5 %) y cortafuegos (35.5 %), implementado hace más de 50 años (Román et al., 2010).

Sitios de estudio

Con el fin de extraer conclusiones generalizables a la totalidad del Parque Nacional de Doñana, e incluso a otras áreas de matorral mediterráneo, todos los objetivos concretos se abordaron en tres sitios de estudio con comunidades vegetales distintas y separados entre sí entre 3 y 14 Km, dentro del Parque Nacional de Doñana:

Matasgordas: finca situada al noreste de la aldea de El Rocío (Fig. 4), en la que se distinguen principalmente dos hábitats:

- **Pastizal adhesionado** (al sur; Fig. 5A), históricamente deforestado para la apertura de pastos para el ganado, dominado por herbáceas y grandes alcornoques (*Quercus suber*) remanentes. Actualmente se observan procesos de recolonización de matorral noble como lentiscos (*Pistacia lentiscus*), piruétanos (*P. bourgaeana*), y sobre todo palmitos (*Chamaerops humilis*) y tarajes (*Tamarix* spp.).

- Matorral mediterráneo (Fig. 5B), localizado al noreste, y dominado principalmente por alcornoques y lentiscos de gran porte (de ahí el nombre de la finca), así como grandes parches de jaguarzo (*H. halimifolium*) y una densidad notable de otros arbustos de frutos carnosos como palmitos, torviscos (*Daphne gnidium*), mirtos, acebuches (*Olea europaea* var. *sylvestris*), olivillas (*Phillyrea angustifolia*) y piruétanos. La investigación tuvo lugar en esta zona de matorral.

Reserva biológica de Doñana (RBD): finca situada en el suroeste del Parque Nacional (Fig. 4) y gestionada por la Estación Biológica de Doñana del CSIC. Pese a su gran extensión y variedad de ecosistemas (matorral, dunas, lagunas, pinares, marisma, etc.), este estudio se desarrolló en un área más reducida, en torno al *camino del control* (Fig. 1). Esta zona está dominada por amplios parches de monte blanco, algunas zonas de monte negro (ligadas a cursos temporales de agua o “caños”, a lagunas y al agua freática) y un sabinar bien desarrollado (Fig. 5C).

La Rocina: zona periférica al arroyo de la Rocina, en el norte del Parque Nacional (Fig. 4). En las inmediaciones del arroyo se observa un bosque de ribera bien desarrollado con madroños, fresnos mediterráneos (*Fraxinus angustifolia*), álamos blancos (*Populus alba*), alcornoques, sauces y tarajes. Rodeando al bosque de ribera se localiza una franja de arbustos como brechinas, acebuches, piruétanos, coscojas (*Quercus coccifera*) y ruscos (*Ruscus aculeatus*). La zona más distante al arroyo está compuesta por matorral mediterráneo dominado por pino piñonero y un denso sotobosque de monte blanco (Fig. 5D). En éste último, además de las especies ya mencionadas, destaca la presencia de escobones (*Cytisus grandiflorus*).

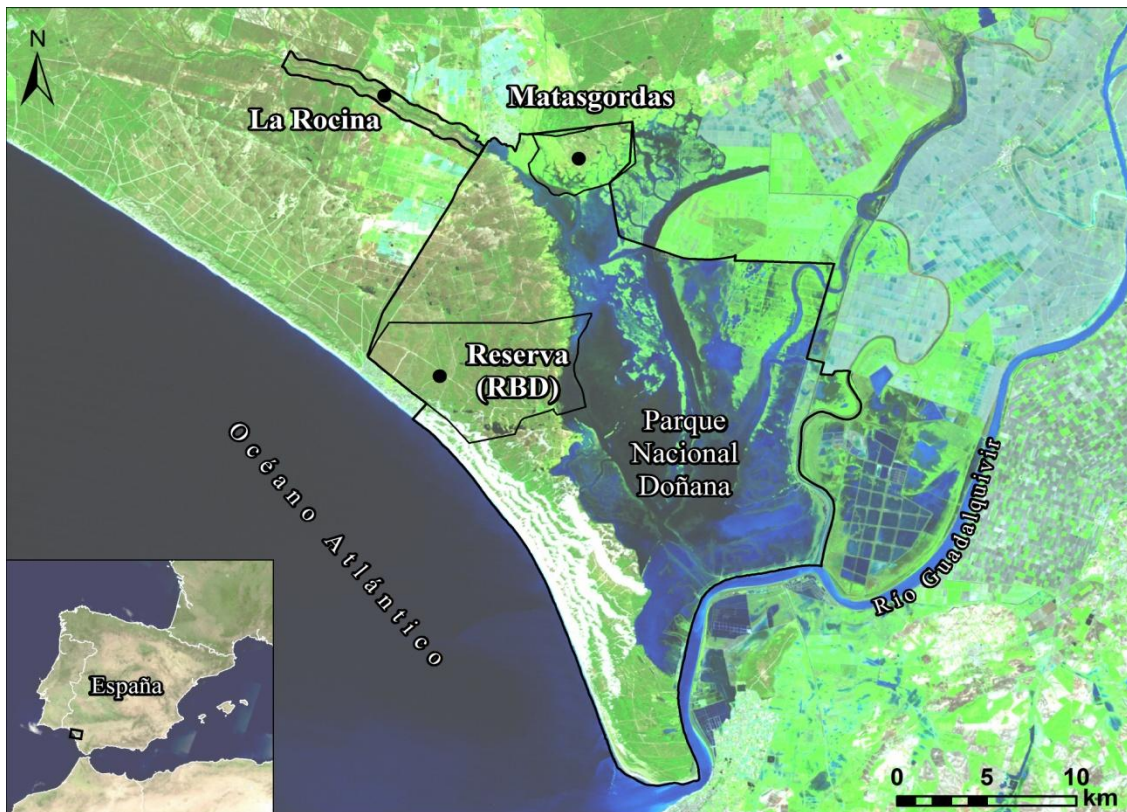


Figura 4: Situación geográfica del Parque Nacional de Doñana, en el que se muestran los tres sitios de estudio donde tuvo lugar la recogida de datos para la realización de esta tesis doctoral.

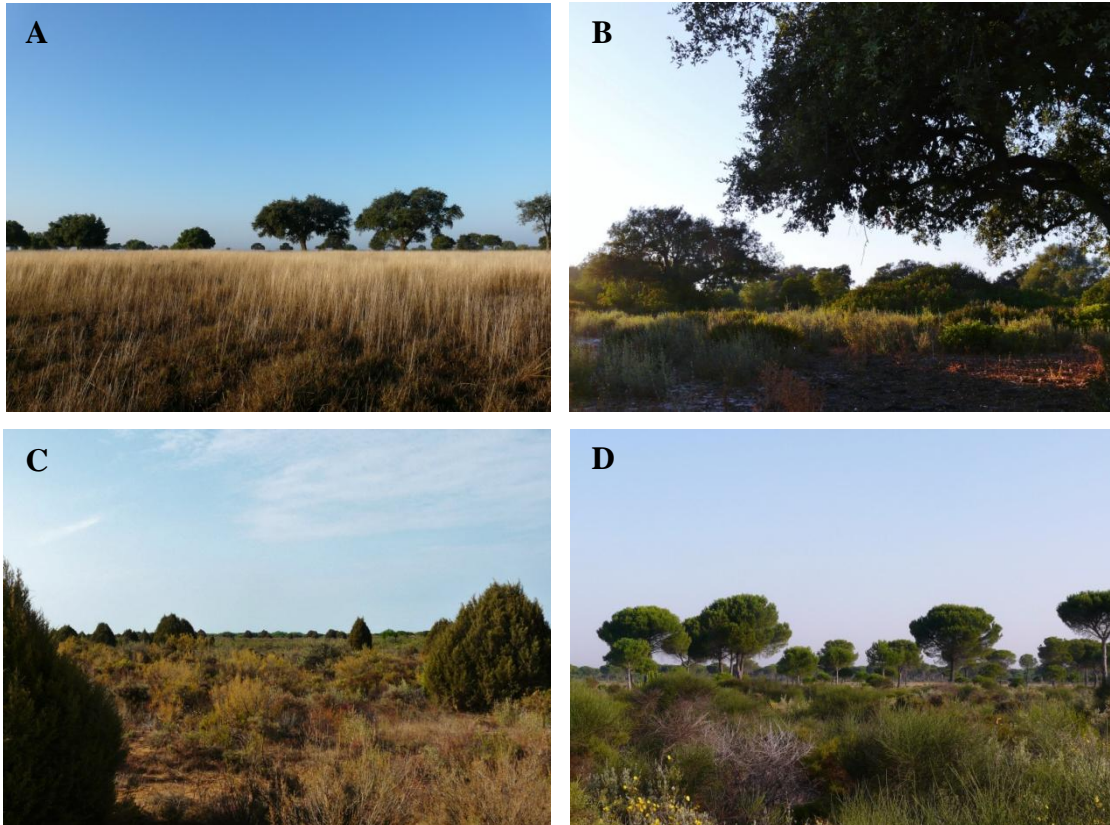


Figura 5: Paisajes representativos de (A) la zona de pastizal adhesado y (B) la zona de matorral mediterráneo de Matasgordas; (C) el entorno del sabinar de la RBD; y (D) los pinares de La Rocina.

Chapter 1

Combined effect of unpaved roads, pollinators and herbivores on the reproductive performance of a dominant Mediterranean shrub



Resumen: La interacción con polinizadores, básica para la producción de frutos y semillas para muchas plantas, puede verse alterada por modificaciones del hábitat como las SLD, y también por herbívoros a través del ramoneo de ramas y flores. En este capítulo se evalúa el efecto de la triple interacción entre polinizadores, herbívoros y SLD sobre el éxito reproductivo de un arbusto mediterráneo: el jaguarzo.

Abstract

Cross-pollination is essential for fruit and seed production in the majority of wild and crop plants. The interaction between pollinators and plants can be altered by habitat features, as well as by large herbivores (e.g. flower and fruit browsing, trampling).

In humanized landscapes, one of the most widespread habitat modifications is the construction of linear developments, such as trails and firebreaks, also called Soft Linear Developments (SLD). SLD are known to alter the spatial behavior of both pollinators and herbivores, but little is known about the combined effect of these three elements on plant reproduction.

We evaluated the combined effect of SLD, pollinators and herbivores (ungulates) on the reproductive output (i.e. fruit and seed set, and seed mass) of a dominant, beetle-pollinated Mediterranean shrub (*Halimium halimifolium*) in three independent sites during two consecutive years. We simulated three scenarios of pollination (total absence, natural level and unlimited pollination) and two scenarios of herbivory (with and without ungulates), at two different habitats (SLD verges vs. the adjacent scrubland).

SLD had conflicting effects on *H. halimifolium* reproduction. Although SLD limited the negative effect of ungulates on fruit set, this benefit was overcome by negative effects on natural pollination that led to an overall lower fruit set along SLD verges than in adjacent scrublands. This lower fruit set along SLD verges was likely due to local deficient pollination. However, the number of seeds produced per fruit did not vary between habitats. Seed mass was negatively correlated with seed number in both SLD and adjacent scrublands.

We propose to promote the establishment (e.g. by seeding or conserving seed dispersers, and avoiding mowing and using herbicides) and conserve woody hedgerows along SLD verges to mitigate their potential negative impacts on pollination, as well as to provide nesting and foraging resources for pollinators.

Introduction

Countless crops and wild plants depend on the exchange of pollen mediated by animal vectors (e.g. insects, birds, bats) to produce seeds (Klein et al., 2007, Ashman et al., 2004, Burd, 1994). Seeds have a magnificent importance on the population dynamics of plants, conditioning for instance their persistence and colonization ability (Howe and Smallwood, 1982). Any disruption in the plant-pollinator interaction can lead to decreased fruit and seed production, with potential negative consequences for plant populations (Anderson et al., 2011, Huang et al., 2009, Wilcock and Neiland, 2002). At present, pollinators are declining globally due to habitat loss and fragmentation (i.e. reduced availability of feeding and nesting resources), agriculture intensification (which usually involves pesticide and herbicide application), the spread of pests and pathogens, alien species and climate change (Potts et al., 2010, Kearns et al., 1998). This is likely to have a huge impact on pollination and thereby on wild plant populations and on agricultural yields in the medium and long term (Hayter and Cresswell, 2006, Wilcock and Neiland, 2002, Garibaldi et al., 2011, Biesmeijer et al., 2006).

At smaller scales, pollinator abundance and behavior can be either negatively or positively influenced by certain human-made habitat transformations (Elliott et al., 2012, Brosi et al., 2007). The presence of human-made linear developments (e.g. roads, trails, firebreaks, railways) usually results in increased habitat fragmentation and edge effects (e.g. dust deposition on flowers, micro-climate extreme conditions, increased pollinator mortality; Cunningham, 2000, Huang et al., 2009, Kolb, 2008, Jules and Rathcke, 1999; but see Magrach et al., 2013) that can reduce the abundance of plants and pollinators, and also affect the behavior of the latter. For example, roads can reduce flower visitation rates by pollinating birds (Geerts and Pauw, 2011; but see Francis et al., 2012, Magrach et al., 2011). This often leads to pollen and thereby to fecundity limitations (Aguilar et al., 2006, Ashman et al., 2004).

On the other hand, linear development verges often host flourishing grasslands that provide suitable habitats for pollinators, favouring their abundance and diversity (Hopwood, 2008, Ries et al., 2001, Noordijk et al., 2009). Furthermore, the verges of linear structures such as trails and firebreaks (also called *Soft Linear Developments*, SLD; Suárez-Esteban et al., 2013a) may host shrub hedgerows (Karim and Mallik, 2008, Suárez-Esteban et al., 2013b) that can also assist pollination by providing habitat, food resources and shelter to pollinators (Schmucki and De Blois, 2009, Rands and Whitney, 2010, Hannon and Sisk, 2009, Van Rossum and Triest, 2012, Morandin and Kremen, 2013). Although SLD are pervasive landscape elements that can affect plant-animal interactions such as seed dispersal (Suárez-Esteban et al., 2013a), little is known about their effect on pollination (but see Huang et al., 2009). For example, vegetation clearings similar to SLD indeed improve (rather than limit) movement rates of pollinators and thereby pollen transfers within a forest matrix (Townsend and Levey, 2005, Tewksbury et al., 2002, Haddad and Tewksbury, 2005).

In addition, SLD may have indirect effects on pollination by altering the outcome of the interactions between plant, herbivores and pollinators. For example, SLD may buffer the negative effects of large herbivores such as ungulates on pollination, since they usually avoid these structures (James and Stuart-Smith, 2000, Suárez-Esteban et al., 2013a). Herbivores can decrease (i) plant and flower density (Kolb, 2008, Gómez, 2003), (ii) flower rewards (Vázquez and Simberloff, 2004), and (iii) the amount of plant resources available for reproduction, by consuming vegetative tissues and by trampling (Vázquez and Simberloff, 2004, Herrera et al., 2002). That usually lead to a reduction in plant attractiveness for pollinators (Söber et al., 2010, Strauss et al., 1996, Lehtilä and Strauss, 1997), and thereby to lower visitation rates and pollen limitation, both in quantity and quality (Aizen and Harder, 2007). Also, herbivores can depredate fruits and seeds already produced, reducing the reproductive output of plants (Herrera et al., 2002).

Summing up, human-made structures such as SLD can have conflicting effects on pollination success. Negative edge and fragmentation effects might be compensated by

other SLD effects such as their potential suitability as habitats for pollinators (Hopwood, 2008), as well as the potential reduction in herbivory. Surprisingly, none study has assessed before the potential consequences of the interaction among human structures such as SLD, pollinators and herbivores on the plant reproductive output.

Here we evaluated the combined effect of SLD, pollinators and herbivory by ungulates on the reproductive output of *H. halimifolium* L. (*Cistaceae*) in several patches of Mediterranean scrubland. In doing so, we compare two measures of reproductive output (fruit and seed set) between two habitats (SLD verges and the scrubland), under two scenarios of herbivory (with and without ungulates). Through flower manipulation, we also performed three pollination treatments (total absence, natural level and unlimited pollination) in order to link pollination success and reproductive output in each target habitat (Cunningham, 2000). Furthermore, we measured seed mass to identify potential trade-offs between the number of seeds produced and their size (Primack, 1987), and evaluated whether such trade-off varied with the presence of SLD.

More specifically, we aimed to answer the following questions: is *H. halimifolium* pollen limited? If so, is pollen limitation affected by the presence of SLD? To what extent are ungulate herbivores limiting the reproductive output? Is that limitation buffered by SLD? Is seed mass affected by the presence of SLD or rather constrained by the number of seeds produced? Based on the literature, we could expect SLD effects on plant reproduction of contrasting strengths and directions. Consequently, the net effect of SLD on *H. halimifolium* predispersal reproductive performance was difficult to anticipate. We will discuss the implications of our findings for management and conservation programs, and provide some recommendations for future research.

Methods

Study system

The Doñana scrubland harbors a diverse community of native Mediterranean shrubs. Among them is our model species, *H. halimifolium* L., an abundant *Cistaceae*

shrub that grows in a wide range of environmental conditions in the Western Mediterranean. At Doñana, it dominates extensive scrubland patches from the marshland limit to mobile dunes (Díaz Barradas et al., 1999). Throughout the study area, it reaches similar high densities both along SLD verges (10.14 ± 1.33 indiv/m²; mean \pm SE) and in the scrubland (9.79 ± 1.13 ; Suárez-Esteban et al., 2013b).

H. halimifolium has large (up to 62 mm of diameter) hermaphrodite yellow flowers that bloom mainly in late-spring and early-summer (May-June; Herrera, 1988). Flowers appear grouped in apical inflorescences and are pollinated mainly by pollinophagous beetles, such as *Heliotaurus ruficollis* (Alleculidae), and less frequently by some bees (Halictidae; Herrera, 1986). Both groups of pollinators are equally observed either far or near from SLD (Authors personal observation). Fecundated flowers lead to small dry fruits that contain 25 seeds on average (Herrera, 1987). After the fruiting period, infrutescences dry off and usually drop their seeds on the ground. Though it lacks of any dispersal specialization, this species seem to have a great colonization ability, as documented in other *Cistaceae* species (Bastida and Talavera, 2002).

Within our study area, browsing ungulates such as the red deer *Cervus elaphus*, the fallow deer *Dama dama*, and livestock (e.g. cows, horses) reach high densities because of the absence of hunting pressure and natural predators. These ungulates can severely damage *H. halimifolium* plants (Silva et al., 1996), even removing entire inflorescences (Authors personal observation).

Experimental design

As pollination success can vary in time and space, we surveyed three different study sites called “Reserva”, “Rocina” and “Matasgordas” (described in detail in “Area de estudio”), during two consecutive years (2010 and 2011). At each site, we set up two independent experimental blocks separated by a minimum of 1 Km (Fig. 6). To assess whether SLD affect *H. halimifolium* reproductive output, we set up four plots (~ 36 m² each) within each experimental block. Two of the plots were set along SLD verges and

the other two were set in the scrubland, 60 meters away from SLD (since most edge effects cease to be significant within 50 m; Murcia, 1995; Fig. 6).

To evaluate whether SLD affect the interaction between pollination and herbivory, from the two plots in each of both habitats (SLD verges and scrubland) one was fenced to exclude large herbivores (e.g. deer, cattle), while another remained completely open (Fig. 6). All plots contained at least ten reproductive *H. halimifolium* individuals.

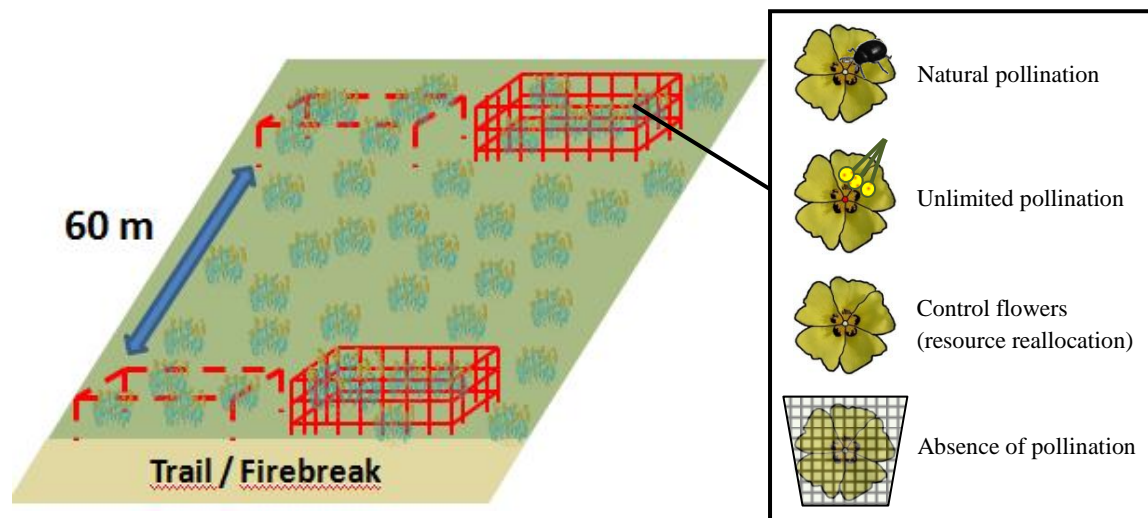


Figure 6: Scheme of one of the two experimental blocks that we set up in each of our three study sites, with open and fenced plots both along SLD verges and in the scrubland. We performed the pollination treatments showed on the right to 10 *H. halimifolium* individuals within each plot, as explained below.

To link pollination success and reproductive output (i.e. fruit and seed set, and seed mass), in each plot we performed three treatments: (a) absence of pollination (by bagging inflorescences), (b) natural pollination (by monitoring flowers), and (c) unlimited pollination (by pollen supplementation).

Absence of pollination

To establish whether SLD effects on pollination were due to changes in plant autogamy rates, after counting the flower-buds, we tagged and bagged a number of inflorescences (five in 2010 and two in 2011) to preclude pollinator access (Parker, 1997) in five randomly selected *H. halimifolium* plants within each plot. For this, we overall tagged and bagged 779 inflorescences with 53152 flowers.

Natural pollination

To evaluate whether SLD, ungulates and their interaction affect natural pollination, we tagged five inflorescences (when possible) of five *H. halimifolium* plants (different from the five used in the previous section) within each plot and counted their flowers that were exposed to natural pollination (hereafter “naturally-pollinated flowers”). For this, we overall tagged 1149 inflorescences with 80038 flowers.

Unlimited pollination

To link potential differences in the reproductive output between habitats with differential pollination requires to confirm that plant reproduction is pollen limited (Cunningham, 2000). In doing so, from the same five *H. halimifolium* plants whose inflorescences were bagged (see above), we randomly selected five open (different) inflorescences and added supplemental pollen by rubbing the stigma (until it was completely covered) of one randomly selected flower per inflorescence (hereafter “supplemented flower”), using collected anthers from distant (20-30 m) conspecifics.

Pollen addition may overestimate the magnitude of pollen limitation if plants reallocate resources from unmanipulated flowers to supplemented flowers (Knight et al., 2006, Haig and Westoby, 1988). To assess whether such resource reallocation occurs (thereby potentially conditioning our results), for each supplemented flower we labeled three control flowers: one within the same inflorescence as the supplemented flower (hereafter “intra-inflorescence control”), one in other inflorescence within the same plant (hereafter “inter-inflorescence level”), and the last one in other surrounding individual outside the plot (hereafter “external control”). All control flowers were exposed to natural pollination (no pollen was added). For this, we tagged and monitored 1034 flowers of each treatment (i.e. 4136 flowers overall).

After the flowering period (July-August), we counted the number of fruits set by all tagged inflorescences (either bagged or naturally-pollinated) and randomly sampled three fruits (when available). We also counted and collected all the fruits set by pollen-

supplemented and control flowers. All collected fruits were stored in paper bags and then lanced in the lab to count up the number of seeds produced per fruit and their mean mass (measured using a precision scale). In 2011 surveys, we selected the same individuals as in 2010 when possible.

Statistical analyses

To compare among pollination treatments, fecundity measures of all kind of flowers (i.e. bagged, naturally-pollinated, and pollen-supplemented) should be ideally analyzed within the same model. However, unbalanced sample sizes (i.e. number of monitored flowers) across treatments prevented to fit such a complex model successfully. Therefore, we opted to analyze separately each of the three treatments mentioned above. Fruit set of bagged flowers was ~2% in both habitats, confirming that *H. halimifolium* is mostly self-incompatible, and thus we excluded this treatment from the analyses.

To assess whether the habitat (SLD verges *vs.* scrubland), herbivory by ungulates (addressed by comparing open *vs.* fenced plots) and their interaction influenced the reproductive output of naturally-pollinated flowers, we fitted three generalized linear mixed models (GLMMs) with three different response variables: (1) the proportion of flowers that set fruits, i.e. fruit set, per inflorescence (using beta distribution and logit-link function), (2) the number of seeds produced per fruit, i.e. seed set (using negative binomial distribution and log-link function), and (3) the mean seed mass per fruit (using Gaussian distribution and identity-link function).

We fitted the same kind of models to address for potential variations in pollen limitation and resource reallocation (using data on supplemented and control flowers) between habitats and between open and fenced plots. When analyzing the fruit set, we fitted in this case a GLMM with logistic response (0 = no fruit set, 1 = fruit set), using binomial distribution and logit-link function. We found no evidence of resources reallocation from control flowers to supplemented flowers neither in the fruiting nor in

the seeding stage at any scale (fruit and seed set were similar among control flowers; $P > 0.05$).

All GLMMs were implemented by means of SAS 9.2 GLIMMIX procedure (Littell et al., 2006). In all models we considered the habitat (SLD verges *vs.* scrubland), herbivory by ungulates (open *vs.* fenced plots), and their interaction as fixed factors. When analyzing whether pollen limitation and resource reallocation varied among factor combinations, we also included the pollination treatment (i.e. pollen-supplemented, intra- and inter-inflorescence, and external controls) and its interactions with habitat and herbivory as fixed factors. When testing the average seed mass per fruit, we include the number of seeds per fruit as a covariate.

To compare the effects of different levels of any main factor, we calculated the differences between their least-square means (Fedriani et al., 2012). Following our experimental design, the year, the study site, the plot (nested within the site), and the plant (nested within plot) were included as random factors to control for temporal and spatial heterogeneity, as well as for potential individual effects. When testing the fruit set of naturally-pollinated flowers, we also included the number of flowers as a random factor to control for potential variations in flowering intensity among plants. For every model concerning seed set and seed weigh, we removed from the dataset all fruits that presented some fault (e.g. with depredated, unripe or rotten seeds), which were a minority.

Results

Natural pollination

Naturally-pollinated flowers set 27689 fruits (overall fruit set 34.6 %; $n = 80038$). We found significant differences in the fruit set between habitats (Table 1). Specifically, the fruit set was a 5.3 % higher in the scrubland as compared with SLD verges (Fig. 7). Overall, inflorescences within fenced plots set a similar proportion of fruits than inflorescences within open plots (herbivory by ungulates did not have an effect as main

factor; Table 1). Although the interaction between habitat and herbivory was not significant (Table 1), the differences in least-square means indicated that, in the scrubland, the fruit set within fenced plots (without ungulate access) was a 15.3 % higher than within open plots (accessible to ungulates; $F_{1,887} = 4.08$; $P = 0.04$; Fig. 7).

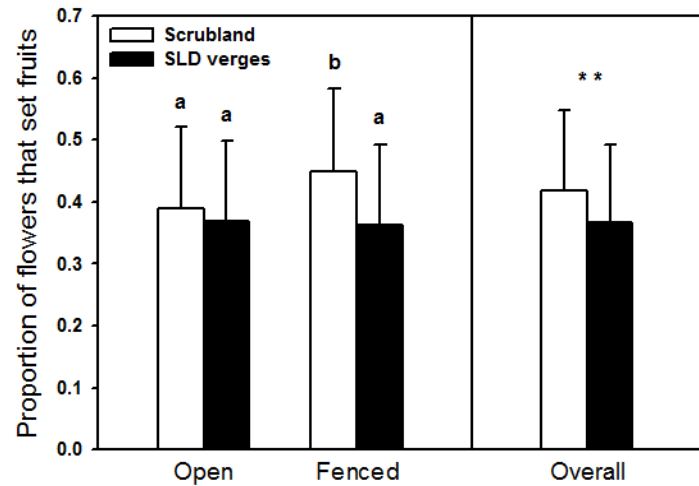


Figure 7: Model-adjusted means (\pm SE) of fruit set by naturally-pollinated flowers along SLD verges (black bars) and in the scrubland (white bars) between open and fenced plots (i.e. with and without ungulates, respectively). Letters and asterisk were used for showing whether the differences between least-square means were significant (** $P < 0.01$).

We collected 2612 fruits (9.43 %) to estimate the number of seeds per fruit set by naturally-pollinated flowers. The number of seeds produced per fruit ranged between 1 and 72. The mean number of seeds produced per fruit was similar between SLD verges (20.12 ± 1.81 ; mean \pm SE) and adjacent scrublands (21.87 ± 1.96 ; Table 1). We did not find a significant effect of herbivory by ungulates on seed set (Table 1). This lack of ungulate effect was consistent in both habitats (the interaction Habitat*Herbivory was not significant; Table 1).

Table 1: Results of the GLMMs fitted for testing the effects of habitat, herbivory, pollen-supplementation (Supplement) and their interactions on the fruit set, seed set and seed mass. P -values are represented by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$).

Factor	Natural pollination						Pollen limitation					
	Fruit set		Seed set		Seed mass		Fruit set		Seed set		Seed mass	
	df	F	df	F	df	F	df	F	df	F	df	F
Habitat	1,887	6.67**	1,2491	1.90	1,2491	0.22	1,4003	0.13	1,1369	3.73	1,1369	0.35
Herbivory	1,887	1.67	1,2491	0.002	1,2491	0.53	1,4003	0.26	1,1369	2.27	1,1369	0.05
Supplement	-	-	-	-	-	-	3,4003	128.06***	3,1369	39.04***	3,1369	17.20*
Habitat*Supplement	-	-	-	-	-	-	3,4003	2.20	3,1369	0.63	3,1369	0.83
Herbivory*Supplement	-	-	-	-	-	-	3,4003	1.75	3,1369	1.62	3,1369	0.93
Habitat*Herbivory	1,887	2.42	1,2491	0.13	1,2491	0.39	1,4003	2.99	1,1369	0.00	1,1369	0.17
Hab*Herb*Supplement	-	-	-	-	-	-	3,4003	0.47	3,1369	1.35	3,1369	3.96**

The averaged seed mass ranged between 0.10 and 1.10 mg. We found a strong negative and significant correlation between the mean number of seeds per fruit and the mean seed mass (slope = -0.004; $R^2 = 0.17$; $F_{1,2490} = 460.86$; $P < 0.0001$). As for the seed set, we did not detect any significant effect of habitat, herbivory, or their interaction on seed mass (Table 1).

Unlimited pollination

Considering supplemented and control flowers altogether, the fruit and the seed set were similar in both habitats and in open and fenced plots (neither habitat nor herbivory had an effect as main factors; Table 1). Pollen supplementation had a significant effect both in the fruit and the seed set (Table 1). As would be expected, supplemented flowers set 2.15-fold more fruits than controls (69.7 % vs. 32.4 % on average, respectively; Fig. 8A), and produced 6.36 more seeds on average than control flowers (Fig. 8B). However, the effect of pollen supplementation on fruit and seed set did not vary between habitats or

between fenced and open plots (Habitat*Supplement and Herbivory*Supplement were insignificant; Table1). Despite the lack of significant differences between habitats in the overall seed set, supplemented flowers produced 3.55 more seeds in the scrubland than along SLD verges on average (Fig. 8B).

Pollen supplementation led to an amplification of the negative and significant correlation between the number of seeds per fruit and the mean seed mass found in

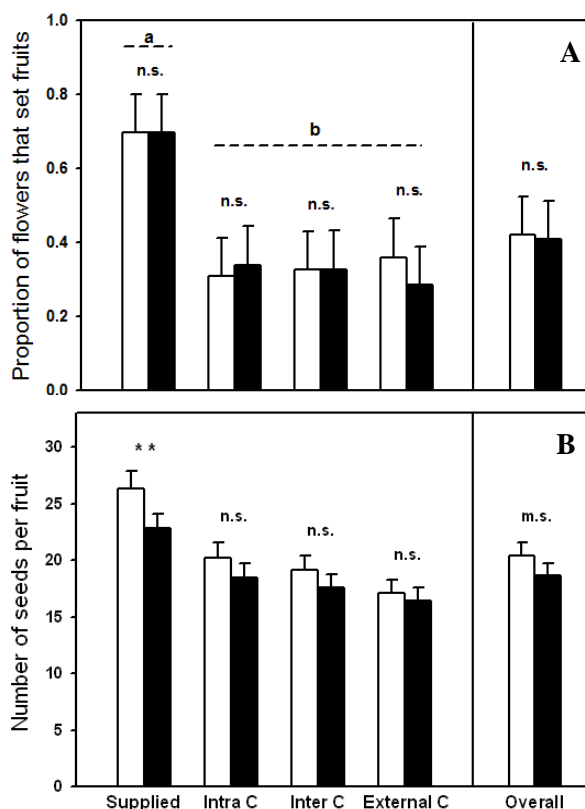


Figure 8: Model-adjusted means (\pm SE) of fruit (A) and seed (B) set by supplemented and control flowers. In general, no significant variations were found between SLD verges (black bars) and the scrubland (white bars). We found no evidence of resource reallocation. n.s. = non significant, $P > 0.05$; m.s. = marginally significant, $P = 0.054$; ** $P < 0.01$.

naturally pollinated flowers (slope = -30.24; $R^2 = 0.11$; $F_{1,1368} = 176.46$; $P < 0.0001$). As supplemented flowers produced more seeds than control flowers, the seeds produced by the latter were 0.19 mg heavier than the former on average. These differences were significant and consistent in both habitats and in both open and fenced plots (Table 1). Despite the third order interaction resulted significant (Table 1), we did not find any consistent trend or significant differences between habitats or between open and fenced plots in the mass of the seeds produced by each kind of flower (test of slices; $F_{3,1368} < 1.14$; $P > 0.45$).

Discussion

SLD effects on pollination

As found by Herrera (1987), bagged *H. halimifolium* barely produce fruits in either habitat, suggesting that this shrub is highly dependent on outcross pollination mediated by insects anywhere. Our study plants did not reallocate resources in response to pollen supplementation. These results suggest that the increased fruit and seed set under pollen supplementation truly represents pollen limitation (Parker, 1997, Burd, 1994). Pollen limitation was consistent in both habitats, i.e. pollen-supplemented flowers at either SLD verges or the scrubland set more fruits and seeds than naturally-pollinated flowers. This suggests that the lower fruit set of naturally-pollinated flowers found along SLD verges (as compared with the scrubland) was due mostly to the reception of fewer or poorer pollen than in the scrubland (Aizen and Harder, 2007).

Lower pollen arrival is usually associated to either lower visitation rates by pollinators (Kolb, 2008, Parker, 1997) or to lower pollinator efficiency in removing and transporting pollen (e.g. due to briefer visits; Wilson and Thomson, 1991, Aizen and Harder, 2007). Beyond pollinators, pollen loads can be also affected by abiotic conditions (Jules and Rathcke, 1999). As a matter of fact, we observed that flowers tended to close with windy weather, and exposition to wind is probably stronger at SLD verges, given the lack of surrounding protective vegetation. This could lead to briefer availability of *H.*

halimifolium open flowers to pollinators along SLD as compared with the scrubland, and therefore to a reduced likelihood of pollen receipt and fecundation.

Considering that naturally-pollinated flowers set more fruits in the scrubland than along SLD verges, the overall production of seeds in the scrubland was higher as compared with SLD verges. Although the number of seeds per fruit set by naturally-pollinated flowers was similar in both habitats, interestingly we found that pollen-supplemented flowers set a significantly higher number of seeds per fruit in the scrubland than along SLD verges (see “Supplied” in Fig. 8B). This suggests the existence of other SLD effects (e.g. dust deposition and interference with pollen, scarcity of resources) that would affect negatively the seed set when pollen is unlimited.

Although identifying the underlying mechanisms driving differences in reproductive output (i.e. fruits and seeds) between SLD verges and the scrubland was out of the scope of this study, all suggested mechanisms can be easily evaluated with a proper combination of observational and experimental approaches. For example, the amount and the quality of pollen that flowers receive can be evaluated by counting pollen tubes within the stigma (Alonso et al., 2012). The effect of dust interference with pollen on the seed set can be tested by comparing flowers that were supplemented with pollen and flowers that were supplemented with both pollen and dust.

Combined effect of SLD and ungulates on plant reproduction

Cadenasso and Pickett (2000) found that big ungulates such as the white-tailed deer (*Odoileicus virginianus*) often forage in the interior wooded areas, far from their edges. Likewise, after searching for ungulate fecal samples both along SLD and the scrubland in our three study sites, we found that these herbivores spent most of their time in the scrubland, far from SLD (Suárez-Esteban et al., 2013a). Thus, SLD may have a beneficial effect on plant life stages affected by large herbivores, such as reproduction. Indeed, ungulates negatively affected *H. halimifolium* fruit set, but only in the scrubland (Fig. 7).

We did not detect any significant effect of herbivory by ungulates on the number of seeds produced per fruit. This suggests that they mainly disrupt fruit set, probably by removing flowers and entire inflorescences (Sõber et al., 2010, Vázquez and Simberloff, 2004). By reducing the fruit set in the scrubland, ungulates reduced in turn the overall production of seeds in that habitat. However, this potentially positive effect of SLD was overcome by other negative effects on pollination (see above). We expect this herbivory repellence by SLD to be rather advantageous in other plant ontogenetic stages, such as the seedling and the sapling stage (Cadenasso and Pickett, 2000).

Seed number and size in relation to SLD

As demonstrated by other studies (e.g. Dupré and Ehrlén, 2002), we detected a strong trade-off between the amount and the size of produced seeds, regardless the presence of SLD (i.e. it occurred both along SLD and the scrubland, and both in naturally-pollinated and pollen-supplemented flowers). To produce many small seeds can be advantageous for colonization in seed limited environments, given that in plants without dispersal adaptations such as *Cistaceae* (Bastida and Talavera, 2002), heavier seeds are likely to disperse shorter distances (Bullock et al., 2003). On the other hand, heavier seeds often result in larger and more competitive seedlings (Krüsi and Debussche, 1988), probably improving local persistence through higher probability of establishment, especially when seed dispersal is not limited. Therefore, the consequences of this trade-off are certainly context-dependent.

Conclusions and implications

Effective management of plant populations in humanized ecosystems requires an understanding of the ecological drivers of plant reproduction and how they interact with pervasive human features. Our results suggest that SLD can have negative effects on pollination and thereby on the reproductive output of *H. halimifolium*, a beetle-pollinated shrub. Limited fruit or seed production do not necessarily mean a negative effect of plant populations (Herrera et al., 2002). Negative effects of SLD on pollination might be

overcome by positive effects on other stages (e.g. seed dispersal; Suárez-Esteban et al., 2013a), being the net effect what ultimately determines plant fitness (Magrath et al., 2013). Despite the importance of considering all ontogenetic stages as a whole, very little is known about whether SLD affect seed predation, germination, and seedling establishment (see following chapters).

Given that *H. halimifolium* readily colonizes SLD after one year without perturbations (*Authors personal observation*), fruit and seed set do not seem to be the most limiting factors for population size. Rather, the availability of empty sites without competitors is likely to be more influent on *H. halimifolium* dynamics. However, the fact that we detected a negative effect of SLD on the reproductive output of such locally widespread and abundant species suggests that SLD disturbances could have a deeper impact on other species (Cunningham, 2000). For instance, those species with small populations, those that depend upon specialist pollinators, or those which fitness relies mainly on sexual reproduction will be probably harmed by SLD. Further research is desirable to address these predictions, especially in endangered species.

In order to reduce the negative effects of SLD on pollination, we propose to conserve roadside native vegetation. SLD verges have the potential to host shrubby hedgerows (Suárez-Esteban et al., 2013b) that can act as dust screens, as well as provide pollinators with habitat for both foraging or nesting (Wratten et al., 2012, Mwangi et al., 2012, Morandín and Kremen, 2013). Natural hedgerows along roadsides can be achieved by conserving endozoochorous seed dispersal vectors that positively select SLD verges for defecation (Suárez-Esteban et al., 2013a) and by promoting shrub establishment along SLD verges (Karim and Mallik, 2008, Suárez-Esteban et al., 2013b).

Chapter 2

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



Resumen: Mientras muchos animales evitan las SLD, algunos mamíferos terrestres la seleccionan para marcar su territorio con sus excrementos, que suelen contener numerosas semillas viables. Por lo tanto, las SLD pueden recibir una gran cantidad y diversidad de semillas, lo que podría tener consecuencias nunca antes exploradas para el reclutamiento de nuevas plantas. En este capítulo se evalúa el potencial papel de las SLD como zonas de recepción de semillas dispersadas por mamíferos terrestres.

Abstract

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.

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-fruited shrubs within faeces and compared their abundance and diversity at SLD verges vs. adjacent scrubland.

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 to faeces of rabbits and especially ungulates.

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. Out of 13 mammal-dispersed shrubs, 4 species were exclusively found along SLD verges, 2 were found only in the scrubland, and 7 were found in both habitats.

By promoting mammal-mediated seed dispersal, soft linear developments (SLD) may act as seed corridors. Given the extremely high density of SLD worldwide, 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.

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 and 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 worldwide (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 extend beyond their boundaries, habitat loss, fragmentation and limited animal and plant dispersal are among their known effects (Forman and Alexander, 1998, Trombulak and 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 and Tewksbury, 2005, Haddad et al., 2003). Moreover, some studies suggested that experimental linear clearings immerse in a forest matrix may enhance ecosystem services such as seed dispersal (Levey et al., 2005, Tewksbury et al., 2002), 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 and Belnap, 2003, Christen and Matlack, 2006), very little is known about their potential effects on native populations (but see Tikka et al., 2001, Karim and 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 (James and Stuart-Smith, 2000, Forman and Alexander, 1998), many seed dispersing mammals all over the world, such as the red fox *Vulpes vulpes* (Rost et al., 2012), the coyote *Canis latrans* Say (Fedriani and Kohn, 2001), the martens *Martes* spp (López-Bao and González-Varo, 2011) and the European rabbit *Oryctolagus cuniculus* (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-fruited plant species worldwide (Matias et al., 2010, Stoner et al., 2007, Myers et al., 2004). 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 and Miriti, 2000, Nathan and 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 and Miriti, 2000), therefore SLD verges could be reforested by some mammal-dispersed plants (Karim and 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 et al., 2010). In the case of endozoochorous plants (plants dispersed through ingestion by animal), the abundance and the spatial distribution of dispersed seeds is determined by the abundance and distribution of faeces containing viable seeds. This in turn is a function of (1) the spatial pattern of defecation of frugivores, (2) their fruit consumption (i.e. proportion of faeces with fruit remains) and (3) 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 southwestern Spain characterized by a diverse community of fleshy-fruited 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 et al., 1999), while ungulates generally avoid these structures (James and Stuart-Smith, 2000). Furthermore, carnivores are recognized as legitimate seed dispersers (Herrera, 1989, López-Bao and González-Varo, 2011), whereas ungulates and rabbits often act as seed predators rather than dispersers (Fedriani and Delibes, 2009b, Perea et al., 2013). Consequently, the potential role of SLD as seed attractors was expected to depend on the species-specific defecation places and dispersal effectiveness (*sensu* Schupp et al., 2010) of dispersal vectors.

Materials and methods

Study sites, plants and their dispersers

To enable assessment of the whole fleshy-fruited shrub community of Doñana, we chose three study sites (called Reserva, Rocina and Matasgordas, respectively) that

contained 48, 36 and 21 km of SLD, respectively. For further description of these sites and the plant communities they contain, see “Area de Estudio” above.

In the Mediterranean basin, fleshy-fruited 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–December (Jordano, 1984a, Fedriani and Delibes, 2009a). Depending on the species, each fruit contains generally from one to eight seeds, though *R. ulmifolius* frequently contain more than 20 seeds per fruit (Jordano, 1995).

In Doñana, most of those plants are dispersed by mammals (Fedriani and Delibes, 2009a, Fedriani and Delibes, 2009b, Herrera, 1989), though some of them are also dispersed by birds (Herrera, 1995, Jordano, 1984b). Specifically, six frugivorous mammals are known to be local important seed dispersers: wild boar (*Sus scrofa*; Matias et al., 2010), red deer (*Cervus elaphus*; Perea et al., 2013), fallow deer (*Dama dama*; Eycott et al., 2007), red fox (Fedriani and Delibes, 2009a), Eurasian badger (*Meles meles*; Fedriani and Delibes, 2009b) and European rabbit (Delibes-Mateos et al., 2008). Genets (*Genetta genetta*) and Egyptian mongooses (*Herpestes ichneumon*) also occur in Doñana, but were not recorded in our surveys. Radio-tracking studies (Fedriani et al., 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 and Delibes, 2009b, Perea et al., 2013). 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 x 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-fruited 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 and Delibes, 2009b, Perea et al., 2013). Though 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 and 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 and 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 2a). Conversely, rabbits and carnivores deposited 2.17 and 5.47 times more faeces along SLD verges than in the scrubland, respectively (Table 2a; Fig. 9A).

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.

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 ± 26.8 % of them contained fruit remains; $n = 76$), whereas fruit prevalence was similar in faeces of rabbits and ungulates (66.7 ± 34.1 %, $n = 325$, and 62.8 ± 41.4 %, $n = 586$, respectively; Table 2b).

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 ± 25.4 % ($n = 4215$), 59.8 ± 18.3 % ($n = 6300$) and 1.8 ± 0.7 % ($n = 10522$) of ingested seeds, respectively (Table 2c). Interestingly, rabbit and ungulate seed damage was 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 3).

Table 2: 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. For the interaction, only the combinations different from zero are shown.

Factor	a) Feces			b) Fruit consumption			c) Seed damage*			d) Seed rain		
	β	SE	P	β	SE	P	β	SE	P	β	SE	P
<u>Habitat</u>												
Scrubland	3.30	0.28	<0001	-0.64	0.97	0.51	0.30	0.46	0.51	3.60	0.68	<0001
SLD	0	-	-	0	-	-	0	-	-	0	-	-
<u>Disperser</u>												
Carnivores	1.45	0.31	<0001	0.89	1.05	0.39	-3.67	0.59	<0001	4.79	0.67	<0001
Rabbits	2.70	0.29	<0001	-0.14	1.00	0.89	0.53	0.51	0.30	5.37	0.76	<0001
Ungulates	0	-	-	0	-	-	0	-	-	0	-	-
<u>Habitat*Disperser</u>												
Scrubland-Carnivores	-5.00	0.44	<0001	1.33	1.35	0.32	1.13	0.80	0.16	-6.67	0.86	<0001
Scrubland-Rabbits	-4.07	0.33	<0001	0.63	1.04	0.55	-0.70	0.55	0.21	-4.86	0.99	<0001

* To achieve model convergence, we did not include month of sampling as random factor in this analysis.

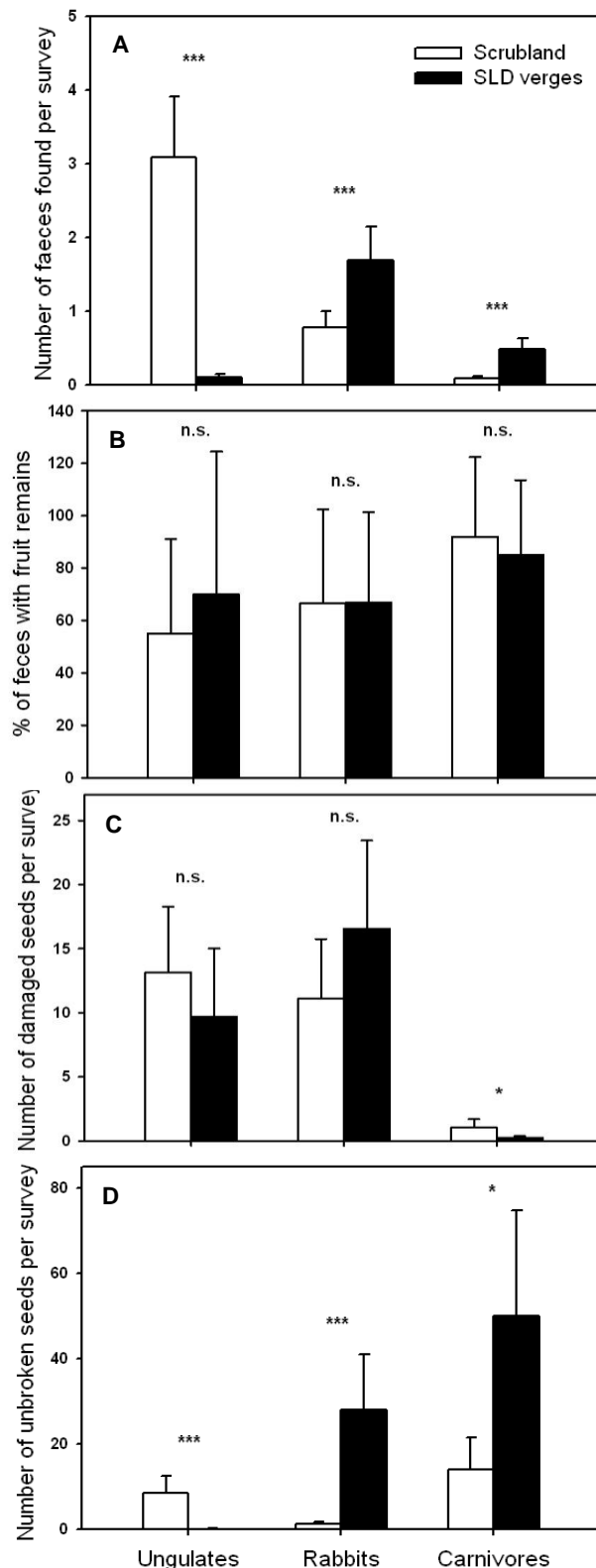


Figure 9: Model-adjusted means (\pm SE) of number of faeces (A), the proportion of faeces containing fruit remains (B), the number of damaged seeds (C) and the estimated number of unbroken seeds (D) found per survey delivered by each disperser group between the scrubland and SLD verges. P values resulted from the test of slices are shown (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$).

Seed rain

Overall, we collected 13931 unbroken seeds from 13 plant species (77.2 % along SLD verges and 22.8 % in the scrubland). 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 2d). 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 2d; Fig. 9D).

Table 3: Relation of damaged and unbroken seeds dispersed by ungulates, rabbits and carnivores along SLD verges and in the scrubland.

Plant species	Ungulates				Rabbits				Carnivores			
	Scrubland		SLD		Scrubland		SLD		Scrubland		SLD	
	Damaged	Unbroken	Damaged	Unbroken	Damaged	Unbroken	Damaged	Unbroken	Damaged	Unbroken	Damaged	Unbroken
<i>Olea europaea</i>	65	2	7	0	0	0	1	0	7	1	3	0
<i>Corema album</i>	1	2	0	0	0	0	0	0	0	0	0	248
<i>Juniperus phoenicea</i>	1	0	0	0	0	0	219	1809	0	0	2	523
<i>J. macrocarpa</i>	0	0	0	0	0	0	0	0	0	0	0	96
<i>Asparagus spp</i>	0	3	0	0	0	3	0	0	0	0	0	0
<i>Pistacia lentiscus</i>	3429	294	64	13	1683	8	249	8	0	0	0	0
<i>Arbutus unedo</i>	0	0	0	0	0	0	1	6	0	0	0	0
<i>Myrtus communis</i>	22	33	44	19	1	2	32	16	0	0	0	0
<i>Phillyrea angustifolia</i>	21	5	0	0	89	123	323	801	0	0	0	0
<i>Chamaerops humilis</i>	0	0	0	0	0	0	0	0	1	93	1	29
<i>Vitis spp</i>	0	0	0	0	0	0	0	0	0	0	0	61
<i>Pyrus bourgaeana</i>	8	2	0	0	0	0	0	0	0	52	4	74
<i>Rubus ulmifolius</i>	65	115	0	0	33	20	708	165	5	2417	17	6888

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-fruited 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. lentiscus*, *P. angustifolia* and *M. communis*) and only two were exclusively found in the scrubland (*Asparagus spp.* and *O. europea*; Table 3). 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 (Levey et al., 2005, Damschen et al., 2006, Ozinga et al., 2009, Tewksbury et al., 2002). 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 (Trombulak and Frissell, 2000, Forman and Alexander, 1998), 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-fruited 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 and 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 and Smith, 2002) in order to better understand the effects of SLD on plant populations and communities.

The strength and direction of SLD effect on seed rains is 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 and 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 which deliver viable seeds in faeces. This positive selection was especially accentuated in the red fox. Though 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 (Vieira and Port, 2007, Fedriani et al., 2001). 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-fruited shrubs in humanized landscapes worldwide (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-fruited shrubs (Traba 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 and 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. 1) may create hedgerows which would provide habitat for some organisms (Pulido-Santacruz and Renjifo, 2011, Lugo and Gucinski, 2000), stop erosion, reduce invasion risk (Grant et al., 2011, Lugo and Gucinski, 2000) and improve the settlement of other plant species by promoting seed arrival (e.g. acting as perches for frugivorous birds; Herrera and García, 2009) or by creating a proper environment (e.g. acting as nurse plants; Armas and 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 and Alexander, 1998) and the increase of human disturbances (Laurance et al., 2009) often lean managers toward 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 and Belnap, 2003, Rost et al., 2012, Christen and Matlack, 2006) 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.

Chapter 3

Are unpaved road margins safe for dispersed seeds? Implications for shrub recruitment and reforestation



Resumen: La llegada de semillas sólo será efectiva para el reclutamiento de nuevas plantas si las semillas sobreviven al ataque de depredadores y patógenos. El comportamiento de los depredadores de semillas puede verse influido por alteraciones del hábitat como las SLD. Al diferir en sus características (e.g. tamaño, nutrientes), es probable que semillas de distintas especies sufran tasas de depredación diferentes. Aquí se evalúa la influencia de las SLD en la supervivencia post-dispersiva de semillas.

Abstract

Post-dispersal seed predation can strongly affect the abundance of dispersed seeds, and thus limit the success of direct seeding during the restoration of native vegetation. Seed predator activity and seed preferences often change among habitats. This may lead to habitat-dependent alterations of the initial seed templates.

In a recent study, we found that hypothetical marginal habitats such as unpaved road (also called *Soft Linear Developments*; SLD) verges can receive a higher amount and a similar diversity of seeds of native fleshy-fruited shrubs than adjacent habitats. We suggested managers to take advantage of this process in order to promote reforestation with native shrubs. However, this would be ineffective if dispersed seeds fail to establish, a premise that remains unexplored.

Through an experimental approach, we evaluated whether post-dispersal seed predation by ants, rodents and birds of a community of Mediterranean fleshy-fruited shrubs was affected by the presence of SLD. We predicted that post-dispersal seed predation may reinforce, counteract, or have a neutral effect on the differences in the spatial abundance of dispersed seeds between SLD verges and adjacent scrublands.

We found that overall post-dispersal seed predation was similar in both habitats. However, seed predation rates of some shrub species varied between habitats. More specifically, *J. phoenicea* and *C. album* seeds were more predated in the scrubland than in SLD verges. Interestingly, more than 99 % of dispersed seeds arrived to SLD verges, the safest habitat. Contrary, *R. ulmifolius* seeds were more predated along SLD verges than in the scrubland. For this species, although SLD verges received most of the seeds, many of them were predated, leading to reduced differences in seed abundance between habitats.

We revealed a weak and inconsistent SLD effect on post-dispersal seed predation across several species of a community of fleshy-fruited Mediterranean shrubs. Given the pervasiveness of SLD, further research on their effects on seeds and other plant stages (e.g. seedlings, saplings, adults) at a community level is needed in order to effectively

manage SLD and to benefit from their potential for natural reforestation and invasion control.

Introduction

Post-dispersal seed predation by both vertebrates and invertebrates is often a major factor limiting seed survival and thereby seedling recruitment (Hulme, 1997, Hulme, 1998, Orrock et al., 2006, Fedriani et al., 2004). Thus, it is a key phenomena potentially impinging plant population dynamics and the diversity and the structure of plant communities (Christianini and Galetti, 2007, Crawley, 2000). Post-dispersal seed predators can respond to diverse factors, including the seed species, the habitat and microhabitat, their perceived predation risk, and the availability of alternative foods (Kollmann et al., 1998, Fedriani and Manzaneda, 2005, Rey et al., 2002, Ostoja et al., 2013).

In particular, habitat attributes play a major role in defining the abundance and foraging behavior of seed predators. Specifically, many granivorous rodents and birds mainly select wooded areas to forage, since the vegetation protect them against potential predators (Craig et al., 2011, Díaz et al., 1999, Vaaland Burkey, 1993, Webb and Willson, 1985). Likewise, ants usually avoid taking seeds from large open patches to minimize the possibility of desiccation (Christianini and Galetti, 2007), and are thereby more active in wooded areas (Ness and Morin, 2008). According to this scenario of habitat use by seed predators, one would expect lower seed predation in open than in wooded areas.

Such general expectation, however, can deviate depending on the identity and the relative abundance of seed predators. For example, some species of rodents (Hay and Fuller, 1981, Ness and Morin, 2008) and ants (Burkey, 1994) are more abundant and/or active in forest edges than in forest interiors. Moreover, habitat changes creating edges (e.g. fragmentation; Magrath et al., 2011, Ness and Morin, 2008, García and Chacoff, 2007, and road construction; Delgado et al., 2001) can also alter the patterns of seed predation.

Species-specific rates of seed predation are also likely given that seed species differ in critical traits (size, chemical and physical defences, nutritional content; Baskin and Baskin, 1998) that conform their attractiveness to contrasting predator guilds (Hulme and Borelli, 1999, Barberá et al., 2006, García-Castaño et al., 2006, Holl and Lulow, 1997). Varying seed predation among seed species or habitats eventually can lead to deep changes in the diversity and the distribution of shrubs. For example, if only one or few species survived in one particular habitat, this habitat would become homogeneous, as found by Arévalo et al. (2010) along roadsides. Thus, evaluating the variations of post-dispersal seed predation between habitats is essential to understand the mechanisms driving plant distribution and diversity.

In a recent study, we showed that the red fox and the European rabbit disperse a substantial amount and diversity of seeds of fleshy-fruited shrubs along the verges of human-made linear structures such as trails and firebreaks (called “Soft Linear Developments”, SLD; Suárez-Esteban et al., 2013a). The disproportionate seed reception by SLD verges may have important implications for the reforestation of humanized habitats, given the pervasiveness of SLD. Indeed, we found that some fleshy-fruited shrubs (e.g. *J. phoenicea*, *P. angustifolia*) were more abundant along SLD verges than in adjacent scrublands, whereas other species (e.g. *C. humilis*) showed the opposite pattern (Suárez-Esteban et al., 2013b). However, differential rates of post-dispersal seed predation may alter the initial pattern of seed deposition, threatening the potential of SLD to assist native plant restoration.

In this study, we evaluated the role of post-dispersal seed predation in defining the potential of SLD verges to host certain species of fleshy-fruited shrubs. In doing so, we performed an experimental seed offering of eight fleshy-fruited shrubs both in SLD verges and the adjacent scrubland, within several patches of Mediterranean scrubland, during two consecutive years, and under four different selective exclosures in order to address the role of different seed predator guilds.

We hypothesized that post-dispersal seed predation would vary between SLD verges and adjacent scrublands, though we did not have a clear expectation concerning the direction of such differences. We considered the following two possibilities: (1) If post-dispersal seed predation is more intense in the scrubland than in SLD verges, it will reinforce the recruitment of species mostly dispersed along SLD verges (e.g. *R. ulmifolius*, *C. album*, *J. phoenicea*), as well as hinder that of species mostly dispersed to the scrubland (e.g. *P. lentiscus*, *C. humilis*), whereas (2) we would expect the opposite if post-dispersal seed predation is more intense along SLD verges than in the scrubland.

Our results provide valuable information for stakeholders in order to realize the actual suitability of SLD verges (Orrock and Damschen, 2005, Birkedal et al., 2010) as safe sites for dispersed seeds and therefore the potential of these hypothetical marginal areas on plant restoration programs (Suárez-Esteban et al., 2013b).

Methods

Study system

Most fleshy-fruited species present in Doñana flower during later winter and spring (Feb-May) and produce drupes (e.g. *P. lentiscus*, *R. ulmifolius*) or berries (e.g. *M. communis*) that ripen during August-December (Jordano, 1984a, Fedriani and Delibes, 2009a). 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). In our study area, they are mainly dispersed by birds and mammals (Jordano, 1984a, Fedriani and Delibes, 2009b, Fedriani and Delibes, 2011). In a previous study about seed rains in relation to SLD, we found most (79.49 %; N = 13066) of *J. phoenicea*, *P. angustifolia* and *R. ulmifolius* mammal-dispersed seeds along SLD verges. Contrary, 88.91 % (N = 451) of *P. lentiscus*, *Asparagus* spp., and *C. humilis* dispersed seeds was found in the scrubland (away from SLD; Suárez-Esteban et al., 2013a).

In Doñana, granivores are mostly represented by ants, rodents and birds. Among ants, the most common seed consumers are *Aphaenogaster senilis* and *Messor* spp.

(Authors personal observation; data from Natural Processes Monitoring Group, Doñana Biological Station, <http://www-rbd.ebd.csic.es/Seguimiento/seguimiento.htm>). Regarding rodents, the most abundant are *Mus spretus* and *Apodemus sylvaticus*, followed by *Rattus norvegicus* and *R. rattus*, being scarce *Elyomys quercinus* (Moreno and Rouco, 2013, Fedriani and Delibes, 2009b). Granivorous birds such as *Carduelis carduelis*, *Carduelis chloris*, *Fringilla coelebs*, *Columba palumbus*, and *Passer domesticus* also occur in the area (González-Varo, 2010b).

Experimental design

In each of our three study sites, we set up four 500 m. transects where mammal-generated seed rains were previously quantified (Suárez-Esteban et al., 2013a). Two of the transects were set along SLD and the other two parallel but 60 m. away from SLD, in the scrubland (see a sketch in Fig. 10A). Along each transect, we placed five independent experimental blocks

separated by 100 m. (Fig. 10A). We finally set 20 experimental blocks per site, 10 in the scrubland and 10 along SLD verges (i.e. overall 60 blocks).

In order to evaluate the relative

removal rates by each seed predator guild, we placed four kinds of enclosure treatments (García-Castaño et al., 2006, Orrock et al., 2003; Fig. 10C) in every experimental block: (i) an open Petri dish accessible to all seed predator guilds (i.e. rodents, birds and ants),

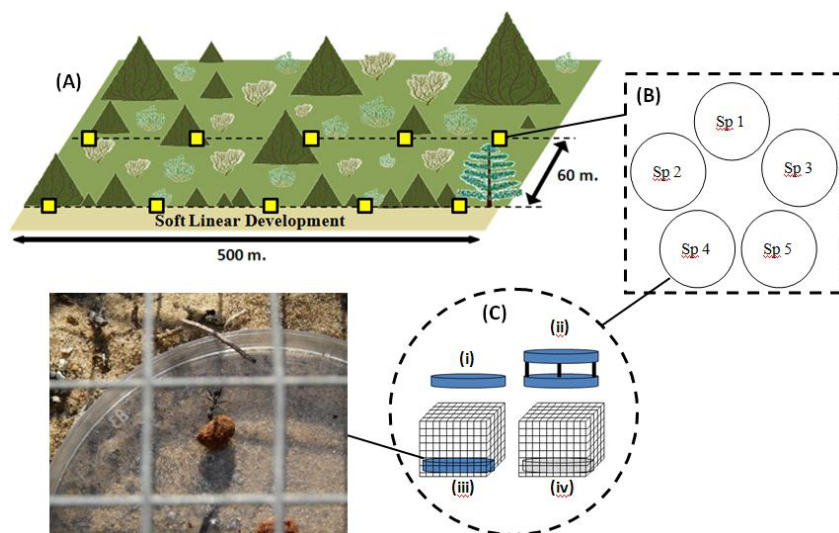


Figure 10: Diagram of the experimental design at different scales: (A) pair of transects, one in the scrubland and another along SLD verges, (B) experimental block with different seed species offered (whose position within the block was random), and (C) treatment enclosures (i open, ii roofed, iii fenced and iv control) set for each plant species. In (D), one ant (*Aphaenogaster senilis*) carrying a *J. macrocarpa* seed out of a fenced Petri dish.

(ii) a roofed Petri dish using a second dish that was held inverted about 2.5-3 cm above the bottom one by means of three thin sticks (to exclude birds; accessible to rodents and ants), (iii) a fenced Petri dish, covered with a cubic wire mesh (to exclude rodents and birds; accessible to ants), and finally (iv) a fenced Petri dish whose edge was greased with Teflon emulsion (Fedriani et al., 2004), to exclude ants besides other seed predators; i.e. the control treatment).

For each block, we estimated the differences in the number of seeds removed between treatment exclosures, which should provide a relative measure of the importance of each predator guild on seed removal (Hulme and Borelli, 1999). Specifically, we assumed that the seeds removed from fenced dishes were harvested by ants, and that, in general, they removed the same number of seeds in the other exclosures. Then, we attribute to rodents the number of seeds removed from roofed dishes, once deducted the number of seeds removed by ants, and assume that, in general, rodents removed the same number of seeds from open dishes. Finally, we attribute to birds the number of seeds removed from open dishes that were not assumed to be removed by ants and rodents.

The control treatment allowed us to discard that any other phenomenon (e.g. wind) led to seed removal. Although controls failed in some blocks close to ant nests (we observed big ants removing seeds without touching the Teflon emulsion used to repel them), in general the number of seeds harvested from this treatment was very low. Thus, for the sake of simplicity when interpreting our results, we did not include the control treatment in the models. Likewise, seeds of *P. bourgaeana* and *C. humilis* were barely predated, and we excluded both species from the analyses.

Within each study site, we set up all four exclosure treatments for each offered seed species in every block (Fig. 10B, C). Every Petri dish contained 10 scattered seeds of the target plant species, obtained by removing the pulp of locally produced fruits. Seed species were selected based on the most abundant plant species found by Suárez-Esteban et al. (2013a) within mammal faeces in each site, which were: *R. ulmifolius*, *J. phoenicea*, *P. angustifolia*, *C. album*, and *J. macrocarpa* in Reserva site; *C. humilis* and *R. ulmifolius*

in Rocina site; and *P. bourgaeana*, *C. humilis* and *P. lentiscus* in Matasgordas site. We assessed seed removal by counting the number of removed seeds in each Petri dish after four, consecutive and non-rainy days, in November (at the end of the seed dispersal season) of two consecutive years (2010 and 2011).

Some of the seed predator guilds considered, such as rodents (Vander Wall et al., 2005) and ants (Christianini and Oliveira, 2009, MacMahon et al., 2000), may occasionally act as secondary seed dispersers. However, we assumed that seed removal is mostly equivalent to seed predation based on our *in situ* observations of hulls from predated seeds, rodent droppings and the absence of reward structures for myrmecochory (i.e. elaiosome) in our target seed species.

Statistical analyses

We evaluated the influence of SLD on seed removal by fitting a generalized linear mixed model (GLMM) using the glimmix procedure in SAS 9.2 (Littell et al., 2006). Our response variable was the number of removed seeds per dish after the four-day experiments. We included the habitat (SLD verges vs. scrubland), the seed predator guild (ants, rodents and birds), the seed species (see above) and their second and third order interactions as fixed factors. When any 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).

We assumed negative binomial error distribution and log-link function. Given that the amount of offered seeds was homogeneous among blocks, species, exclosures, and habitats, we did not include the number of offered seeds as an offset variable. Adjusted means and standard errors were calculated using the LSMEANS statement, and back-transformed using the appropriate Taylor’s series approach (Littell et al., 2006). The year, and the experimental block were included as random factors to control for potential environmental and temporal variations.

Results

From 8400 offered seeds overall, 22.2 % was removed from our experimental blocks after four days in the field. The percentage of seeds removed per dish varied between 0 % (61.2 % of the cases, $n = 840$) and 100 % (11.0 % of the cases). These results suggest that once seed predators found a seed depot, they usually depleted it.

Table 4: Results of the GLMMs fitted to evaluate whether SLD affect seed predation.

Factor	Num df	Den df	F value	P value
Habitat	1	775	0.39	0.53
Predator	2	775	10.78	< 0.001
Seed species	5	775	3.11	< 0.01
Habitat*Predator	2	775	0.93	0.40
Habitat*Seed species	5	775	2.91	0.01
Seed species*Predator	10	775	2.27	0.01
Habitat*Seed sp*Predator	10	775	0.64	0.78

Although all seed species undergo seed losses, the overall intensity of seed removal varied significantly among seed species (Table 4). Specifically, *J. macrocarpa*, *P. lentiscus* and *C. album* were the most intensively removed, with 1.11 ± 0.25 , $1.06 \pm$

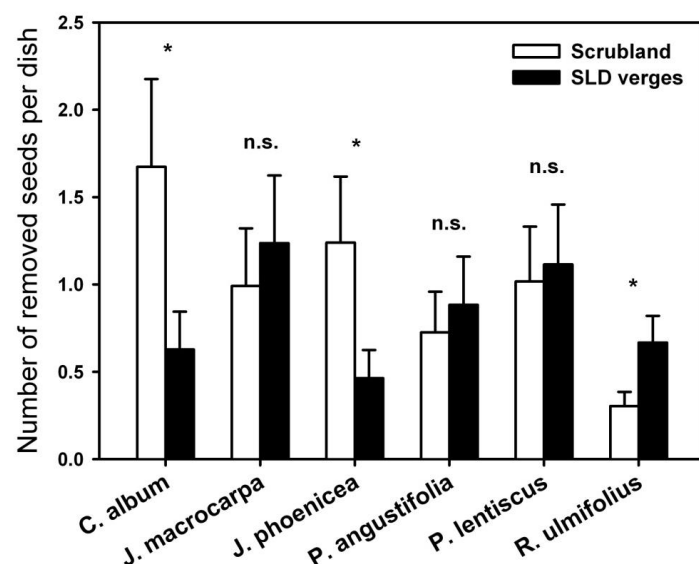


Figure 11: Model-adjusted mean (\pm SE) number of removed seeds per Petri dish of each seed species in the scrubland (white bars) and along SLD verges (black bars). P values resulted from the test of slices are shown (* $P < 0.05$), indicating whether the differences between habitat were significant.

0.23 and 1.02 ± 0.23 seeds removed per block (mean \pm SE), respectively. Whereas, *P. angustifolia*, *J. phoenicea*, and *R. ulmifolius* were the least intensively removed species, with 0.80 ± 0.18 , 0.76 ± 0.18 and 0.45 ± 0.08 seeds removed per block, respectively (Fig. 11).

Conversely, the overall number of removed seeds per

dish did not significantly vary between SLD verges (0.79 ± 0.10 ; mean \pm SE) and the scrubland (0.88 ± 0.11 ; i.e. lack of significant effect of habitat as main factor, Table 4). Interestingly, however, the interaction between habitat and seed species was significant (Table 4), suggesting that the effect of habitat on seed removal was inconsistent across seed species. Specifically, the numbers of *C. album* and *J. phoenicea* removed seeds were 2.67 times higher in the scrubland than along SLD verges in both species (Fig. 11). Contrary, the number of *R. ulmifolius* removed seeds was 2.20 times higher along SLD verges than in the scrubland (Fig. 11). Seed removal was similar between both habitats for *J. macrocarpa*, *P. angustifolia* and *P. lentiscus* (Fig. 11).

The number of removed seeds by each predator guild was significantly different (see Predator in Table 4). Specifically, ants removed 2.69 and 1.90 times more seeds on average than birds and rodents, respectively. Furthermore, there was a significant interaction between the predator guild and the seed species (Table 4), suggesting that the

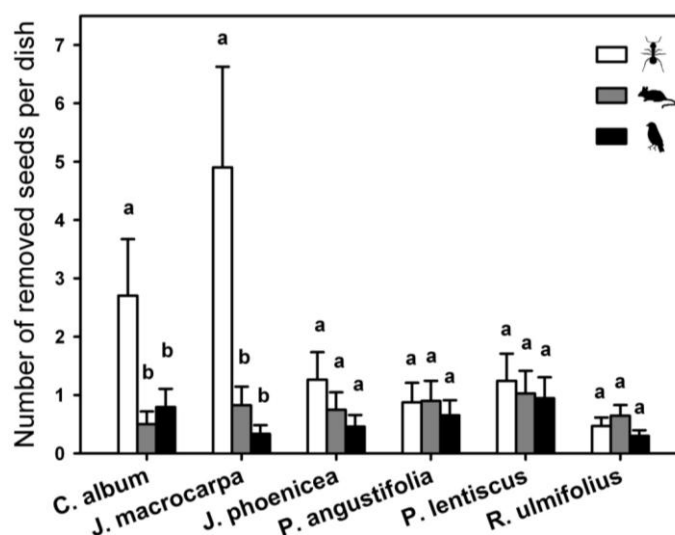


Figure 12: Model-adjusted mean (\pm SE) number of removed seeds per Petri dish of each seed species by ants (white bars), rodents (grey bars) and birds (black bars). For each species, bars with similar letters (a, b) are not significantly different.

relative number of seeds removed by each predator varied among seed species. Ants removed 5.42 and 3.40 times more *J. macrocarpa* seeds, and 5.94 and 14.61 times more *C. album* seeds than rodents and birds, respectively (Fig. 12). All predator guilds removed a similar number of *J. phoenicea*, *P. angustifolia*, *P. lentiscus* and *R. ulmifolius* seeds (Fig. 12).

The overall number of seeds removed by the different predator guilds was consistent between habitats (the interaction Habitat*Predator was insignificant; Table 4),

as well as their mentioned seed-species preferences (i.e. the third order interaction was neither significant; Table 4).

Discussion

Seed arrival will be effective for plant recruitment and restoration only if post-dispersal seed predation and other mortality factors do not limit seed availability. In a previous study, we have demonstrated that SLD verges could receive a substantial and higher amount of seeds of many fleshy-fruited shrubs than adjacent habitats (Suárez-Esteban et al., 2013a). Our results here suggest that overall seed survival is similar in SLD verges than in adjacent Mediterranean scrublands. Thus, we support that SLD do not alter overall post-dispersal seed survival.

Several studies comparing post-dispersal seed predation between different habitats have shown different outcomes. Specifically, Webb and Willson (1985), and Díaz et al. (1999) found higher seed predation rates by rodents and birds in forest interiors than in forest edges and gaps. Contrary, Delgado et al. (2001) found that rates of seed predation by rats were higher along forest edges (associated to roadsides) than in forest interiors. Therefore, seed survival is probably strongly context-dependent. According to this, we suggest to evaluate whether seeds arriving to SLD verges in other ecosystems survive and hold their potential to lead to successful plant recruitment, which certainly has important management implications, both for native plant restoration and for plant invasion control (Wandrag et al., 2013, Suárez-Esteban et al., 2013b).

As detected by other studies (e.g. García-Castaño et al., 2006, Holl and Lulow, 1997), there were variations in seed survival between habitats for certain shrub species. These differences led to our two described potential effects of post-dispersal seed predation on initial seed rains. For some species, post-dispersal seed predation can reinforce the observed differences in seed abundance between habitats. Interestingly, the most intensively predated species in the scrubland (i.e. *C. album* and *J. phoenicea*) were almost exclusively (more than 99 % of the seeds; $n = 250$, and $n = 2332$, respectively)

dispersed along SLD verges by foxes and rabbits (Suárez-Esteban et al., 2013a). Thus, these seed dispersers are likely providing an important service to those plants by dispersing their seeds to safe sites (i.e. where seed predation is low as compared with other habitats) that, in addition, seem to be suitable for shrub establishment (Suárez-Esteban et al., 2013b). This can be considered as an example of species-specific directed dispersal (Wenny, 2001).

Under other circumstances, post-dispersal seed predation can reduce the differences in seed abundance between habitats. For example, in the case of *R. ulmifolius*, although SLD verges received 2.76 times more seeds than the scrubland (Suárez-Esteban et al., 2013a), 2.20 times more seeds were predated in SLD verges as compared with the scrubland. After considering both phenomena, the detected significant differences in the abundance of *R. ulmifolius* seeds between habitats (Suárez-Esteban et al., 2013a) will probably disappear. However, we still found more *R. ulmifolius* shrubs along SLD verges than in the scrubland (Suárez-Esteban et al., 2013b). This suggests that other post-dispersal processes (e.g. seedling emergence and survival) are promoting *R. ulmifolius* establishment along SLD verges rather than in adjacent scrublands.

For other species, apparently post-dispersal seed predation may have not a deep effect on the differences in seed abundance between habitats. For example, most of *P. lentiscus* seeds (more than 90 %; n = 326) were dispersed to the scrubland, whereas most of *J. macrocarpa* and *P. angustifolia* seeds were dispersed along SLD verges (100 %, and 89 % of the seeds; n = 96, and n = 929, respectively). Seed predation of all three species was similar between habitats. Thus, post-dispersal seed predation can reinforce seed limitation in SLD verges for *P. lentiscus* and in the scrubland for *J. macrocarpa* (assuming occasional arrival) and *P. angustifolia*, but we would not expect a change in the proportion of seeds in each habitat for these species.

Shrub species varied in their susceptibility to seed predation, such as found by other studies (García-Castaño et al., 2006, Holl and Lulow, 1997, Perea et al., 2011). This suggests that including several species is needed in order to make generalizations about

the potential recruitment limitations driven by seed predation at a community level. An endangered species, *J. macrocarpa*, was the most intensively predated (in a similar way in both habitats). We therefore suggest managers interested in sowing seeds for the restoration of *J. macrocarpa* populations to protect them against seed predators, especially against ants. In order to exclude ants, we recommend the use of physical barriers (e.g. wire/plastic mesh with holes small enough to preclude ant access).

Considering the whole fleshy-fruited shrub community, ants were the main seed predators both in SLD verges and the scrubland. Specifically, ants were much more efficient predated *J. macrocarpa* and *C. album* seeds than rodents and birds (Fig. 3). This high seed removal success by ants could have limited the access of rodents and birds to the seeds of these two species (Orrock et al., 2003). However, the nested design of our enclosure treatments may have made seed removal by rodents and especially by birds more difficult to detect, since ants have access to all enclosures.

The intensity of predation of all three seed predator guilds did not show significant differences between habitats. That matched our previous results on rodent trapping (*Authors' unpublished data*). Probably, the presence and the activity of rodents relies on the availability of protecting shrubs (García-Castaño et al., 2006, Fedriani and Manzaneda, 2005), independently of their distance to SLD. Likewise, ant and bird activity seemed to be unaffected by SLD.

Conclusions

Overall, SLD had no effect on post-dispersal seed predation. This result is consistent with the strong observed coupling between mammal-generated seed rains and the relative abundance of fleshy-fruited shrubs in SLD verges and adjacent scrublands (Suárez-Esteban et al., 2013a, Suárez-Esteban et al., 2013b). However, as we found for seed dispersal, differences in seed predation between habitats occurred in some species, and therefore the general pattern is not translatable to the whole fleshy-fruited shrub community. We identified that, depending on the seed species, post-dispersal seed

predation can reinforce, counteract, or have a neutral effect on the differences between habitats in the abundance of dispersed seeds.

Our results suggest that seed addition (either dispersed by natural vectors or sowed by humans) will lead to different outcomes of seedling recruitment depending on seed species identity, both at SLD verges and at the scrubland. In order to restore native shrubs along SLD verges, we suggest the use of *C. humilis* and *P. bourgaeana* seeds, given that they were barely predated. Nonetheless, sowing programs for SLD reforestation must consider that there are other key ecological filters with the potential to limit plant establishment, such as the summer drought (Gulias et al., 2004, Rey and Alcántara, 2000, Gómez-Aparicio, 2008). Whether these other filters interact with SLD will be evaluated in chapter 4.

We revealed a weak and inconsistent SLD effect on post-dispersal seed predation across several species of a community of fleshy-fruited Mediterranean shrubs. The extrapolation of our results to other ecosystems (e.g. temperate, tropical or boreal forest) must proceed with caution, given the extremely spatial, temporal and species-specific variations of seed predation rates (Fedriani et al., 2004, Webb and Willson, 1985, García-Castaño et al., 2006, Díaz et al., 1999). As SLD are pervasive in almost all terrestrial ecosystems, further research on their effects on seeds and other plant stages (e.g. seedlings, saplings, adults) at a community level is needed in order to effectively manage SLD and to benefit from their potential for natural reforestation and invasion control (Suárez-Esteban et al., 2013b).

Chapter 4

Identifying key determinants for native fleshy-fruited shrub recruitment along unpaved road verges



Resumen: La llegada y la supervivencia de semillas no garantizan el reclutamiento de nuevas plantas. Para ello, las semillas supervivientes deben germinar, dando lugar a plántulas. Debido a su pequeño tamaño, las plántulas son muy sensibles a factores ambientales como la humedad, y a factores biológicos como los herbívoros, ambos susceptibles de ser afectados por SLD. En este capítulo se evalúa el efecto de las SLD en la emergencia y supervivencia temprana de plántulas de arbustos de frutos carnosos.

Abstract

Extensive forests and scrublands have been relegated to small patches due to agricultural intensification and other land-use changes like the construction of linear developments such as trails and firebreaks (also called Soft Linear Developments, SLD). In those small patches the regeneration of native woody plants is thought to be unlikely. Their conservation and restoration require explicitly recognizing and making use of particularly suitable habitats for recruitment (i.e. hotspots).

Interestingly, in a recent study we found that SLD verges hold more native fleshy-fruited shrubs than adjacent, unaltered scrublands. Therefore, SLD verges could act as those required hotspots for the restoration of native scrublands. In order to do so, SLD verges should receive a high and constant amount of seeds, and these seeds must lead to seedlings that do not experience a disproportionately high mortality. Whereas the former condition has been demonstrated, the latter remains unexplored.

To evaluate the effect of SLD on seedling emergence and survival, and therefore their potential to become hotspots of shrub recruitment, we sowed seeds of 8 fleshy-fruit shrubs both in SLD verges and in adjacent scrublands within three, distant patches of Mediterranean scrubland. We then monitored seedling emergence and survival during 30 months.

Overall, both the magnitude and the temporal pattern of seedling emergence and survival were similar in SLD verges and in adjacent scrublands. Seedling emergence and survival were different among shrub species, suggesting the existence of species-specific requirements. Nonetheless, those requirements were consistent in both habitats. Thus, SLD verges seem to be as suitable habitats for seedling emergence and survival as adjacent, unaltered scrublands. Their suitability along with the intense seed arrival, suggest that the verges of these pervasive, ignored structures can become hotspots of native shrub recruitment, and thereby they can be used in restoration programs.

Introduction

The expansion of urban and agricultural land has relegated ancient, extensive wooded areas (e.g. forests, scrublands) to small patches (Lambin and Geist, 2006, Fearnside, 2005) within which natural recruitment of native plants is often limited (Aparicio, 2008, Gómez-Aparicio et al., 2004). Thus, their conservation and restoration require explicitly recognizing and making use of particularly suitable habitats for recruitment (i.e. hotspots; Gómez-Aparicio, 2008, Hampe et al., 2008). Furthermore, land-use changes are usually associated with pervasive habitat alterations like the construction of linear developments (Forman et al., 2003, Cropper et al., 2001) such as highways, roads, as well as other, generally narrower structures such as trails and firebreaks (also called Soft Linear Developments, SLD; Suárez-Esteban et al., 2013a).

These human-made structures are usually associated with negative effects on biodiversity (Trombulak and Frissell, 2000, Forman et al., 2003). Surprisingly, they can also hold potential conservation values. For example, in a previous study we found that SLD verges can house a higher number of native fleshy-fruited shrubs than adjacent, unaltered scrublands, potentially acting as hotspots of shrub recruitment and establishment (Suárez-Esteban et al., 2013b). This requires not only that SLD verges receive a high and constant amount of seeds, but also that seeds lead to seedlings that do not experience a disproportionately high mortality (Hampe et al., 2008, Chambers, 2000).

The former condition has been thoroughly evaluated. Indeed, we have demonstrated that SLD modify the behavior of frugivorous mammals such as the red fox and the European rabbit, which positively selected these pervasive structures for defecation (Suárez-Esteban et al., 2013a). As a consequence, many SLD verges received more dispersed seeds of fleshy-fruited shrubs than adjacent, unaltered scrublands (Suárez-Esteban et al., 2013a). However, from a plant perspective, only seeds leading to seedlings represent effective dispersal (Schupp et al., 2010), and have the potential to influence plant abundance, diversity and distribution (Bleher and Böhning-Gaese, 2001, Herrera et

al., 1994, Houle, 1992). Yet, whether SLD verges are suitable habitats for seedling emergence and survival of fleshy-fruited shrubs (i.e. the second premise for these verges acting as hotspots of shrub recruitment and establishment) remains unexplored.

Spatial patterns of seedling emergence and survival are often strongly affected by the environmental heterogeneity, especially by habitat variations (Gómez-Aparicio, 2008). The presence of SLD may increase habitat heterogeneity and the range of potential recruitment niches (Schupp, 1988, Lugo and Gucinski, 2000). For example, roadsides and SLD verges can accumulate water that would promote their colonization by some species (Lelong et al., 2007, Jodoin et al., 2008, Buckley et al., 2003). Also, these structures can be light- (Parendes and Jones, 2000) and nutrient-richer environments (Angold, 1997), as well as they can hold less competitors (Jongejans et al., 2007) than adjacent, unaltered scrublands. This can potentially assist seedling emergence and establishment of certain species, especially of exotics (Flory and Clay, 2009, Harper et al., 2005), though very few studies have investigated these intriguing possibilities (e.g. Veldman and Putz, 2010).

SLD may also have negative effects on seedling recruitment. For example, soil water availability can be briefer along road embankments than in adjacent habitats, limiting plant establishment (Bochet and García-Fayos, 2004, Tormo et al., 2006). Furthermore, the presence of SLD may lead to negative effects that hinder seedling emergence and survival, such as pollution (Legret and Pagotto, 2006), salinity (Czerniawska-Kusza et al., 2004), dust deposition (Walker and Everett, 1987), and lack of shade and thus harsh micro-climate conditions (Addison et al., 2007). Therefore, the overall effect of SLD on seedling fate is difficult to forecast and likely strongly context-dependent, making necessary comprehensive evaluations in representative humanized landscapes.

In this study we experimentally evaluate for the first time the potential of SLD verges as suitable habitats for seedling emergence and survival of a community of fleshy-fruited Mediterranean shrubs. By using experimental field sowings, we compared seedling emergence and early survival along SLD verges and in adjacent, unaltered

scrublands. Regarding seedling emergence, not only the proportion of emerged seedlings is relevant, but also the temporal pattern, since early emergence is often related with high seedling survival rates (Huxtable and Whalley, 1999, Verdú and Traveset, 2005, Fedriani et al., 2012). Likewise, the temporal pattern of seedling survival can be used as a surrogate of the probability of plant recruitment in a certain habitat (González-Varo et al., 2012).

Seedling recruitment is likely dependent on different ecological requirements of particular shrub species (Myers and Harms, 2011). In order to draw conclusions at the community level, we sowed seeds of eight fleshy-fruited shrub species. As different habitats are usually subjected to different biotic and abiotic conditions (Castro et al., 2004), we compared both seedling emergence and survival in SLD verges and in adjacent scrublands in three distant Mediterranean scrublands with contrasting plant communities. In addition, the quality of different habitats may fluctuate over time due to variation in climatic conditions (Gómez-Aparicio et al., 2005, Hampe et al., 2008). To take into account these potential temporal variations, we extended our study during 30 months, thoroughly evaluating whether SLD affect seedling emergence and survival.

Materials and methods

Study area and species

The regeneration of most of these fleshy-fruit shrubs in Doñana and in Mediterranean ecosystems in general, is known to be strongly limited by seedling survival, especially during the harsh summer droughts. This is specifically the case of, for example, *C. humilis* (Fedriani and Delibes, 2011), *M. communis* (González-Varo et al., 2012), *O. europaea* (Rey and Alcántara, 2000), and *P. bourgaeana* (Fedriani et al., 2012).

Experimental field sowing

The magnitude and the speed of seedling emergence and survival were experimentally evaluated by sowing seeds both in SLD verges and in adjacent scrublands. In October 2010, we extracted seeds from fruits harvested from the eight fleshy-fruit

shrub species (from 10-20 individuals per species) with the highest prevalence within mammals feces (Suárez-Esteban et al., 2013a). Specifically, our target species were: *C. humilis*, *P. lentiscus* and *P. bourgaeana* in Matasgordas, *C. album*, *J. macrocarpa*, *J. phoenicea*, *P. angustifolia* and *R. ulmifolius* in Reserva, and *C. humilis* and *R. ulmifolius* in Rocina.

In each of our three study sites, we established two pairs (more than 1 km apart; i.e. considered independent) of two 500 m. transects each, one set along SLD verges and the other one set parallel to it but 60 m away from SLD, in the scrubland (i.e. the same transects where mammal-generated seed rains were recently quantified (Suárez-Esteban et al., 2013a). Along each transect we placed five experimental blocks separated by 100 m (Fig. 13). Thus, we overall set up 60 experimental blocks (5 blocks x 2 transects x 2 habitats x 3 sites).

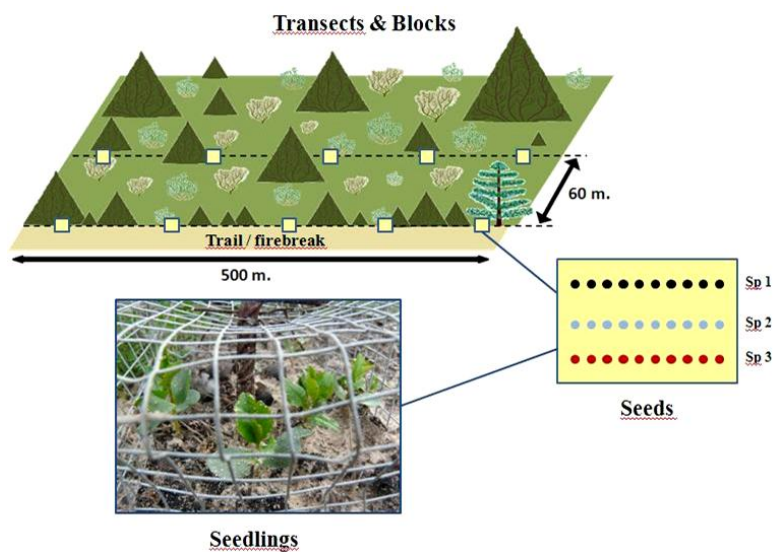


Figure 13: Scheme of the experimental sowings used to evaluate the role of SLD on seedling emergence and early survival. We set two groups of transects (dashed lines) as the one the figure is showing in each study site. In every block (yellow boxes), we sowed 10 seeds in each of as many parallel lines as species considered in each study site. Then, we covered the sowing with a wire mesh to preclude predator access.

Within each block, we sowed 10 seeds of the corresponding target species at each site. Seeds were placed around 1-2 cm apart from each other and at a depth similar to the size of the seed, following parallel lines (one line per species; Fig. 13). Given their small size, we sowed 20 seeds of *C. album* and *R. ulmifolius* instead of 10.

We removed any natural seed or seedling prior to sowing. Previous similar experiments indicated that our procedure ensured that arrival of non-experimental seeds was unlikely

(Fedriani and Delibes, 2009a), and no evidence of it was noted throughout the study. We covered each sowing with a wire 1-cm mesh cage (30 x 21 x 13 cm) to preclude the access of seed predators and herbivores (Fig. 13) until the end of the experiment (June 2013).

To evaluate the effect of habitat (SLD verges *vs.* adjacent scrublands) excluding the potential confounding effect of microhabitat, we placed all sowings next and at the north side of a dominant shrub (e.g. *P. lentiscus* in Matasgordas, *J. phoenicea* and *Stauracanthus* spp. in Reserva, *H. halimifolium* and *C. grandiflorus*. in Rocina). We monitored monthly the emergence and survival of each individual seedling separately until the end of the study (i.e. during 30 months). Our schedule allowed us to register the most likely cause of seedling mortality (i.e. drought, fungal infection and invertebrate herbivory). Because none *C. album* seed germinated by the end of the study, it was excluded from analyses.

Statistical analyses

Seedling emergence

To assess whether the magnitude of seedling emergence differed between SLD verges and adjacent scrublands, we performed a generalized linear mixed model (GLMM) by means of GLIMMIX procedure in SAS 9.2 (Littell et al., 2006). We used the number of emerged seedlings per block by the end of the study as response variable (which was fit to a negative binomial distribution and log-link function), corrected by the number of sowed seeds of each species per block (included as offset variable).

Because the GLMM did not allow us to assess the temporal pattern of seedling emergence, we used failure-time analyses by fitting a Cox proportional hazard regression model (e.g. Fedriani et al., 2012, Fedriani and Delibes, 2011) by means of the *coxph* function included in the *survival* package (Therneau, 2013) in R 3.0.1 (R Development Core Team, 2013). We used the number of weeks between the sowing date and the seedling emergence date as response variable, modeled as non-censored since more than

99 % of the seedlings emerged within the first two years and any additional emergence would be unlikely to modify our results.

Seedling survival

To evaluate whether the magnitude of final seedling survival differed between SLD verges and adjacent scrublands, we fitted a GLMM following a similar procedure as above. We use the proportion of surviving seedlings (considering the number of emerged seedlings of each shrub species) per block by the end of the study as response variable (which was fit to a binomial distribution and logit-link function). A preliminary model fit including also plant species as main factor did not converge, likely due to great inter-specific variations and the small number of survivors; thus, we only considered the habitat as fixed factor in our final model.

In order to assess the temporal pattern of seedling survival (i.e. speed of seedling mortality), we fit a Cox proportional hazard regression model following the same methodology as above. We used the number of weeks between seedling emergence (i.e. using only data concerning emerged seedlings) and death as response variable, modeled as right-censored since remaining seedlings (survivors) could eventually die after the end of our study (Therneau and Grambsch, 2000). Given the variations we found in the date of emergence of each seedling and its potential effect on seedling survival (e.g. Fedriani et al., 2012), we included this factor as a covariate to control for its potential effect.

In all models (GLMM and Cox regressions), we considered the habitat (SLD verges vs. scrubland), the plant species (except for the GLMM analyzing the magnitude of final seedling survival) and their interaction as fixed factors. The experimental block was included as random (or *frailty* in the case of Cox regressions) factor to control for potential environmental heterogeneity.

Results

Seedling emergence

From 2200 sowed seeds, we detected 784 (35.6 %) emergences. From these, 51.5 % emerged within the first six months, reaching a 92.6 % of emergence after 13 months from the sowing date. Considering shrub species altogether, the percentage of emerged seedlings per block varied between 0 % and 80 %. Seedling emergence (i.e. presence of at least one seedling) took place in most (98.3 %; $n = 60$) experimental blocks.

Overall, the number of emerged seedlings per block by the end of the study did not significantly differ ($F_{1,137} = 2.39$; $P = 0.12$) between SLD verges (1.31 ± 0.12 ; mean \pm SE) and the scrubland (1.51 ± 0.13 ; Fig. 14A). However, seedling emergence strongly varied among shrub species ($F_{6,137} = 20.77$; $P < 0.0001$). Specifically, *P. bourgaeana* showed the highest average emergence (2.90 ± 0.39 mean number of seedlings emerged per block \pm SE), followed by *C. humilis* (1.86 ± 0.20), *J. phoenicea* (1.85 ± 0.28), *P. angustifolia* (1.81 ± 0.27), *J. macrocarpa* (1.17 ± 0.20), *P. lentiscus* (1.15 ± 0.19), and finally by *R. ulmifolius*, which showed the lowest emergence (0.45 ± 0.07).

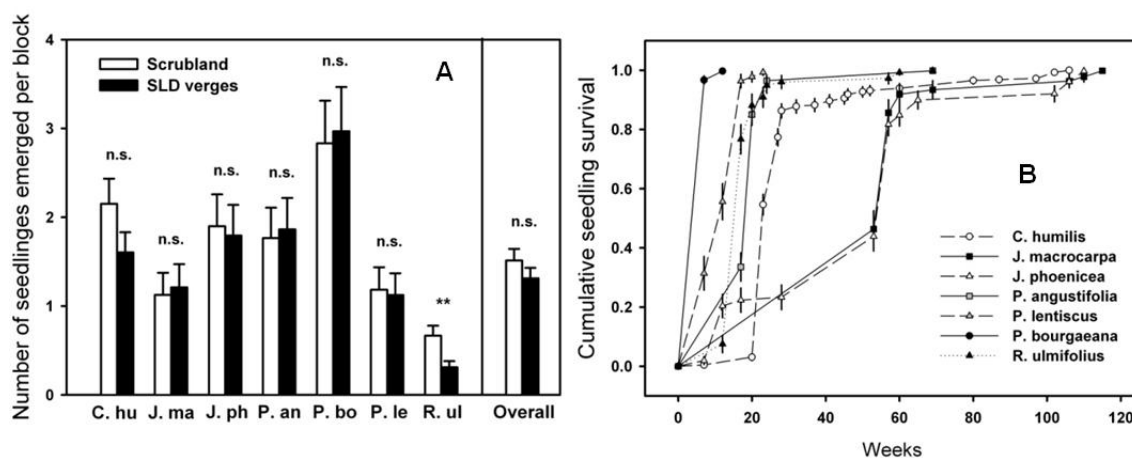


Figure 14: Variations among shrub species in (A) the mean (\pm SE) number of seedlings emerged per block by the end of the study, and in (B) the temporal pattern of seedling emergence. In A, results of the differences of least square means are shown, indicating whether the differences between habitats were significant (** $P < 0.01$) or not (n.s. non-significant) for each species.

The interaction between habitat and plant species was insignificant ($F_{6,137} = 1.44$; $P = 0.20$), indicating that, in general, the number of emerged seedlings of each plant species per block was consistent in both habitats (Fig. 14A). Indeed, in a series of comparisons for individual species using the differences in least-square means, we only detected significant differences between habitats in the case of *R. ulmifolius*, with

seedling emergence being 2.15-fold higher in the scrubland than in SLD verges (Fig. 14A).

The temporal pattern of seedling emergence was similar between habitats ($\chi^2_1 = 1.71$; $P = 0.19$), but varied strongly among shrub species ($\chi^2_6 = 998.62$; $P < 0.0001$). Specifically, we detected two different major patterns (i.e. groups of species). The first group of shrubs (i.e. *C. humilis*, *P. angustifolia*, *P. lentiscus*, *P. bourgaeana* and *R. ulmifolius*) showed an early emergence, with more than 80 % of the seedlings emerging within the first 30 weeks (Fig. 14B). Among them, *P. bourgaeana* seedlings showed the earliest and fastest emergence (it reached 100 % of emergence in 12 weeks; Fig. 14B). However, the second group of shrubs (i.e. *J. macrocarpa* and *J. phoenicea*) showed a slower seedling emergence pattern, with a sharp increase around 55 weeks after the sowing date (perhaps matching the brake of dormancy), and taking around 60 weeks to reach the 80 % of seedling emergence (Fig. 14B).

The interaction between habitat and shrub species was insignificant ($\chi^2_6 = 6.08$; $P = 0.41$), indicating that for each shrub species its temporal pattern of seedling emergence was similar in both habitats.

Seedling survival

From 784 emerged seedlings, only 120 (15.3 %) survived by the end of the study. From these, 66.6 %, 30.0 %, 1.7 % and 1.7 % belonged to *C. humilis*, *P. bourgaeana*, *J. macrocarpa* and *P. lentiscus*, respectively. From the 664 dead seedlings by the end of the study, 93.7 % died apparently because of water stress, 4.7 % because of fungal infection, 1.2 % was predated by invertebrates (e.g. caterpillars) and the remaining 0.4 % was buried by nearby activity of wild boars (*Sus scrofa*). These percentages were rather consistent between habitats. The number of surviving seedlings per block by the end of the study was not significantly different ($F_{1,27} = 0.04$; $P = 0.84$) between SLD verges (0.03 ± 0.11 ; mean \pm SE) and the scrubland (0.04 ± 0.12).

However, the temporal trend of seedling survival showed marginally significant differences between habitats ($\chi^2_1 = 3.41$; $P = 0.06$). Specifically, overall seedling survival was very similar between habitats at the beginning (0-25 weeks) and at the end (62-125 weeks) of the study. However, between 25 and 62 weeks from the date of emergence, overall seedling survival was, on average, a 45.0 % higher in the scrubland than in SLD verges (Fig. 15A).

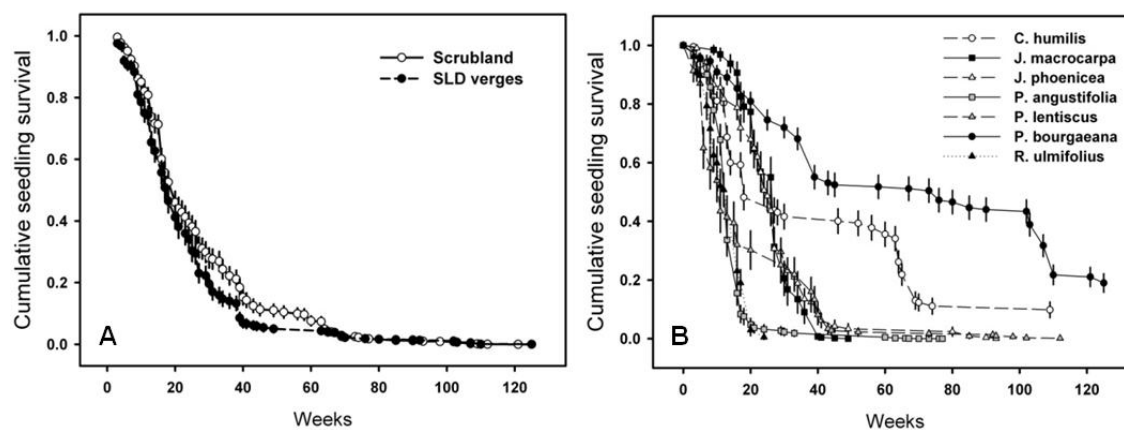


Figure 15: Differences in the temporal pattern of seedling survival between habitats (A) and among shrub species (B). In A, note the differences between habitats between about the 25th and the 62th weeks.

The temporal trend of seedling survival varied greatly among plant species ($\chi^2_6 = 297.25$; $P < 0.0001$), with survival of *C. humilis* and *P. bourgaeana* seedlings decreasing slowest, and fastest in the case of *P. angustifolia* and *R. ulmifolius* seedlings (Fig. 15B). The temporal pattern of survival decreasing in *J. macrocarpa*, *J. phoenicea*, and *P. lentiscus* seedlings was intermediate (Fig. 15B). Interestingly, the interaction Habitat*shrub species was significant ($\chi^2_6 = 16.76$; $P = 0.01$), suggesting that the temporal trend of seedling survival of some shrub species varied between habitats. Specifically, the survival of *P. angustifolia* seedlings decreased faster in SLD verges (seedling survival declined a 43.9 % between the 11st and the 13th week) than in the scrubland (where seedling survival only declined a 19.5 % during the same period). Despite these strong differences in the temporal trend of seedling survival of *P. angustifolia* seedlings between habitats ($\chi^2_1 = 9.29$; $P < 0.01$), we did not detect significant differences for the remaining shrub species ($\chi^2_1 < 2.21$; $P > 0.13$).

Discussion

In most humanized ecosystems, where SLD are usually pervasive, understanding the interactions between these structures and ecological processes is a key stage toward a more effective conservation and management of ecosystems and the services they provide (Dobson et al., 1997, Tylianakis et al., 2008), which mostly rely on plants (Isbell et al., 2011). In this study, we evaluated for the first time whether SLD verges, thought to act as hotspots of fleshy-fruited shrub recruitment and establishment (Suárez-Esteban et al., 2013b), are suitable habitats for seedling emergence and survival of these native shrubs.

In general, both the magnitude and the temporal pattern of seedling emergence were similar in SLD verges and in adjacent, unaltered scrublands. This suggests that SLD verges provide a habitat similarly suitable (but not better) for seedling emergence as the scrublands. We detected strong variations in the magnitude and the temporal pattern of seedling emergence among species, which suggests species-specific emergence behaviours and/or requirements (Hampe et al., 2008). *P. bourgaeana* was the species that emerged the most, the earliest and the fastest. Nonetheless, both aspects of seedling emergence were consistent between habitats in 6 of our 7 target species (*R. ulmifolius* showed a higher magnitude of emergence in the scrubland than in SLD verges), reinforcing the idea of a generally neutral effect of SLD on seedling emergence.

As for seedling emergence, the magnitude and the temporal pattern of seedling survival were similar in both habitats for most considered shrubs. Nevertheless, we detected wide variations in the magnitude and the temporal pattern of seedling survival among shrub species. The species that showed the highest seedling survival at the end of the study, and also with highest temporal pattern of survival, were *C. humilis* and *P. bourgaeana*. This was probably related to an extensively developed root system that allowed them to both resist the summer drought (Fedriani et al., 2012, Fedriani and Delibes, 2011) and to resprout after this stressful season. Indeed, 33.8 % (n = 80) and 69.4 % (n = 36) of *C. humilis* and *P. bourgaeana* surviving seedlings, respectively, were

dried out along the study, but eventually resprouted in a similar proportion in both habitats. This highlights the importance of long-term monitoring in studies evaluating seedling survival and establishment.

All species showed an abrupt fall of seedling survival within their first 40 weeks of life (largely coinciding with the summer period), followed by a much lighter decrease later on (Fig. 15B). This suggests that, as found for other Mediterranean species such as *O. europaea* (Rey and Alcántara, 2000), *Phillyrea latifolia* (Herrera et al., 1994), and *Acer opalus* subsp. *granatense* (Gómez-Aparicio, 2008), seedling survival expectancy is much higher in the second than in the first year of life, both in SLD verges and in the scrubland. In the case of *P. angustifolia*, seedling survival decreased much faster in SLD verges than in the scrubland. This might suggest that SLD verges are worse habitats for the recruitment of this species, although it could be a consequence of little sample size (we monitored the fate of 99 *P. angustifolia* emerged seedlings).

The summer drought was the main cause of seedling mortality in both habitats by large (Rey and Alcántara, 2000, Gómez-Aparicio et al., 2005, Castro et al., 2004, Fedriani et al., 2012). Therefore, water limitation in SLD verges was likely as intense as in adjacent scrublands, contrary to found previously for roadsides (Jodoin et al., 2008, Lelong et al., 2007) and SLD verges (Buckley et al., 2003). This contradiction occurred probably because SLD construction does not always involve the implementation of large ditches with the potential to gather water, as in the case of paved roads or highways (Lugo and Gucinski, 2000). Therefore, it is important to distinguish between different linear development types when analyzing the effects of these structures on plant populations (Lugo and Gucinski, 2000, Suárez-Esteban et al., 2013a).

We did not take into account the effect of herbivore vertebrates (e.g. rabbits, deer, voles), which can strongly limit seedling survival (Cadenasso et al., 2002, Hulme, 1996, Ibáñez and Schupp, 2001, Olofsson et al., 2005, Porensky et al., 2013). Indeed, in a similarly designed study we found that *P. bourgaeana* seedlings exposed to herbivores did not survive longer than 20 weeks, being such massive and quick mortality similar

both in SLD verges and the scrubland ($P = 0.75$). This contrasts with the relatively high survival of *P. bourgaeana* seedlings in absence of herbivores, and highlights the importance of these animals in limiting seedling establishment (Lopez and Terborgh, 2007, Clark et al., 2012).

Given the lack of SLD effect on seedling emergence and survival, we would expect to find the same number of naturally-recruited seedlings in both habitats. However, in a previous study, we detected 5.2 times more seedlings of fleshy-fruited shrubs in SLD verges than in the scrubland (along the same transects surveyed here; (Suárez-Esteban et al., 2013b). This pattern was particularly marked in the case of shrubs dispersed by the red fox and the European rabbit (e.g. *J. phoenicea*, *P. angustifolia*, *R. ulmifolius*), probably related with the preferential use of SLD verges by these animals for defecation and seed dispersal (they dispersed overall four-fold more seeds along SLD verges than in the scrubland; Suárez-Esteban et al., 2013a). Our result is consistent with those of Veldman and Putz (2010), who found that the higher densities of invasive grasses along trails verges as compared with forest interiors and forest gaps were related to a disproportional arrival of seeds to these verges dispersed by logging trucks rather than to seedling fate.

Since the habitat that received more seeds is also the habitat with higher number of recruits, we can assume that the recruitment of most fleshy-fruit shrubs in our study area is seed-limited rather than microsite-limited. Thus, we can assume that the role of SLD verges as hotspots for the recruitment and the establishment of native fleshy-fruited shrubs rely on seed dispersal by animals that positively select these verges for movement and defecation, such as foxes and rabbits in our study area (Suárez-Esteban et al., 2013a). These results highlight the potential benefits and the suitability of seed addition, either by human sowing (a commonly used, widespread method for plant restoration; (Brudvig et al., 2011, Tormo et al., 2006, Huxtable and Whalley, 1999), or mediated by animal seed dispersal (Suárez-Esteban et al., 2013a), for Mediterranean shrub restoration along SLD verges.

Conclusions

Seedling emergence and especially survival are often strong bottlenecks for plant recruitment (e.g. Gulias et al., 2004, González-Varo et al., 2012). Therefore, these two processes have often a deep influence on the suitability of certain habitats as plant recruitment hotspots. Surprisingly, we found no overall effect of SLD on both the magnitude and the temporal pattern of seedling emergence and survival. Thus, the higher abundance of fleshy-fruited shrubs along SLD verges as compared with adjacent scrublands (Suárez-Esteban et al., 2013b) is probably related to a disproportional arrival of seeds to these verges dispersed by foxes and rabbits (Suárez-Esteban et al., 2013a). This highlights the need of the conservation of these and other seed vectors that positively use SLD verges in order to promote the reforestation of SLD verges by native shrubs whenever it is a management aim.

Chapter 5

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



Resumen: Hábitats considerados como marginales también pueden tener un importante valor para la conservación. Mamíferos frugívoros como el zorro o el conejo dispersan semillas viables a lo largo de los bordes de SLD. Sin embargo, la mera llegada de semillas no garantiza el reclutamiento de nuevas plantas, ya que otros muchos procesos como los anteriormente tratados pueden alterar la abundancia espacial inicial de las semillas. En este capítulo se evalúa el papel de los bordes de SLD como potenciales *puntos calientes* de reclutamiento y establecimiento de arbustos mediterráneos.

Abstract

Hypothetical low-quality habitats can hold an overlooked conservation value. Some frugivorous mammals such as the red fox and the European rabbit 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 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 favour the diversity and the structural complexity of native vegetation while preventing the spread of invasive species.

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 (Nathan and Muller-Landau, 2000, Howe and Miriti, 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 (Shiels and Walker, 2003, Herrera and García, 2009, Harvey, 2000, Russo et al., 2006).

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 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 (Sagnard et al., 2007, Hampe, 2011). 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 et al., 2006, Damschen and Brudvig, 2012). In the same line, a recent study in SW Spain (Suárez-Esteban et al., 2013a) 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 and red foxes, which positively select SLD verges for defecation (Suárez-Esteban et al., 2013a). 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., 2013a). 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., 2013a) 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 (which defecated mainly in the scrubland; Suárez-Esteban et al., 2013a), 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 (Gómez-Aparicio, 2008, Fedriani et al., 2012), 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., 2013a), 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.

Material and Methods

Study area and species

In Doñana most of the fleshy-fruited species flower during later winter and spring (Feb-May) and produce drupes (e.g., *P. lentiscus*, *R. ulmifolius*) or berries (e.g., *M. communis*) that ripen during August-December (Jordano, 1984a, Fedriani and Delibes, 2009a). 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 (Jordano, 1984a, Fedriani and Delibes, 2009b, Fedriani and Delibes, 2011). 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. (2013a) 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 = 13066) 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, the fallow deer and the wild boar (boar and both deer species will be subsequently referred to as “ungulates”).

Sampling design

In each of our three study sites, we setup 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 in Matasgordas and Reserva, we sampled fifteen (12 m²) plots placed equidistantly (around 27 m 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 (24 m²) 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 5): (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, 1984a, Jordano, 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 100 cm³), adults (plants with flowers, fruits or their remains and/or with a volume higher than 8.5 m³), 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).

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, 2013) 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.

Results

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 located 678 fleshy-fruited shrubs belonging to 14 species (Table 5), with 59.14% and 40.86% of individuals found within SLD and scrubland plots, respectively. Rockroses were more

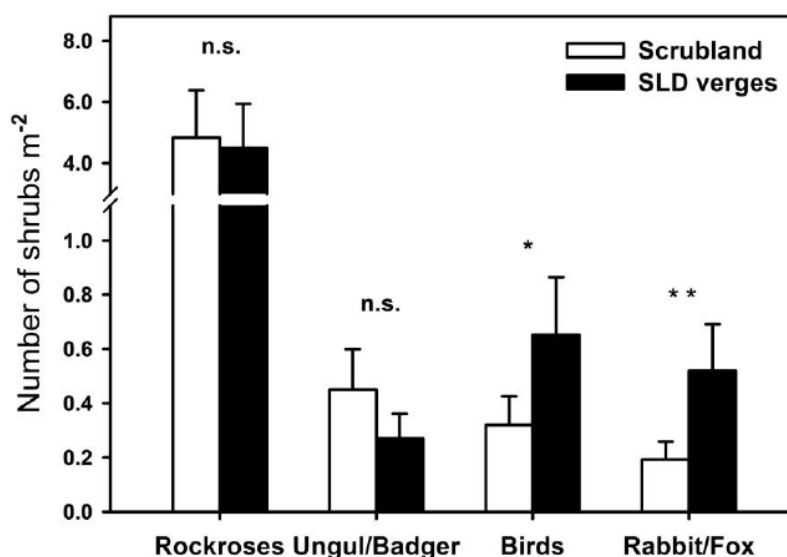


Figure 16: Differences in the adjusted mean density (\pm SE) of rockroses and fleshy-fruited shrubs between habitats. *P*-values of the corresponding test of slices are shown, indicating whether the differences between habitats were significant (n.s., non significant; * $P < 0.05$, ** $P < 0.01$).

abundant but less diverse than fleshy-fruited shrubs. Overall, we found 2754 individuals belonging to only five rockrose species (Table 5), 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. 16).

Table 5: Mean (\pm SE) density of each shrub taxa per plot (12 m²) along SLD verges and 60 m 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	Reference
Fleshy-fruited shrubs				
<i>Asparagus</i> spp.	0.32 \pm 0.09	0.67 \pm 0.30	Ungulate	a
<i>Pistacia lentiscus</i>	0.23 \pm 0.11	0.20 \pm 0.06	Ungulate	a
<i>Myrtus communis</i>	0.03 \pm 0.02	0.18 \pm 0.12	Ungulate	a
<i>Chamaerops humilis</i>	0.17 \pm 0.07	0.36 \pm 0.18	Badger	a, b
<i>Pyrus bourgasana</i>	0.10 \pm 0.09	0.08 \pm 0.06	Badger	a, c
<i>Rubia</i> spp.	1.01 \pm 0.46	0.27 \pm 0.25	Birds	d, e
<i>Osyris alba</i>	0.44 \pm 0.32	0.33 \pm 0.23	Birds	d, e
<i>Rhamnus oleoides</i>	0.30 \pm 0.10	0.29 \pm 0.09	Birds	d, e
<i>Daphne gnidium</i>	0.27 \pm 0.10	0.11 \pm 0.06	Birds	d, e
<i>Olea europaea sylvestris</i>	0.02 \pm 0.02	0.02 \pm 0.02	Birds	d, e
<i>Tamus communis</i>	0.01 \pm 0.01	0.00 \pm 0.00	Birds	d, e
<i>Juniperus phoenicea turbinata</i>	0.60 \pm 0.19	0.13 \pm 0.07	Rabbit/Fox	a
<i>Phillyrea angustifolia</i>	0.87 \pm 0.36	0.43 \pm 0.18	Rabbit	a
<i>Rubus ulmifolius</i>	0.08 \pm 0.05	0.01 \pm 0.01	Fox	a
Rockroses				
<i>Halimium halimifolium</i>	10.14 \pm 1.33	9.79 \pm 1.13	None	f
<i>Halimium calicinum</i>	3.18 \pm 0.59	3.44 \pm 0.47	None	f
<i>Cistus salvifolius</i>	0.90 \pm 0.37	0.87 \pm 0.27	None	f
<i>Cistus libanotis</i>	0.29 \pm 0.10	1.92 \pm 0.47	None	f
<i>Cistus crispus</i>	0.07 \pm 0.04	0.00 \pm 0.00	None	f

References: a: Suárez-Esteban et al. (2013a), b: Fedriani and Delibes (2011), c: Fedriani and Delibes (2009b), d: Jordano (1984a), e: Jordano (1995), f: Bastida and Talavera (2002).

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.

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. 17).

Nonetheless, while the density of saplings was similar between habitats for every plant functional group (Fig. 17), the differences in the density of seedlings

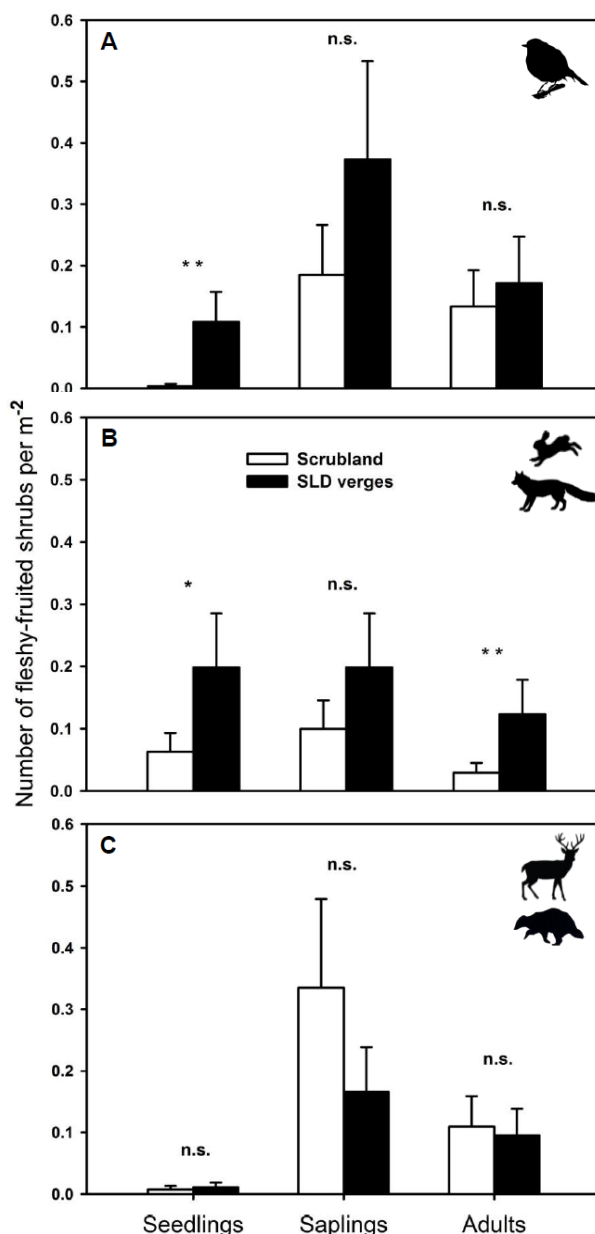


Figure 17: Differences in the mean density (\pm SE) of shrub size classes between habitats in the three functional groups of fleshy-fruited shrubs (bird-dispersed, above; rabbit/fox-dispersed, middle; ungulate/badger, below). P -values of the differences of least square means are shown, indicating whether the differences between habitats were significant in each case (n.s., non significant; ** $P < 0.01$; *** $P < 0.0001$)

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. 17A). 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. 17B). 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. 17A, B). However, the absence of differences between habitats in the density of ungulate/badger-dispersed species was consistent for all size classes (Fig. 17C).

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., 2013a), 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 (Suárez-Esteban et al., 2013a, Perea 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 (Suárez-Esteban et al., 2013a, Fedriani et al., 2010, Perea et al., 2013), promoting plant spatial heterogeneity. Therefore, the maintenance of diverse communities of frugivores is necessary to ensure plant diversity conservation (Ozinga et al., 2009, McConkey et al., 2012) 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. 17). 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., 2013a) 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., 2013a). 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 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.

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 favourable 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 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 (Jump and Peñuelas, 2005, Hampe, 2011). 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 et al., 2006, Damschen and Brudvig, 2012).

To take advantage of all the described potential benefits of SLD verges holding shrubs, which certainly deserve further research (Ries et al., 2001, Haddad and Tewksbury, 2005), these stripes of habitat must be cautiously managed. Traditional roadside and hedgerow management practices, including periodical mowing and the use of herbicides, are highly inadvisable (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 forestation efforts are necessary.

Síntesis y discusión general

Como consecuencia de la intensificación de las actividades humanas, la densidad de estructuras lineales como caminos y cortafuegos (i.e. estructuras lineales suaves; SLD) se ha incrementado de forma exponencial en las últimas décadas. Incluso emblemáticos parques nacionales como Yellowstone (EEUU), Jasper (Canadá) y Kruger (Sudáfrica) albergan más de 2000 Km de SLD cada uno. El Parque Nacional de Doñana es un ejemplo extremo, con más de 2000 Km de estas estructuras repartidos en apenas 543 Km² de superficie (el 6 % de la superficie de Yellowstone). Dada su extremadamente alta densidad, considerar todos los potenciales efectos de las SLD, tanto positivos como negativos, es un requerimiento imprescindible para gestionar estas estructuras con precisión y éxito (Lugo and Gucinski, 2000, Watkins et al., 2003).

La importancia de una gestión eficaz de las estructuras humanas es aún mayor ante la creciente desaparición y fragmentación de los hábitats naturales (Fahrig, 2003, Vitousek et al., 1997, Foley et al., 2005), ante el vertiginoso cambio climático (Schröter et al., 2005, Bertrand et al., 2011), y ante la omnipresente invasión de especies (Hulme et al., 2008, Mack et al., 2000). Estos y otros fenómenos conllevan una pérdida alarmante de biodiversidad (Brook et al., 2008, Western and Pearl, 1989), poniendo seriamente en entredicho nuestra capacidad para sobrevivir en el futuro (Barnosky et al., 2012, Hulme, 2013, Isbell et al., 2011, Lindenmayer and Possingham, 2013, MacDougall et al., 2013).

Esta tesis explora los efectos, hasta ahora ignorados, de SLD sobre las interacciones planta-animal, y sus consecuencias para la regeneración de arbustos mediterráneos (un buen ejemplo de organismos cuya distribución se ha visto seriamente reducida por las actividades humanas; Aparicio, 2008). Para ello se compararon las consecuencias para las plantas de sus interacciones con distintos animales tanto en los bordes de SLD como en el matorral adyacente (a 60 m de las SLD), un hábitat sin dicha intervención humana (i.e. “control”). Tal y como se ha ido viendo a lo largo de esta tesis, en el caso concreto de Doñana, los efectos de las SLD sobre el matorral variaron en signo

e intensidad dependiendo de las interacciones planta-animal y de las especies consideradas.

En cuanto a la producción de frutos y semillas del jaguarzo (especie seleccionada por cuestiones logísticas), las SLD tuvieron efectos contrastados. Por ejemplo, la depredación de flores y frutos por ungulados ramoneadores (e.g. ciervo, gamo) fue mayor en el interior del matorral que en los bordes de SLD. Esto concuerda con los resultados de Cadenasso and Pickett (2000), que demostraron que los ciervos se alimentan preferentemente en el interior del bosque y evitan sus bordes. Pese a esta reducción de la herbivoría, potencialmente positiva, las SLD tuvieron un efecto negativo aun mayor sobre la polinización (principalmente por escarabajos en esta cistácea; Herrera, 1986). Como consecuencia, la producción total de frutos y de semillas del jaguarzo fue menor en los bordes de SLD que en el matorral. Esto concuerda con las averiguaciones de Huang et al. (2009), que mostraron que la presencia de caminos en el Parque Nacional Huanglong (China) reducía la actividad de los polinizadores, disminuyendo el éxito reproductivo de dos especies de orquídeas.

En cuanto a la dispersión de semillas de arbustos de frutos carnosos, los bordes de SLD recibieron 3.4 veces más semillas que los matorrales adyacentes, de un total de 11 especies de arbustos fundamentalmente dispersadas por mamíferos como el zorro y el conejo, que seleccionaron positivamente los bordes de SLD para defecar (comportamiento probablemente asociado al marcaje territorial). Por el contrario, en los matorrales adyacentes se recibieron las semillas de 9 especies de arbustos de frutos carnosos, fundamentalmente dispersadas por otros mamíferos como el ciervo, el gamo, el jabalí y el tejón, que generalmente evitaron defecar en los bordes de SLD. La diversidad de especies dispersadas fue similar en los bordes de SLD y en los matorrales adyacentes (e.g. 7 de las 11 especies dispersadas en los bordes de SLD fueron también dispersadas en el matorral).

Para que la dispersión de semillas sea efectiva, las semillas deben, en primer lugar, sobrevivir al ataque de depredadores y patógenos (Hulme, 1997). Las SLD no

mostraron ningún efecto sobre la supervivencia post-dispersiva total de semillas, es decir, el número total de semillas supervivientes fue, en general, equivalente en los bordes de SLD y en los matorrales adyacentes. En segunda instancia, la dispersión efectiva de semillas depende del reclutamiento, es decir, de la emergencia y supervivencia de plántulas (Schupp et al., 2010). Ni la magnitud ni la velocidad de la emergencia y la supervivencia totales de plántulas se vio afectada por las SLD (i.e. ambos procesos dieron un resultado similar en los bordes de SLD y en el matorral).

Los efectos de las SLD fueron, en muchos casos, diferentes según la especie de arbusto. Para aquellas especies de las que se recogió una información más completa, calculamos la probabilidad acumulada de reclutamiento (en adelante PAR; i.e. el producto de los resultados de cada interacción planta-animal evaluada, desde el estadio de semilla hasta el de plántula), en los bordes de SLD y en los matorrales adyacentes. Cuando el resultado de una interacción planta-animal fue cero (e.g. la proporción de semillas de enebro dispersadas en el matorral), consideramos una probabilidad de 1 entre mil (ya que no es biológicamente imposible que esa interacción ocurra). Después, comparamos gráficamente la PAR con el patrón observado de abundancia relativa de cada especie de arbusto en cada hábitat, descrito en el capítulo 5 (Fig. 18).

En la Figura 18 se observa que la abundancia relativa de cada especie de arbusto en cada hábitat concuerda con el patrón esperado en base a su PAR (representada por el último punto de la curva). Dicho de otra forma, para las especies cuya PAR fue superior en los bordes de SLD que en el matorral adyacente (i.e. todas excepto el palmito), la abundancia relativa de arbustos fue también superior en los bordes de SLD, y viceversa. Pese a que no se detectaron arbustos de camarina y de enebro marítimo en los muestreos del capítulo 5, datos previos de nuestro equipo de investigación tomados en la Reserva Biológica de Doñana (RBD) demuestran que ambas especies alcanzan densidades muy superiores en los bordes de SLD que en el matorral adyacente (J.M. Fedriani & M. Delibes, *datos sin publicar*), con lo que para estas especies también se daría esa coincidencia (Fig. 18).

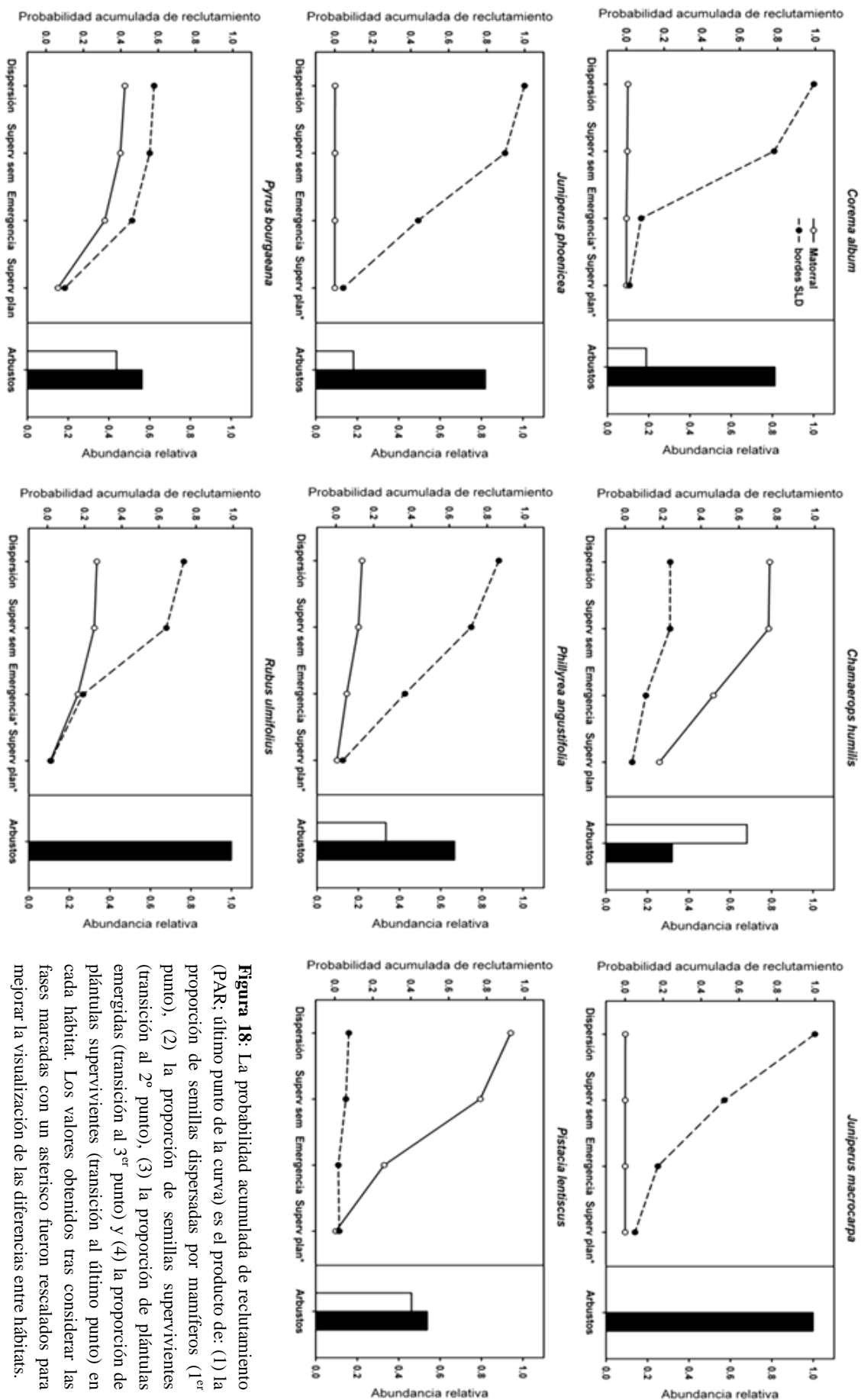


Figura 18: La probabilidad acumulada de reclutamiento (PAR; último punto de la curva) es el producto de: (1) la proporción de semillas dispersadas por mamíferos (1^{er} punto), (2) la proporción de semillas supervivientes (transición al 2^o punto), (3) la proporción de plántulas emergidas (transición al 3^{er} punto) y (4) la proporción de plántulas supervivientes (transición al último punto) en cada hábitat. Los valores obtenidos tras considerar las fases marcadas con un asterisco fueron rescalados para mejorar la visualización de las diferencias entre hábitats.

Sin embargo, la magnitud de las diferencias en la probabilidad de reclutamiento entre hábitats no se correspondió de forma precisa con la magnitud de las diferencias observadas de abundancia relativa de arbustos. Esto puede deberse a que, pese a que este estudio ha tratado de ser muy comprensivo, no ha tenido la duración suficiente como para valorar los potenciales efectos de las SLD sobre la transición del estadio de plántula al de juvenil y, finalmente, al de adulto reproductor.

Además, existen numerosos factores ecológicos que también condicionan el establecimiento de los arbustos mediterráneos y no se han tenido en cuenta. Entre ellos podemos incluir la producción de frutos y semillas (evaluada solamente en el caso del jaguarzo; Cranmer et al., 2012), la dispersión de semillas por aves (cuantiosa en multitud de las especies de arbustos estudiadas; Jordano, 1984a), la dispersión secundaria de semillas (Vander Wall et al., 2005), la herbivoría (Verkaar, 1987, Hulme, 1996), la influencia de factores abióticos (e.g. radiación solar, humedad, temperatura, concentración de nutrientes; Pearson et al., 2009) y la estocasticidad ambiental, presente en todos los procesos naturales (Lande, 1993).

Aunque las variaciones interanuales, así como la ausencia de datos en cuanto al crecimiento y la supervivencia tardía de plántulas y juveniles, puedan limitar la capacidad predictiva de este estudio, el hecho de que los patrones de probabilidad de reclutamiento y de abundancia relativa de arbustos en cada hábitat tiendan a coincidir (Fig. 18), pone de manifiesto la robustez de los resultados expuestos en esta tesis.

Contextualización de los resultados

Numerosos estudios han evidenciado la importancia de las interacciones planta-animal en la regeneración de árboles y arbustos mediterráneos como el acebuche (Rey and Alcántara, 2000), el aladierno (*Rhamnus alaternus*; Gulias et al., 2004), el arce (*Acer opalus* subsp. *granatense*; Gómez-Aparicio, 2008), la encina (*Quercus ilex*; Pulido and Díaz, 2005), el labiérnago (*P. latifolia*; Herrera et al., 1994), el palmito (Fedriani and Delibes, 2011), el piruétano (Fedriani et al., 2012) y el rotaboc (*Rhamnus ludovici-*

salvatoris; Traveset et al., 2003). Sin embargo, faltan estudios que integren este conocimiento con los efectos de las alteraciones humanas que tengan el potencial de modificar el devenir de las interacciones entre plantas y animales (e.g. la fragmentación de los hábitats; González-Varo, 2010a). El escaso conocimiento de esta triple interacción entre plantas, animales y actividades humanas limita nuestra capacidad de minimizar los efectos negativos de la explotación y la transformación del medio natural (Laurance et al., 2009, Auld and Keith, 2009), así como la de restaurar hábitats y ecosistemas degradados (Brunet, 2007, Dobson et al., 1997).

Los resultados de esta tesis indican que las diferencias observadas en cuanto a la abundancia y diversidad de arbustos entre los bordes de SLD y los matorrales adyacentes fueron debidas fundamentalmente a una dispersión de semillas diferencial (salvo en el caso del lentisco; Fig. 18). Siendo la dispersión de semillas un proceso fundamental a la hora de definir el efecto global de las SLD sobre la distribución espacial, abundancia y diversidad del matorral mediterráneo (Nathan and Muller-Landau, 2000, Hampe et al., 2008, Suárez-Esteban et al., 2013a), quisimos comprobar la generalidad de este resultado en otros ecosistemas y zonas del mundo mediante una revisión bibliográfica.

A priori podría esperarse que la influencia de las SLD en la lluvia de semillas fuera generalizada, ya que muchas especies de vertebrados parcialmente frugívoros de todo el mundo utilizan las SLD para desplazarse y/o defecar. Por citar unos pocos ejemplos, tal es el caso de la garduña (*Martes foina*) y la marta (*Martes martes*) en Europa (López-Bao and González-Varo, 2011), la marta (*Martes melampus*) y la comadreja (*Mustela itatsi*) japonesas en Asia (Tsuji et al., 2011), el casuario (*Casuarius casuarius*) en Oceanía (Stocker and Irvine, 1983; Westcott & McKeown *comunicación personal*), el zorro cangrejero (*Cerdocyon thous*) y el zorro de la pampa (*Pseudalopex gymnocercus*) en Sudamérica (Vieira and Port, 2007), y el coyote en Norteamérica (Fedriani and Kohn, 2001), etc.

Sin embargo, después de revisar 185 artículos, sólo 9 comparan la cantidad de semillas dispersadas en los bordes de SLD y en hábitats adyacentes. De ellos, 3

encontraron más semillas en los bordes de SLD (Veldman and Putz, 2010, Honu and Gibson, 2008, Pons and Pausas, 2007), 5 encontraron menos (Gorchov et al., 1993, Gorchov et al., 2013, Greene and Johnson, 1996, Restrepo et al., 1999, Wieland et al., 2011) y el restante, no encontró diferencias (Mayfield et al., 2006). Esto sugiere que, pese a su omnipresencia y su potencial importancia sobre el paisaje vegetal, el efecto de las SLD sobre la dispersión de semillas permanece prácticamente inexplorado en la mayor parte de los ecosistemas (Suárez-Esteban et al., Submitted). Esto ilustra el novedoso enfoque y el importante aporte de esta tesis doctoral, que podría ser utilizada como guía metodológica para evaluar los efectos de las SLD sobre el paisaje vegetal en otras zonas del mundo.

Regeneración del matorral mediterráneo en los bordes de SLD: implicaciones para la reforestación de paisajes humanizados.

En Doñana, conejos y zorros dispersan las semillas de al menos 11 especies de arbustos de frutos carnosos (e.g. camarina, sabina, enebro marítimo, zarzamora, olivilla) a lo largo de los bordes de SLD. Esta dispersión diferencial de semillas es el fenómeno que más influye en la abundancia y la diversidad de arbustos mediterráneos de frutos carnosos en las SLD, lo que pone de manifiesto el papel de estos mamíferos como auténticos *ingenieros del paisaje* (Jones et al., 1994). La conservación de estos dispersores de semillas, ambos sometidos a una alta presión humana (i.e. caza, control de depredadores, etc.) es necesaria para el mantenimiento y, en su caso, expansión del matorral mediterráneo (Damschen et al., 2008, McConkey et al., 2012). La pervivencia de este valioso servicio ecosistémico debe ser considerada a la hora de manejar las poblaciones de éstos mamíferos (Schröter et al., 2005). La depauperación o extinción de las poblaciones locales de estos animales conllevaría probablemente la pérdida del potencial de las SLD para albergar arbustos autóctonos (Brederveld et al., 2011, Schröter et al., 2005, Ozinga et al., 2009), cuya regeneración parece estar limitada por la llegada de semillas.

El hecho de que los bordes de SLD sean focos no sólo de recepción de semillas (Suárez-Esteban et al., 2013a), sino también de reclutamiento y establecimiento de arbustos de frutos carnosos, los convierte en potenciales puntos calientes o «*hotspots*» de regeneración, e incluso en frentes de colonización para arbustos autóctonos, algunos de los cuales ostentan categorías de amenaza (e.g. enebro marítimo; Fig. 19; (Suárez-Esteban et al., 2013b, Suárez-Esteban et al., Submitted). Este efecto, potencialmente beneficioso, abre nuevas oportunidades para el manejo de la vegetación en ambientes humanizados (Lugo and Gucinski, 2000). Por ejemplo, las SLD pueden actuar como refugios y reservorios de arbustos autóctonos, especialmente en paisajes profundamente transformados como los agrícolas (en los que la vegetación natural persiste únicamente en zonas marginales -no cultivadas- como los bordes de SLD; Lugo and Gucinski, 2000, Suárez-Esteban et al., 2013b).

Así, en caso de producirse el abandono de los campos, las SLD funcionarían como focos de producción de semillas para la reforestación de dichos campos (Blitzer et al., 2012, Brudvig et al., 2009), impidiendo, o al menos dificultando, el asentamiento de especies invasoras que



Figura 19: Enebro marítimo (*J. macrocarpa*) establecido en el borde del camino del control, en la RBD.

perjudicarían a la biodiversidad local (Byun et al., 2013, Hulme, 2007, Reinhardt Adams and Galatowitsch, 2008).

Si, como ocurre en Doñana, los arbustos autóctonos se establecen y forman verdaderos setos a lo largo de los bordes de SLD (Fig. 1 & Fig. 19), esto puede tener importantes ventajas de cara a la conservación de la biodiversidad y la atenuación de los posibles efectos perjudiciales de las SLD (Suárez-Esteban et al., 2013b). Por ejemplo, estos setos pueden (1) reducir la erosión (un problema recurrente asociado a las SLD;

Laurance et al., 2009), (2) actuar como barreras frente al establecimiento de especies invasoras (también común a lo largo de las SLD; Baret and Strasberg, 2005, Campbell and Gibson, 2001, Tyser and Worley, 1992), (3) disminuir los efectos de borde de las SLD (e.g. alta velocidad del viento, depósito de polvo, alta temperatura; Harvey, 2000), (4) proporcionar hábitat para multitud de organismos (e.g. aves, Pulido-Santacruz and Renjifo, 2011; murciélagos, Boughey et al., 2011; mamíferos terrestres, Gelling et al., 2007; insectos polinizadores, Morandin and Kremen, 2013; otros artrópodos, Pollard and Holland, 2006), y (5) mejorar la colonización de otras plantas (Wehling and Diekmann, 2009, Suárez-Esteban et al., 2013b), promoviendo tanto la llegada de semillas (por ejemplo, proporcionando posaderos para aves frugívoras) como el reclutamiento y establecimiento de nuevas plántulas (al generar un micro-ambiente favorable; Harvey, 2000).

Asimismo, los bordes de SLD pueden facilitar la creación de nuevos núcleos de arbustos reproductores (Fig. 20) que, a medio plazo, probablemente mejorarían la conectividad (i.e. el intercambio de genes e individuos) entre poblaciones aisladas de arbustos (Damschen et al., 2008), actuando como poblaciones puente o «*stepping stones*» (Harvey, 2000, Suárez-Esteban et al., 2013b).

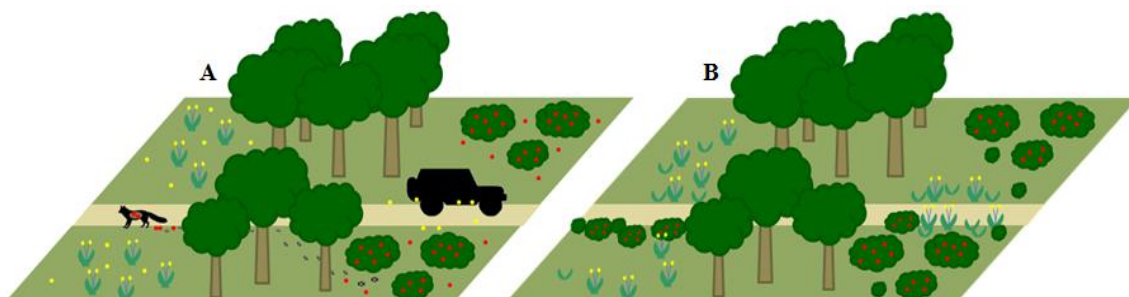


Figura 20: Esquema que muestra el potencial de las SLD como zonas de recepción de semillas (A) que posteriormente dan lugar a la creación de nuevos núcleos reproductores de arbustos a lo largo de sus bordes (B), tal y como se ha constatado que ocurre en el Parque Nacional de Doñana.

El incremento de la conectividad favorecería a su vez la riqueza y diversidad de arbustos a escala de paisaje (Damschen and Brudvig, 2012, Damschen et al., 2006). Además, las SLD podrían actuar como corredores, facilitando la migración de arbustos lo que, a largo plazo, probablemente incrementaría su capacidad de persistencia frente al

cambio climático (Williams et al., 2005) y otras perturbaciones o fenómenos estocásticos (e.g. incendios, plagas).

El reclutamiento y establecimiento de arbustos nativos en los bordes de SLD está condicionado por el manejo de estas estructuras (Avon et al., 2013). Si se pretende aprovechar el papel de los bordes de SLD como núcleos de regeneración de la vegetación autóctona, es desaconsejable la realización de desbroces y quemas (Jantunen et al., 2007), la utilización de herbicidas (Tyser et al., 1998), y la aplicación de sal (Czerniawska-Kusza et al., 2004) en éstas zonas. La ausencia de perturbaciones humanas en los bordes de SLD no está, a priori, reñida con la función que desempeñan estas estructuras (e.g. mejorar el acceso humano, evitar la expansión del fuego en caso de incendio). Recomendamos el uso de métodos selectivos (e.g. podas manuales) para controlar la expansión del matorral al interior de las SLD (lo que conllevaría una pérdida funcional de la estructura), sin poner en entredicho el incremento de la diversidad y la complejidad estructural del matorral en los bordes de las SLD y sus potenciales beneficios.

No se puede pasar por alto que los mencionados efectos positivos de las SLD podrían tornarse negativos si, por ejemplo, las especies dispersadas a lo largo de SLD fueran exóticas (e.g. Padrón et al., 2011). En tal caso, las SLD actuarían como corredores peligrosos (Proches et al., 2005), facilitando la expansión de plantas exóticas (Christen and Matlack, 2006) y con ello la pérdida de diversidad de especies vegetales nativas (Hulme, 2007), así como de las especies que interactúan con ellas (Traveset and Richardson, 2006) y de los servicios ecosistémicos que proveen (Isbell et al., 2011). En el caso de las invasiones biológicas, se podría usar a las SLD como zonas fácilmente identificables y accesibles donde incrementar los esfuerzos de erradicación de dichas especies (Buckley et al., 2006).

Además, es necesario considerar que los efectos de las SLD sobre las interacciones planta-animal son contexto-dependientes. Incluso considerando una misma interacción planta-animal (e.g. la dispersión de semillas, su supervivencia post-dispersiva, etc.) los efectos de las SLD dependieron de la identidad las especies de animales y

arbustos involucrados en la interacción. Por ejemplo, los bordes de SLD actuaron como receptores de semillas para arbustos dispersados por zorros y conejos, pero no para aquéllos dispersados por ungulados y tejones. Asimismo, los bordes de SLD supusieron lugares seguros para las semillas de algunas especies como la camarina y la sabina, pero no para la zarzamora. Esto pone de manifiesto la dependencia de los efectos de las SLD del contexto ecológico (i.e. de la identidad, la distribución y la abundancia relativa de las especies que conforman el ecosistema y de sus interacciones). Por lo tanto, aunque los patrones aquí descritos no pueden ser extrapolados directamente a otros ecosistemas, el marco conceptual y métodos aquí propuestos probablemente serán de mucha utilidad en futuras, similares investigaciones.

Como se ha demostrado en esta tesis, las alteraciones humanas (en este caso la presencia de SLD) pueden tener efectos ecológicos de naturaleza muy dispar, desde efectos de atracción (por ejemplo, de semillas dispersadas por zorros y conejos) hasta efectos disuasorios (por ejemplo, sobre los herbívoros), relevantes para la configuración espacial, abundancia y diversidad del matorral mediterráneo. Dada la elevada densidad de SLD y estructuras humanas afines en prácticamente todos los ecosistemas terrestres (Forman, 1998), así como su persistencia, considerar todos sus potenciales efectos es un requerimiento imprescindible para manejarlas de forma efectiva. Por esto y por su contexto-dependencia, proponemos que efectos como los demostrados en este proyecto sean evaluados en otras partes del mundo.

Conclusiones

1. En Doñana, las SLD limitan la polinización, y con ello a la producción de frutos y de semillas del jaguarzo. Pese a este efecto negativo, la densidad de jaguarzos es similar en las lindes de SLD y en el matorral adyacente. Esto sugiere que la regeneración de esta especie no está limitada por la cantidad de semillas, y que la menor producción relativa de frutos y semillas en los bordes de SLD se ve compensada en otras fases del ciclo de regeneración.
2. Los bordes de SLD reciben más semillas de arbustos de frutos carnosos fundamentalmente aquéllos dispersados por zorros y conejos (e.g. camarina, olivilla, sabina, enebro marítimo, zarzamora, madroño) que los matorrales adyacentes. Por el contrario, los matorrales reciben más semillas de arbustos dispersados fundamentalmente por ungulados y tejones (e.g. lentisco, esparraguera, palmito). Por lo tanto, la identidad y abundancia relativa de distintos dispersores de semillas determinarán la distribución y la diversidad de las semillas dispersadas cerca y lejos de las SLD.
3. En general, la presencia de SLD no alteró la supervivencia post-dispersiva de las semillas de arbustos de frutos carnosos. No obstante, las semillas de algunas especies fueron más depredadas en el matorral que en los bordes de SLD (e.g. camarina, sabina), mientras que las de otras especies mostraron el patrón opuesto (e.g. zarzamora).
4. Tanto la emergencia como la supervivencia temprana de plántulas fueron equivalentes en el interior del matorral mediterráneo y en los bordes de SLD, tanto en magnitud como en velocidad. La supervivencia de plántulas fue muy baja en todas las especies consideradas. El principal factor de mortalidad fue la sequía estival, aunque la herbivoría podría ser un factor muy limitante para la supervivencia temprana de plántulas de algunas especies.

5. Los bordes de SLD pueden ser hábitats favorables, e incluso «*hotspots*» para el reclutamiento y el establecimiento de una amplia diversidad de arbustos autóctonos, algunos de ellos amenazados (e.g. enebro marítimo). Por tanto, pueden tener un papel destacado en la conservación y la restauración de la vegetación nativa en ambientes humanizados.
6. De todas las interacciones planta-animal examinadas, la más decisiva a la hora de definir la configuración espacial, la abundancia y la diversidad de arbustos mediterráneos de frutos carnosos en relación a las SLD fue la dispersión de semillas por mamíferos. Esto muestra el papel de estos animales como *ingenieros ecológicos* y pone de manifiesto que la regeneración de los arbustos de frutos carnosos en Doñana está limitada por la llegada de semillas.
7. El efecto de las SLD sobre cada interacción planta-animal es variable según la identidad de las especies involucradas en la interacción. Por ejemplo, en cuanto a la dispersión de semillas, la identidad del vector de dispersión condiciona si las semillas son dispersadas a lo largo o lejos de los bordes de SLD. Esto sugiere que las consecuencias globales de las SLD sobre la regeneración del matorral están ligadas a la identidad de las especies que conforman el ecosistema y son, por lo tanto, contexto-dependientes.
8. Las alteraciones humanas (en este caso la presencia de SLD) pueden tener efectos ecológicos de naturaleza muy dispar, desde efectos de atracción (por ejemplo, de semillas dispersadas por zorros y conejos) hasta efectos disuasorios (por ejemplo, sobre los herbívoros), relevantes para la configuración espacial, abundancia y diversidad del matorral mediterráneo. Dada la omnipresencia de SLD en prácticamente todos los ecosistemas terrestres, es necesario evaluar exhaustivamente sus papeles ecológicos, tanto positivos como negativos, para gestionarlas de forma efectiva. Esta tesis puede servir como guía metodológica para investigar el efecto neto de las SLD sobre la regeneración de la vegetación en otras partes del mundo.

Referencias

Addison, S. J., Farrell, T., Roberts, G. N. & Rogers, D. J. (2007) Roadside surveys support predictions of negligible naturalisation potential for cotton (*Gossypium hirsutum*) in north-east Australia. *Weed Research*, **47**, 192-201.

Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M. A. (2006) Plant reproductive susceptibility to habitat fragmentation: Review and synthesis through a meta-analysis. *Ecology Letters*, **9**, 968-980.

Aizen, M. A. & Harder, L. D. (2007) Expanding the limits of the pollen-limitation concept: Effects of pollen quantity and quality. *Ecology*, **88**, 271-281.

Alisa W, C. (2007) From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography*, **15**, 396-406.

Alonso, C., Herrera, C. M. & Ashman, T. L. (2012) A piece of the puzzle: A method for comparing pollination quality and quantity across multiple species and reproductive events. *New Phytologist*, **193**, 532-542.

Anderson, S. H., Kelly, D., Ladley, J. J., Molloy, S. & Terry, J. (2011) Cascading effects of bird functional extinction reduce pollination and plant density. *Science*, **331**, 1068-1071.

Angold, P. G. (1997) The impact of a road upon adjacent heathland vegetation: Effects on plant species composition. *Journal of Applied Ecology*, **34**, 409-417.

Aparicio, A. (2008) Descriptive analysis of the 'relictual' Mediterranean landscape in the Guadalquivir River valley (southern Spain): A baseline for scientific research and the development of conservation action plans. *Biodiversity and Conservation*, **17**, 2219-2232.

Arévalo, J. R., Otto, R., Escudero, C., Fernández-Lugo, S., Arteaga, M., Delgado, J. D. & Fernández-Palacios, J. M. (2010) Do anthropogenic corridors homogenize plant

communities at a local scale? A case studied in Tenerife (Canary Islands). *Plant Ecology*, **209**, 23-35.

Armas, C. & Pugnaire, F. I. (2009) Ontogenetic shifts in interactions of two dominant shrub species in a semi-arid coastal sand dune system. *Journal of Vegetation Science*, **20**, 535-546.

Arteaga, M. A., Delgado, J. D., Otto, R., Fernández-Palacios, J. M. & Arévalo, J. R. (2009) How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. *Biological Invasions*, **11**, 1071-1086.

Ashman, T. L., Knight, T. M., Steets, J. A., Amarasekare, P., Burd, M., Campbell, D. R., Dudash, M. R., Johnston, M. O., Mazer, S. J., Mitchell, R. J., Morgan, M. T. & Wilson, W. G. (2004) Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology*, **85**, 2408-2421.

Auld, T. D. & Keith, D. A. (2009) Dealing with threats: Integrating science and management. *Ecological Management & Restoration*, **10**, S79-S87.

Avon, C., Bergès, L., Dumas, Y. & Dupouey, J. L. (2010) Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. *Forest Ecology and Management*, **259**, 1546-1555.

Avon, C., Dumas, Y. & Bergès, L. (2013) Management practices increase the impact of roads on plant communities in forests. *Biological Conservation*, **159**, 24-31.

Bacles, C. F. E., Lowe, A. J. & Ennos, R. A. (2006) Effective seed dispersal across a fragmented landscape. *Science*, **311**, 628.

Barberá, G. G., Navarro-Cano, J. A. & Castillo, V. M. (2006) Seedling recruitment in a semi-arid steppe: The role of microsite and post-dispersal seed predation. *Journal of Arid Environments*, **67**, 701-714.

Baret, S. & Strasberg, D. (2005) The effects of opening trails on exotic plant invasion in protected areas on la Réunion Island (Mascarene Archipelago, Indian Ocean). *Revue d'Ecologie (La Terre et la Vie)*, **60**, 325-332.

Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A., Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall, C., Matzke, N., Mindell, D. P., Revilla, E. & Smith, A. B. (2012) Approaching a state shift in Earth's biosphere. *Nature*, **486**, 52-58.

Bascompte, J., Jordano, P. & Olesen, J. M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, **312**, 431-433.

Baskin, C. C. & Baskin, J. M. (1998) *Seeds: ecology, biogeography, and evolution of dormancy and germination*. Academic Press, San Diego.

Bastida, F. & Talavera, S. (2002) Temporal and spatial patterns of seed dispersal in two *Cistus* species (Cistaceae). *Annals of Botany*, **89**, 427-434.

Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B. & Bascompte, J. (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, **458**, 1018-1020.

Bennett, A. F. (1991) Roads, roadsides and wildlife conservation: a review. *Nature conservation 2: the role of corridors*, 99-117.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J. C. & Gégout, J. C. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature*.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. & Kunin, W. E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351-354.

Birkedal, M., Löf, M., Olsson, G. E. & Bergsten, U. (2010) Effects of granivorous rodents on direct seeding of oak and beech in relation to site preparation and sowing date. *Forest Ecology and Management*, **259**, 2382-2389.

Blake, R. J., Westbury, D. B., Woodcock, B. A., Sutton, P. & Potts, S. G. (2012) Enhancement of buffer strips can improve provision of multiple ecosystem services. *Outlooks on Pest Management*, **23**, 258-262.

Bleher, B. & Böhning-Gaese, K. (2001) Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia*, **129**, 385-394.

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A.-M., Rand, T. A. & Tschamntke, T. (2012) Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, **146**, 34-43.

Bochet, E. & García-Fayos, P. (2004) Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. *Restoration Ecology*, **12**, 166-174.

Boughey, K. L., Lake, I. R., Haysom, K. A. & Dolman, P. M. (2011) Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biological Conservation*, **144**, 1790-1798.

Boyles, J. G., Cryan, P. M., McCracken, G. F. & Kunz, T. H. (2011) Economic importance of bats in agriculture. *Science*, **332**, 41-42.

Bray, J. R. & Curtis, J. T. (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, **27**, 325-349.

Brederveld, R. J., Jähnig, S. C., Lorenz, A. W., Brunzel, S. & Soons, M. B. (2011) Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *Journal of Applied Ecology*, **48**, 1241-1250.

Brook, B. W., Sodhi, N. S. & Bradshaw, C. J. A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453-460.

Brosi, B. J., Daily, G. C. & Ehrlich, P. R. (2007) Bee community shifts with landscape context in a tropical countryside. *Ecological Applications*, **17**, 418-430.

Brown, G. P., Phillips, B. L., Webb, J. K. & Shine, R. (2006) Toad on the road: Use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biological Conservation*, **133**, 88-94.

Brudvig, L. A., Damschen, E. I., Tewksbury, J. J., Haddad, N. M. & Levey, D. J. (2009) Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 9328-9332.

Brudvig, L. A., Mabry, C. M. & Mottl, L. M. (2011) Dispersal, not Understory Light Competition, Limits Restoration of Iowa Woodland Understory Herbs. *Restoration Ecology*, **19**, 24-31.

Brunet, J. (2007) Plant colonization in heterogeneous landscapes: An 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology*, **44**, 563-572.

Buckley, D. S., Crow, T. R., Nauertz, E. A. & Schulz, K. E. (2003) Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in Upper Michigan, USA. *Forest Ecology and Management*, **175**, 509-520.

Buckley, Y. M., Anderson, S., Catterall, C. P., Corlett, R. T., Engel, T., Gosper, C. R., Nathan, R., Richardson, D. M., Setter, M., Spiegel, O., Vivian-Smith, G., Voigt, F. A., Weir, J. E. S. & Westcott, D. A. (2006) Management of plant invasions mediated by frugivore interactions. *Journal of Applied Ecology*, **43**, 848-857.

Bullock, J. M., Moy, I. L., Coulson, S. J. & Clarke, R. T. (2003) Habitat-specific dispersal: Environmental effects on the mechanisms and patterns of seed movement in a grassland herb *Rhinanthus minor*. *Ecography*, **26**, 692-704.

Burd, M. (1994) Bateman's principal and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review*, **60**, 83-139.

Burkey, T. V. (1994) Tropical tree species diversity: A test of the Janzen-Connell model. *Oecologia*, **97**, 533-540.

Byun, C., de Blois, S. & Brisson, J. (2013) Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology*, **101**, 128-139.

Cadenasso, M. L. & Pickett, S. T. A. (2000) Linking forest edge structure to edge function: Mediation of herbivore damage. *Journal of Ecology*, **88**, 31-44.

Cadenasso, M. L., Pickett, S. T. A. & Morin, P. J. (2002) Experimental test of the role of mammalian herbivores on old field succession: Community structure and seedling survival. *Journal of the Torrey Botanical Society*, **129**, 228-237.

Campbell, J. E. & Gibson, D. J. (2001) The effect of seeds of exotic species transported via horse dung on Vegetation along trail corridors. *Plant Ecology*, **157**, 23-35.

Castro, J., Zamora, R., Hódar, J. A. & Gómez, J. M. (2004) Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: Consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*, **92**, 266-277.

Chambers, J. C. (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. *Ecological Applications*, **10**, 1400-1413.

Chen, H., Liu, J., Xue, T. & Wang, R. (2012) Roads accelerate the invasion process of alien species. *Advanced Materials Research*, **347-353**, 1483-1487.

Christen, D. C. & Matlack, G. R. (2006) The role of roadsides in plant invasions: A demographic approach. *Conservation Biology*, **20**, 385-391.

Christen, D. C. & Matlack, G. R. (2009) The habitat and conduit functions of roads in the spread of three invasive plant species. *Biological Invasions*, **11**, 453-465.

Christianini, A. V. & Galetti, M. (2007) Spatial variation in post-dispersal seed removal in an Atlantic forest: Effects of habitat, location and guilds of seed predators. *Acta Oecologica*, **32**, 328-336.

Christianini, A. V. & Oliveira, P. S. (2009) The relevance of ants as seed rescuers of a primarily bird-dispersed tree in the Neotropical cerrado savanna. *Oecologia*, **160**, 735-745.

Clark, C. J., Poulsen, J. R. & Levey, D. J. (2012) Vertebrate herbivory impacts seedling recruitment more than niche partitioning or density-dependent mortality. *Ecology*, **93**, 554-564.

Craig, D. J., Craig, J. E., Abella, S. R. & Vanier, C. H. (2010) Factors affecting exotic annual plant cover and richness along roadsides in the eastern Mojave Desert, USA. *Journal of Arid Environments*, **74**, 702-707.

Craig, M. T., Orrock, J. L. & Brudvig, L. A. (2011) Edge-mediated patterns of seed removal in experimentally connected and fragmented landscapes. *Landscape Ecology*, **26**, 1373-1381.

Cranmer, L., McCollin, D. & Ollerton, J. (2012) Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos*, **121**, 562-568.

Crawley, M. J. (2000) Seed Predators and Plant Population Dynamics. *Seeds. The Ecology of Regeneration in Plant Communities* (ed M. Fenner), pp. 167-182. CABI Publishing.

Cropper, M., Puri, J. & Griffiths, C. (2001) Predicting the location of deforestation: The role of roads and protected areas in North Thailand. *Land Economics*, **77**, 172-186.

Cunningham, S. A. (2000) Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 1149-1152.

Czerniawska-Kusza, I., Kusza, G. & Dużyński, M. (2004) Effect of deicing salts on urban soils and health status of roadside trees in the Opole Region. *Environmental Toxicology*, **19**, 296-301.

D'Hondt, B., Vansteenbrugge, L., van den Berge, K., Bastiaens, J. & Hoffmann, M. (2011) Scat analysis reveals a wide set of plant species to be potentially dispersed by foxes. *Plant Ecology and Evolution*, **144**, 106-110.

Damschen, E. I. & Brudvig, L. A. (2012) Landscape connectivity strengthens local-regional richness relationships in successional plant communities. *Ecology*, **93**, 704-710.

Damschen, E. I., Brudvig, L. A., Haddad, N. M., Levey, D. J., Orrock, J. L. & Tewksbury, J. J. (2008) The movement ecology and dynamics of plant communities in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19078-19083.

Damschen, E. I., Haddad, N. M., Orrock, J. L., Tewksbury, J. J. & Levey, D. J. (2006) Corridors increase plant species richness at large scales. *Science*, **313**, 1284-1286.

Delgado, J. D., Arévalo, J. R. & Fernández-Palacios, J. M. (2001) Road and topography effects on invasion: Edge effects in rat foraging patterns in two oceanic island forests (Tenerife, Canary Islands). *Ecography*, **24**, 539-546.

Delibes-Mateos, M., Delibes, M., Ferreras, P. & Villafuerte, R. (2008) Key role of European rabbits in the conservation of the western Mediterranean Basin hotspot. *Conservation Biology*, **22**, 1106-1117.

Delibes, M., Corbacho, C., Calvo, G. & Fedriani, J. M. (2012) Agriculture as matchmaker of an unexpected mutualism: Great bustard disperses and enhances emergence of domestic olive seeds. *Basic and Applied Ecology*, **13**, 125-131.

Develey, P. F. & Stouffer, P. C. (2001) Effects of roads on movements by understory birds in mixed-species flocks in Central Amazonian Brazil. *Conservation Biology*, **15**, 1416-1422.

Díaz Barradas, M. C., Zunzunegui, M. & García Novo, F. (1999) Autecological traits of *Halimium halimifolium* in contrasting habitats under a Mediterranean type climate - a review. *Folia Geobotanica*, **34**, 189-208.

Díaz, I., Papic, C. & Armesto, J. J. (1999) An assessment of post-dispersal seed predation in temperate rain forest fragments in Chiloe Island, Chile. *Oikos*, **87**, 228-238.

Dobson, A. P., Bradshaw, A. D. & Baker, A. J. M. (1997) Hopes for the Future: Restoration Ecology and Conservation Biology. *Science*, **277**, 515-522.

Dupré, C. & Ehrlén, J. (2002) Habitat configuration, species traits and plant distributions. *Journal of Ecology*, **90**, 796-805.

Elliott, C. P., Lindenmayer, D. B., Cunningham, S. A. & Young, A. G. (2012) Landscape context affects honeyeater communities and their foraging behaviour in Australia: Implications for plant pollination. *Landscape Ecology*, **27**, 393-404.

Ellstrand, N. C. (2005) *Dangerous liaisons? When cultivated plants mate with their wild relatives*. The John Hopkins University Press, Baltimore, Maryland.

Eycott, A. E., Watkinson, A. R., Hemami, M. R. & Dolman, P. M. (2007) The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. *Oecologia*, **154**, 107-118.

Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, pp. 487-515.

Fahrig, L. & Rytwinski, T. (2009) Effects of roads on animal abundance: An empirical review and synthesis. *Ecology and Society*, **14**.

Fearnside, P. M. (2005) Deforestation in Brazilian Amazonia: History, Rates, and Consequences. *Conservation Biology*, **19**, 680-688.

Fedriani, J. M. & Delibes, M. (2009a) Functional diversity in fruit-frugivore interactions: A field experiment with Mediterranean mammals. *Ecography*, **32**, 983-992.

Fedriani, J. M. & Delibes, M. (2009b) Seed dispersal in the Iberian pear, *Pyrus bourgaeana*: A role for infrequent mutualists. *Ecoscience*, **16**, 311-321.

Fedriani, J. M. & Delibes, M. (2011) Dangerous liaisons disperse the Mediterranean dwarf palm: Fleshy-Pulp defensive role against seed predators. *Ecology*, **92**, 304-315.

Fedriani, J. M., Fuller, T. K. & Sauvajot, R. M. (2001) Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography*, **24**, 325-331.

Fedriani, J. M. & Kohn, M. H. (2001) Genotyping faeces links individuals to their diet. *Ecology Letters*, **4**, 477-483.

Fedriani, J. M. & Manzaneda, A. J. (2005) Pre- and postdispersal seed predation by rodents: Balance of food and safety. *Behavioral Ecology*, **16**, 1018-1024.

Fedriani, J. M., Palomares, F. & Delibes, M. (1999) Niche relations among three sympatric Mediterranean carnivores. *Oecologia*, **121**, 138-148.

Fedriani, J. M., Rey, P. J., Garrido, J. L., Guitián, J., Herrera, C. M., Medrano, M., Sánchez-Lafuente, A. M. & Cerdá, X. (2004) Geographical variation in the potential of mice to constrain an ant-seed dispersal mutualism. *Oikos*, **105**, 181-191.

Fedriani, J. M., Wiegand, T. & Delibes, M. (2010) Spatial pattern of adult trees and the mammal-generated seed rain in the Iberian pear. *Ecography*, **33**, 545-555.

Fedriani, J. M., Zywiec, M. & Delibes, M. (2012) Thieves or mutualists? Pulp feeders enhance endozoochore local recruitment. *Ecology*, **93**, 575-587.

Fleming, T. H. & Estrada, A. (1993) *Frugivory and seed dispersal: ecological and evolutionary aspects*.

Flory, S. L. & Clay, K. (2009) Effects of roads and forest successional age on experimental plant invasions. *Biological Conservation*, **142**, 2531-2537.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. (2005) Global consequences of land use. *Science*, **309**, 570-574.

Forman, R. T. T. (1998) Road ecology: A solution for the giant embracing us. *Landscape Ecology*, **13**, iii-v.

Forman, R. T. T. (2000) Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology*, **14**, 31-35.

Forman, R. T. T. (2004) Road Ecology's Promise: What's Around the Bend? *Environment*, **46**, 8-21.

Forman, R. T. T. & Alexander, L. E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, **29**, 207-231.

Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., Fahrig, L., France, R., Goldman, C. R., Heanue, K., Jones, J. A., Swanson, F. J., Turrentine, T. & Winter, T. C. (2003) *Road Ecology: Science and Solutions*. Island Press, Washington.

Francis, C. D., Kleist, N. J., Ortega, C. P. & Cruz, A. (2012) Noise pollution alters ecological services: Enhanced pollination and disrupted seed dispersal. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2727-2735.

Freemark, K. E., Boutin, C. & Keddy, C. J. (2002) Importance of farmland habitats for conservation of plant species. *Conservation Biology*, **16**, 399-412.

Fuentes-Montemayor, E., Cuarón, A. D., Vázquez-Domínguez, E., Benítez-Malvido, J., Valenzuela-Galván, D. & Andresen, E. (2009) Living on the edge: Roads and edge effects on small mammal populations. *Journal of Animal Ecology*, **78**, 857-865.

Fuentes-Montemayor, E., Goulson, D. & Park, K. J. (2011) Pipistrelle bats and their prey do not benefit from four widely applied agri-environment management prescriptions. *Biological Conservation*, **144**, 2233-2246.

García-Castaño, J. L., Kollmann, J. & Jordano, P. (2006) Spatial variation of post-dispersal seed removal by rodents in highland microhabitats of Spain and Switzerland. *Seed Science Research*, **16**, 213-222.

García, D. & Chacoff, N. P. (2007) Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. *Conservation Biology*, **21**, 400-411.

Garibaldi, L. A., Aizen, M. A., Klein, A. M., Cunningham, S. A. & Harder, L. D. (2011) Global growth and stability of agricultural yield decrease with pollinator dependence. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 5909-5914.

Geerts, S. & Pauw, A. (2011) Easy technique for assessing pollination rates in the genus *Erica* reveals road impact on bird pollination in the Cape fynbos, South Africa. *Austral Ecology*, **36**, 656-662.

Gelbard, J. L. & Belnap, J. (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology*, **17**, 420-432.

Gelling, M., Macdonald, D. W. & Mathews, F. (2007) Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. *Landscape Ecology*, **22**, 1019-1032.

Gómez-Aparicio, L. (2008) Spatial patterns of recruitment in Mediterranean plant species: Linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. *Journal of Ecology*, **96**, 1128-1140.

Gómez-Aparicio, L., Gómez, J. M. & Zamora, R. (2005) Microhabitats shift rank in suitability for seedling establishment depending on habitat type and climate. *Journal of Ecology*, **93**, 1194-1202.

Gómez-Aparicio, L., Zamora, R., Gómez, J. M., Hódar, J. A., Castro, J. & Baraza, E. (2004) Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, **14**, 1128-1138.

Gómez, J. M. (2003) Herbivory Reduces the Strength of Pollinator-Mediated Selection in the Mediterranean Herb *Erysimum mediohispanicum*: Consequences for Plant Specialization. *The American Naturalist*, **162**, 242-256.

González-Varo, J. P. (2010a) *Biología de la conservación de Myrtus communis en un paisaje fragmentado: ecología de la reproducción, efectos genéticos y regeneración*. PhD Thesis, Universidad de Sevilla.

González-Varo, J. P. (2010b) Fragmentation, habitat composition and the dispersal/predation balance in interactions between the Mediterranean myrtle and avian frugivores. *Ecography*, **33**, 185-197.

González-Varo, J. P., Nora, S. & Aparicio, A. (2012) Bottlenecks for plant recruitment in woodland remnants: An ornithochorous shrub in a Mediterranean 'relictual' landscape. *Perspectives in Plant Ecology, Evolution and Systematics*, **14**, 111-122.

Gorchov, D. L., Cornejo, F., Ascorra, C. & Jaramillo, M. (1993) The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio*, **107-108**, 339-349.

Gorchov, D. L., Rondon, X. J., Cornejo, F., Schaefer, R. L., Janosko, J. M. & Sultz, G. (2013) Edge effects in recruitment of trees, and relationship to seed dispersal patterns, in cleared strips in the Peruvian Amazon. *Ecological Research*, **28**, 53-65.

Grant, A. S., Nelson, C. R., Switalski, T. A. & Rinehart, S. M. (2011) Restoration of Native Plant Communities after Road Decommissioning in the Rocky Mountains: Effect of Seed-Mix Composition on Vegetative Establishment. *Restoration Ecology*, **19**, 160-169.

Greene, D. F. & Johnson, E. A. (1996) Wind dispersal of seeds from a forest into a clearing. *Ecology*, **77**, 595-609.

Gulias, J., Traveset, A., Riera, N. & Mus, M. (2004) Critical Stages in the Recruitment Process of *Rhamnus alaternus* L. *Annals of Botany*, **93**, 723-731.

Guzmán, B. & Vargas, P. (2009) Long-distance colonization of the Western Mediterranean by *Cistus ladanifer* (*Cistaceae*) despite the absence of special dispersal mechanisms. *Journal of Biogeography*, **36**, 954-968.

Haddad, N. M., Bowne, D. R., Cunningham, A., Danielson, B. J., Levey, D. J., Sargent, S. & Spira, T. (2003) Corridor use by diverse taxa. *Ecology*, **84**, 609-615.

Haddad, N. M. & Tewksbury, J. J. (2005) Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications*, **15**, 250-257.

Haig, D. & Westoby, M. (1988) On limits to seed production. *American Naturalist*, **131**, 757-759.

Hampe, A. (2011) Plants on the move: The role of seed dispersal and initial population establishment for climate-driven range expansions. *Acta Oecologica*, **37**, 666-673.

Hampe, A., Garcia-Castaño, J. L., Schupp, E. W. & Jordano, P. (2008) Spatio-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. *Journal of Ecology*, **96**, 668-678.

Hannon, L. E. & Sisk, T. D. (2009) Hedgerows in an agri-natural landscape: Potential habitat value for native bees. *Biological Conservation*, **142**, 2140-2154.

Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosofske, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D., Jaiteh, M. S. & Esseen, P. A. (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, **19**, 768-782.

Harvey, C. A. (2000) Colonization of agricultural windbreaks by forest trees: Effects of connectivity and remnant trees. *Ecological Applications*, **10**, 1762-1773.

Hay, M. E. & Fuller, P. J. (1981) Seed Escape from Heteromyid Rodents: The Importance of Microhabitat and Seed Preference. *Ecology*, **62**, 1395-1399.

Hayter, K. E. & Cresswell, J. E. (2006) The influence of pollinator abundance on the dynamics and efficiency of pollination in agricultural Brassica napus: Implications for landscape-scale gene dispersal. *Journal of Applied Ecology*, **43**, 1196-1202.

Herrera, C. M. (1989) Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. *Oikos*, **55**, 250-262.

Herrera, C. M. (1995) Plant-vertebrate seed dispersal systems in the Mediterranean: Ecology, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics*, **26**, 705-727.

Herrera, C. M., Jordano, P., Lopez-Soria, L. & Amat, J. A. (1994) Recruitment of a mast-fruited, bird-dispersed tree: Bridging frugivore activity and seedling establishment. *Ecological Monographs*, **64**, 315-344.

Herrera, C. M., Medrano, M., Rey, P. J., Sánchez-Lafuente, A. M., García, M. B., Guitián, J. & Manzaneda, A. J. (2002) Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism- and antagonism-related traits. *Proceedings of the National Academy of Sciences*, **99**, 16823-16828.

Herrera, J. (1986) Flowering and fruiting phenology in the coastal shrublands of Doñana, south Spain. *Vegetatio*, **68**, 91-98.

Herrera, J. (1987) Flower and fruit biology in southern Spanish Mediterranean shrublands. *Annals - Missouri Botanical Garden*, **74**, 69-78.

Herrera, J. (1988) Pollination relationships in southern Spanish Mediterranean shrublands. *Journal of Ecology*, **76**, 274-287.

Herrera, J. M. & García, D. (2009) The role of remnant trees in seed dispersal through the matrix: Being alone is not always so sad. *Biological Conservation*, **142**, 149-158.

Higgins, S. I., Nathan, R. & Cain, M. L. (2003) Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology*, **84**, 1945-1956.

Hille Ris Lambers, J. & Clark, J. S. (2003) Effects of dispersal, shrubs, and density-dependent mortality on seed and seedling distributions in temperate forests. *Canadian Journal of Forest Research*, **33**, 783-795.

Hinsley, S. A. & Bellamy, P. E. (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. *Journal of Environmental Management*, **60**, 33-49.

Holl, K. D. & Lulow, M. E. (1997) Effects of Species, Habitat, and Distance from Edge on Post-dispersal Seed Predation in a Tropical Rainforest. *Biotropica*, **29**, 459-468.

Honu, Y. A. K. & Gibson, D. J. (2008) Patterns of invasion: Trends in abundance of understory vegetation, seed rain, and seed bank from forest edge to interior. *Natural Areas Journal*, **28**, 228-239.

Hopwood, J. L. (2008) The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation*, **141**, 2632-2640.

Houle, G. (1992) Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *Journal of Ecology*, **80**, 99-108.

Howe, H. F. & Miriti, M. N. (2000) No question: Seed dispersal matters. *Trends in Ecology and Evolution*, **15**, 434-436.

Howe, H. F. & Smallwood, J. (1982) Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics*, **13**, 201-228.

Huang, B. Q., Sun, Y. N., Yu, X. H., Luo, Y. B., Hutchings, M. J. & Tang, S. Y. (2009) Impact of proximity to a pathway on orchid pollination success in Huanglong National Park, South-West China. *Biological Conservation*, **142**, 701-708.

Hulme, P. E. (1996) Herbivory, plant regeneration, and species coexistence. *Journal of Ecology*, **84**, 609-615.

Hulme, P. E. (1997) Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. *Oecologia*, **111**, 91-98.

Hulme, P. E. (1998) Post-dispersal seed predation: Consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics*, **1**, 32-46.

Hulme, P. E. (2007) Biological invasions in Europe: Drivers, pressures, states, impacts and responses. *Biodiversity under threat* (eds R. E. Hester & R. M. Larrison), pp. 56-80. The Royal Society of Chemistry, Cambridge.

Hulme, P. E. (2013) Environmental health crucial to food safety. *Science*, **339**, 522.

Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., Pergl, J., Pysek, P., Roques, A., Sol, D., Solarz, W. & Vilá, M. (2008) Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology*, **45**, 403-414.

Hulme, P. E. & Borelli, T. (1999) Variability in post-dispersal seed predation in deciduous woodland: Relative importance of location, seed species, burial and density. *Plant Ecology*, **145**, 149-156.

Huxtable, C. H. A. & Whalley, R. D. B. (1999) Emergence and survival of three native grass species sown on roadsides on the Northern Tablelands, New South Wales, Australia. *Australian Journal of Botany*, **47**, 221-235.

Ibáñez, I. & Schupp, E. W. (2001) Positive and negative interactions between environmental conditions affecting *Cercocarpus ledifolius* seedling survival. *Oecologia*, **129**, 543-550.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B. J., Zavaleta, E. S. & Loreau, M. (2011) High plant diversity is needed to maintain ecosystem services. *Nature*, **477**, 199-202.

James, A. R. C. & Stuart-Smith, A. K. (2000) Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management*, **64**, 154-159.

Jantunen, J., Saarinen, K., Valtonen, A. & Saarnio, S. (2007) Flowering and seed production success along roads with different mowing regimes. *Applied Vegetation Science*, **10**, 285-292.

Janzen, D. H. (1970) Herbivores and the number of tree species in Tropical forests. *The American Naturalist*, **104**, 501-528.

Jodoin, Y., Lavoie, C., Villeneuve, P., Theriault, M., Beaulieu, J. & Belzile, F. (2008) Highways as corridors and habitats for the invasive common reed *Phragmites australis* in Quebec, Canada. *Journal of Applied Ecology*, **45**, 459-466.

Johnson, V. C. & Adkisson, C. S. (1985) Dispersal of beech nuts by blue jays in fragmented landscapes. *American Midland Naturalist*, **113**, 319-324.

Jones, C. G., Lawton, J. H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373-386.

Jongejans, E., Skarpaas, O., Tipping, P. W. & Shea, K. (2007) Establishment and spread of founding populations of an invasive thistle: The role of competition and seed limitation. *Biological Invasions*, **9**, 317-325.

Jordano, P. (1984a) *Relaciones entre plantas y aves frugívoras en el matorral mediterráneo del área de Doñana*. Ph.D. Thesis, University of Seville.

Jordano, P. (1984b) Seed weight variation and differential avian dispersal in blackberries *Rubus ulmifolius*. *Oikos*, **43**, 149-153.

Jordano, P. (1995) Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist*, **145**, 163-191.

Jordano, P., Forget, P.-M., Lambert, J. E., Böhning-Gaese, K., Traveset, A. & Wright, S. J. (2011) Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters*, **7**, 321-323.

Jordano, P., García, C., Godoy, J. A. & García-Castaño, J. L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 3278-3282.

Jules, E. S. & Rathcke, B. J. (1999) Mechanisms of Reduced Trillium Recruitment along Edges of Old-Growth Forest Fragments. *Conservation Biology*, **13**, 784-793.

Jump, A. S. & Peñuelas, J. (2005) Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010-1020.

Karim, M. N. & Mallik, A. U. (2008) Roadside revegetation by native plants. I. Roadside microhabitats, floristic zonation and species traits. *Ecological Engineering*, **32**, 222-237.

Kearns, C. A., Inouye, D. W. & Waser, N. M. (1998) Endangered mutualisms: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, **29**, 83-112.

Kerley, L. L., Goodrich, J. M., Miquelle, D. G., Smirnov, E. N., Quigley, H. B. & Hornocker, M. G. (2002) Effects of roads and human disturbance on Amur tigers. *Conservation Biology*, **16**, 97-108.

Kitajima, K. & Fenner, M. (2005) Ecology of seedling regeneration. *Seeds. The ecology of regeneration in plant communities* (ed M. Fenner), pp. 331-360. CABI Publishing, Wallingford.

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303-313.

Knight, T. M., Steets, J. A. & Ashman, T. L. (2006) A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. *American Journal of Botany*, **93**, 271-277.

Kolb, A. (2008) Habitat fragmentation reduces plant fitness by disturbing pollination and modifying response to herbivory. *Biological Conservation*, **141**, 2540-2549.

Kollmann, J., Coomes, D. A. & White, S. M. (1998) Consistencies in Post-Dispersal Seed Predation of Temperate Fleshy-Fruited Species Among Seasons, Years and Sites. *Functional Ecology*, **12**, 683-690.

Kremen, C. (2005) Managing ecosystem services: What do we need to know about their ecology? *Ecology Letters*, **8**, 468-479.

Krüsi, B. O. & Debussche, M. (1988) The fate of flowers and fruits of *Cornus sanguinea* L. in three contrasting Mediterranean habitats. *Oecologia*, **74**, 592-599.

Kuefler, D., Hudgens, B., Haddad, N. M., Morris, W. F. & Thurgate, N. (2010) The conflicting role of matrix habitats as conduits and barriers for dispersal. *Ecology*, **91**, 944-950.

Lambin, E. F. & Geist, H. (2006) *Land-Use and Land-Cover Changes. Local Processes and Global Impacts*. Springer, Berlin.

Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, **142**, 911-927.

Laurance, W. F., Croes, B. M., Guissouegou, N., Buij, R., Dethier, M. & Alonso, A. (2008) Impacts of roads, hunting, and habitat alteration on nocturnal mammals in African rainforests. *Conservation Biology*, **22**, 721-732.

Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., Campbell, P. & Ondzeano, C. (2006) Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, **20**, 1251-1261.

Laurance, W. F., Goosem, M. & Laurance, S. G. W. (2009) Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution*, **24**, 659-669.

Legret, M. & Pagotto, C. (2006) Heavy Metal Deposition and Soil Pollution Along Two Major Rural Highways. *Environmental Technology*, **27**, 247-254.

Lehtilä, K. & Strauss, S. Y. (1997) Leaf damage by herbivores affects attractiveness to pollinators in wild radish, *Raphanus raphanistrum*. *Oecologia*, **111**, 396-403.

Leidner, A. K. & Haddad, N. M. (2011) Combining measures of dispersal to identify conservation strategies in fragmented landscapes. *Conservation Biology*, **25**, 1022-1031.

Lelong, B., Lavoie, C., Jodoin, Y. & Belzile, F. (2007) Expansion pathways of the exotic common reed (*Phragmites australis*): a historical and genetic analysis. *Diversity and Distributions*, **13**, 430-437.

Lenda, M., Skórka, P., Knops, J. M. H., Moroń, D., Tworek, S. & Woyciechowski, M. (2012) Plant establishment and invasions: An increase in a seed disperser combined with land abandonment causes an invasion of the non-native walnut in Europe. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1491-1497.

Levey, D. J., Bolker, B. M., Tewksbury, J. J., Sargent, S. & Haddad, N. M. (2005) Ecology: Effects of landscape corridors on seed dispersal by birds. *Science*, **309**, 146-148.

Levin, S. A., Muller-Landau, H. C., Nathan, R. & Chave, J. (2003) The Ecology and Evolution of Seed Dispersal: A Theoretical Perspective. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 575-604.

Lindenmayer, D. B. & Possingham, H. P. (2013) No Excuse for Habitat Destruction. *Science*, **340**, 680.

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D. & Schabenberger, O. (2006) *SAS for mixed models*. Cary NC: SAS Institute Inc.

Loiselle, B. A., Blendinger, P. G., Blake, J. G. & Ryder, T. B. (2007) Ecological redundancy in seed dispersal systems: A comparison between manakins (Aves: *Pipridae*) in two tropical forests. *Seed dispersal. Theory and its application in a changing world* (eds A. J. Dennis, E. W. Schupp, R. J. Green & D. A. Westcott), pp. 178-199. CAB International, Wallingford.

López-Bao, J. V. & González-Varo, J. P. (2011) Frugivory and spatial patterns of seed deposition by carnivorous mammals in anthropogenic landscapes: A multi-scale approach. *PLoS ONE*, **6**.

Lopez, L. & Terborgh, J. (2007) Seed predation and seedling herbivory as factors in tree recruitment failure on predator-free forested islands. *Journal of Tropical Ecology*, **23**, 129-137.

Lugo, A. E. & Gucinski, H. (2000) Function, effects, and management of forest roads. *Forest Ecology and Management*, **133**, 249-262.

MacDougall, A. S., McCann, K. S., Gellner, G. & Turkington, R. (2013) Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature*, **494**, 86-89.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. & Bazzaz, F. A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689-710.

MacMahon, J. A., Mull, J. F. & Crist, T. O. (2000) Harvester ants (*Pogonomyrmex* spp.): Their community and ecosystem influences. *Annual Review of Ecology and Systematics*, **31**, 265-291.

Mader, H. J. (1984) Animal habitat isolation by roads and agricultural fields. *Biological Conservation*, **29**, 81-96.

Magrach, A., Guitián, J. & Larrinaga, A. R. (2011) Land-use and edge effects unbalance seed dispersal and predation interactions under habitat fragmentation. *Ecological Research*, **26**, 851-861.

Magrach, A., Santamaría, L. & Larrinaga, A. R. (2013) Forest edges show contrasting effects on an austral mistletoe due to differences in pollination and seed dispersal. *Journal of Ecology*, **101**, 713-721.

Malo, J. E. & Suarez, F. (1996) *Cistus ladanifer* recruitment - Not only fire, but also deer. *Acta Oecologica*, **17**, 55-60.

Matias, L., Zamora, R., Mendoza, I. & Hódar, J. A. (2010) Seed Dispersal Patterns by Large Frugivorous Mammals in a Degraded Mosaic Landscape. *Restoration Ecology*, **18**, 619-627.

Mayfield, M. M., Ackerly, D. & Daily, G. C. (2006) The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *Journal of Ecology*, **94**, 522-536.

McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., Rogers, H. & Santamaria, L. (2012) Seed dispersal in changing landscapes. *Biological Conservation*, **146**, 1-13.

McLellan, B. N. & Shackleton, D. M. (1988) Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. *Journal of Applied Ecology*, **25**, 451-460.

Morandin, L. A. & Kremen, C. (2013) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, **23**, 829-839.

Moreno, S. & Rouco, C. (2013) Responses of a small-mammal community to habitat management through controlled burning in a protected Mediterranean area. *Acta Oecologica*, **49**, 1-4.

Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, **10**, 58-62.

Mwangi, D., Kasina, M., Nderitu, J., Hagen, M., Gikungu, M. & Kraemer, M. (2012) Diversity and abundance of native bees foraging on hedgerow plants in the Kakamega farmlands, western Kenya. *Journal of Apicultural Research*, **51**, 298-305.

Myers, J. A. & Harms, K. E. (2011) Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology*, **92**, 676-686.

Myers, J. A., Vellend, M. & Gardescu, S. (2004) Seed dispersal by white-tailed deer: Implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia*, **139**, 35-44.

Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786-788.

Nathan, R. & Katul, G. G. (2005) Foliage shedding in deciduous forests lifts up long-distance seed dispersal by wind. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8251-8256.

Nathan, R. & Muller-Landau, H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278-285.

Ness, J. H. & Morin, D. F. (2008) Forest edges and landscape history shape interactions between plants, seed-dispersing ants and seed predators. *Biological Conservation*, **141**, 838-847.

Noordijk, J., Delille, K., Schaffers, A. P. & Sýkora, K. V. (2009) Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, **142**, 2097-2103.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2012) vegan: Community Ecology Package. R package version 2.0-5.

Olofsson, J., Hulme, P. E., Oksanen, L. & Suominen, O. (2004) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, **106**, 324-334.

Olofsson, J., Hulme, P. E., Oksanen, L. & Suominen, O. (2005) Effects of mammalian herbivores on revegetation of disturbed areas in the forest-tundra ecotone in northern Fennoscandia. *Landscape Ecology*, **20**, 351-359.

Orrock, J. L. & Damschen, E. I. (2005) Corridors cause differential seed predation. *Ecological Applications*, **15**, 793-798.

Orrock, J. L., Danielson, B. J., Burns, M. J. & Levey, D. J. (2003) Spatial ecology of predator-prey interactions: Corridors and patch shape influence seed predation. *Ecology*, **84**, 2589-2599.

Orrock, J. L., Levey, D. J., Danielson, B. J. & Damschen, E. I. (2006) Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. *Journal of Ecology*, **94**, 838-845.

Ostoja, S. M., Schupp, E. W., Durham, S. & Klinger, R. (2013) Seed harvesting is influenced by associational effects in mixed seed neighbourhoods, not just by seed density. *Functional Ecology*, **27**, 775-785.

Ozinga, W. A., Römermann, C., Bekker, R. M., Prinzing, A., Tamis, W. L. M., Schaminée, J. H. J., Hennekens, S. M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J. P. & Van Groenendael, J. M. (2009) Dispersal failure contributes to plant losses in NW Europe. *Ecology Letters*, **12**, 66-74.

Padrón, B., Nogales, M., Traveset, A., Vilà, M., Martínez-Abraín, A., Padilla, D. P. & Marrero, P. (2011) Integration of invasive *Opuntia* spp. by native and alien seed dispersers in the Mediterranean area and the Canary Islands. *Biological Invasions*, **13**, 831-844.

Parendes, L. A. & Jones, J. A. (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. *Conservation Biology*, **14**, 64-75.

Parker, I. M. (1997) Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. *Ecology*, **78**, 1457-1470.

Pearson, G. A., Lago-Leston, A. & Mota, C. (2009) Frayed at the edges: Selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. *Journal of Ecology*, **97**, 450-462.

Perea, R., Delibes, M., Polko, M., Suárez-Esteban, A. & Fedriani, J. M. (2013) Context-dependent fruit–frugivore interactions: partner identities and spatio-temporal variations. *Oikos*, **122**, 943-951.

Perea, R., San Miguel, A. & Gil, L. (2011) Disentangling factors controlling fruit and seed removal by rodents in temperate forests. *Seed Science Research*, **21**, 227-234.

Pollard, K. A. & Holland, J. M. (2006) Arthropods within the woody element of hedgerows and their distribution pattern. *Agricultural and Forest Entomology*, **8**, 203-211.

Pons, J. & Pausas, J. G. (2007) Acorn dispersal estimated by radio-tracking. *Oecologia*, **153**, 903-911.

Porensky, L. M., Wittman, S. E., Riginos, C. & Young, T. P. (2013) Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. *Oecologia*, 1-12.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W. E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution (Personal edition)*, **25**, 345-353.

Primack, R. B. (1987) Relationships among flowers, fruits, and seeds. *Annual review of ecology and systematics. Vol. 18*, 409-430.

Proches, S., Wilson, J. R. U., Veldtman, R., Kalwij, J. M., Richardson, D. M., Chown, S. L., Levey, D. J., Bolker, B. M., Tewksbury, J. J., Sargent, S. & Haddad, N. M. (2005) Landscape corridors: Possible dangers? *Science*, **310**, 779-783.

Pulido-Santacruz, P. & Renjifo, L. M. (2011) Live fences as tools for biodiversity conservation: A study case with birds and plants. *Agroforestry Systems*, **81**, 15-30.

Pulido, F. J. & Díaz, M. (2005) Regeneration of a Mediterranean oak: A whole-cycle approach. *Ecoscience*, **12**, 92-102.

Quinn, G. G. P. & Keough, M. J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press.

R Development Core Team. (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramp, D., Wilson, V. K. & Croft, D. B. (2006) Assessing the impacts of roads in peri-urban reserves: Road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. *Biological Conservation*, **129**, 348-359.

Rands, S. A. & Whitney, H. M. (2010) Effects of pollinator density-dependent preferences on field margin visitations in the midst of agricultural monocultures: A modelling approach. *Ecological Modelling*, **221**, 1310-1316.

Reed, R. A. (1996) Contribution of roads to forest fragmentation in the Rocky Mountains. *Conservation Biology*, **10**, 1098-1106.

Reinhardt Adams, C. & Galatowitsch, S. (2008) The transition from invasive species control to native species promotion and its dependence on seed density thresholds. *Applied Vegetation Science*, **11**, 131-138.

Restrepo, C., Gomez, N. & Heredia, S. (1999) Anthropogenic edges, treefall gaps, and fruit-frugivore interactions in a neotropical montane forest. *Ecology*, **80**, 668-685.

Rey, P. J. & Alcántara, J. M. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): Connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, **88**, 622-633.

Rey, P. J., Garrido, J. L., Alcántara, J. M., Ramírez, J. M., Aguilera, A., García, L., Manzaneda, A. J. & Fernández, R. (2002) Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. *Functional Ecology*, **16**, 773-781.

Ries, L., Debinski, D. M. & Wieland, M. L. (2001) Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology*, **15**, 401-411.

Román, J., Barón, A. & Revilla, E. (2010) Evaluación de los efectos del tránsito a motor sobre especies y comunidades de interés en el Espacio Natural de Doñana. pp. 236. Consejería de Medio Ambiente, Junta de Andalucía. Estación Biológica de Doñana, CSIC.

Rost, J., Pons, P. & Bas, J. M. (2012) Seed dispersal by carnivorous mammals into burnt forests: An opportunity for non-indigenous and cultivated plant species. *Basic and Applied Ecology*.

Russo, S. E., Portnoy, S. & Augspurger, C. K. (2006) Incorporating animal behavior into seed dispersal models: Implications for seed shadows. *Ecology*, **87**, 3160-3174.

Sage Jr, R. W., Tierson, W. C., Mattfeld, G. F. & Behrend, D. F. (1983) White-tailed deer visibility and behavior along forest roads. *Journal of Wildlife Management*, **47**, 940-953.

Sagnard, F., Pichot, C., Dreyfus, P., Jordano, P. & Fady, B. (2007) Modelling seed dispersal to predict seedling recruitment: Recolonization dynamics in a plantation forest. *Ecological Modelling*, **203**, 464-474.

Schlaepfer, M. A., Runge, M. C. & Sherman, P. W. (2002) Ecological and evolutionary traps. *Trends in Ecology and Evolution*, **17**, 474-480.

Schmucki, R. & De Blois, S. (2009) Pollination and reproduction of a self-incompatible forest herb in hedgerow corridors and forest patches. *Oecologia*, **160**, 721-733.

Schröter, D., Cramer, W., Leemans, R., Prentice, I. C., Araújo, M. B., Arnell, N. W., Bondeau, A., Bugmann, H., Carter, T. R., Gracia, C. A., De La Vega-Leinert, A. C., Erhard, M., Ewert, F., Glendining, M., House, J. I., Kankaanpää, S., Klein, R. J. T., Lavorel, S., Lindner, M., Metzger, M. J., Meyer, J., Mitchell, T. D., Reginster, I., Rounsevell, M., Sabaté, S., Sitch, S., Smith, B., Smith, J., Smith, P., Sykes, M. T., Thonicke, K., Thuiller, W., Tuck, G., Zaehle, S. & Zierl, B. (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science*, **310**, 1333-1337.

Schupp, E. W. (1988) Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos*, **51**, 71-78.

Schupp, E. W., Jordano, P. & Gómez, J. M. (2010) Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, **188**, 333-353.

Shiels, A. B. & Walker, L. R. (2003) Bird perches increase forest seeds on Puerto Rican landslides. *Restoration Ecology*, **11**, 457-465.

Silva, F. J. A., Barradas, M. C. D. & Zunzunegui, M. (1996) Growth in *Halimium halimifolium* under simulated and natural browsing in the Donana National Park (SW Spain). *Journal of Vegetation Science*, **7**, 609-614.

Söber, V., Moora, M. & Teder, T. (2010) Florivores decrease pollinator visitation in a self-incompatible plant. *Basic and Applied Ecology*, **11**, 669-675.

Spiegel, O. & Nathan, R. (2010) Incorporating density dependence into the directed-dispersal hypothesis. *Ecology*, **91**, 1538-1548.

Standish, R. J., Cramer, V. A. & Hobbs, R. J. (2008) Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. *Journal of Applied Ecology*, **45**, 1576-1583.

Stocker, G. C. & Irvine, A. K. (1983) Seed Dispersal by Cassowaries (*Casuarius casuarius*) in North Queensland's Rainforests. *Biotropica*, **15**, 170-176.

Stoner, K. E., Riba-Hernández, P., Vulinec, K. & Lambert, J. E. (2007) The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. *Biotropica*, **39**, 316-327.

Strauss, S. Y., Conner, J. K. & Rush, S. L. (1996) Foliar herbivory affects floral characters and plant attractiveness to pollinators: Implications for male and female plant fitness. *American Naturalist*, **147**, 1098-1107.

Suárez-Esteban, A., Delibes, M. & Fedriani, J. M. (2013a) Barriers or corridors? The overlooked role of unpaved roads in endozoochorous seed dispersal. *Journal of Applied Ecology*, **50**, 767-774.

Suárez-Esteban, A., Delibes, M. & Fedriani, J. M. (2013b) Unpaved road verges as hotspots of fleshy-fruited shrub recruitment and establishment. *Biological Conservation*, **167**, 50-56.

Suárez-Esteban, A., Fahrig, L., Delibes, M. & Fedriani, J. M. (Submitted) Do human-made linear gaps assist plant expansion? Current evidence and future steps.

Taylor, B. D. & Goldingay, R. L. (2004) Wildlife road-kills on three major roads in north-eastern New South Wales. *Wildlife Research*, **31**, 83-91.

Tewksbury, J. J., Levey, D. J., Haddad, N. M., Sargent, S., Orrock, J. L., Weldon, A., Danielson, B. J., Brinkerhoff, J., Damschen, E. I. & Townsend, P. (2002) Corridors

affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 12923-12926.

Therneau, T. (2013) A package for survival analysis in S. R package version 2.37-4.

Therneau, T. & Grambsch, P. M. (2000) *Modeling survival data: Extending the Cox model*. Springer, New York.

Thompson, J. N. (2005) *The geographic mosaic of coevolution*. The University of Chicago press, London.

Tikka, P. M., Högmander, H. & Koski, P. S. (2001) Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology*, **16**, 659-666.

Tomimatsu, H., Sasaki, T., Kurokawa, H., Bridle, J. R., Fontaine, C., Kitano, J., Stouffer, D. B., Vellend, M., Bezemer, T. M., Fukami, T., Hadly, E. A., van der Heijden, M. G. A., Kawata, M., Kéfi, S., Kraft, N. J. B., McCann, K. S., Mumby, P. J., Nakashizuka, T., Petchey, O. L., Romanuk, T. N., Suding, K. N., Takimoto, G., Urabe, J. & Yachi, S. (2013) Sustaining ecosystem functions in a changing world: a call for an integrated approach. *Journal of Applied Ecology*, *In press*.

Tormo, J., Bochet, E. & García-Fayos, P. (2006) Is seed availability enough to ensure colonization success? An experimental study in road embankments. *Ecological Engineering*, **26**, 224-230.

Townsend, P. A. & Levey, D. J. (2005) An experimental test of whether habitat corridors affect pollen transfer. *Ecology*, **86**, 466-475.

Traba, J., Arrieta, S., Herranz, J. & Clamagirand, M. C. (2006) Red fox (*Vulpes vulpes* L.) favour seed dispersal, germination and seedling survival of Mediterranean Hackberry (*Celtis australis* L.). *Acta Oecologica*, **30**, 39-45.

Traveset, A. (1998) Effect of seed passage through vertebrate frugivores' guts on germination: A review. *Perspectives in Plant Ecology, Evolution and Systematics*, **1**, 151-190.

Traveset, A., Gulias, J., Riera, N. & Mus, M. (2003) Transition Probabilities from Pollination to Establishment in a Rare Dioecious Shrub Species (*Rhamnus ludovici-salvatoris*) in Two Habitats. *Journal of Ecology*, **91**, 427-437.

Traveset, A. & Richardson, D. M. (2006) Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, **21**, 208-216.

Trombulak, S. C. & Frissell, C. A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18-30.

Tsuji, Y., Tatewaki, T. & Kanda, E. (2011) Endozoochorous seed dispersal by sympatric mustelids, *Martes melampus* and *Mustela itatsi*, in western Tokyo, central Japan. *Mammalian Biology*, **76**, 628-633.

Tylianakis, J. M., Didham, R. K., Bascompte, J. & Wardle, D. A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351-1363.

Tyser, R. W., Asebrook, J. M., Potter, R. W. & Kurth, L. L. (1998) Roadside revegetation in Glacier National Park, USA: effects of herbicide and seeding treatments. *Restoration Ecology*, **6**, 197-206.

Tyser, R. W. & Worley, C. A. (1992) Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana, (USA). *Conservation Biology*, **6**, 253-262.

Vaaland Burkey, T. (1993) Edge effects in seed and egg predation at two neotropical rainforest sites. *Biological Conservation*, **66**, 139-143.

Van Rossum, F. & Triest, L. (2012) Stepping-stone populations in linear landscape elements increase pollen dispersal between urban forest fragments. *Plant Ecology and Evolution*, **145**, 332-340.

Vander Wall, S. B., Kuhn, K. M. & Beck, M. J. (2005) Seed removal, seed predation, and secondary dispersal. *Ecology*, **86**, 801-806.

Vázquez, D. P. & Simberloff, D. (2004) Indirect effects of an introduced ungulate on pollination and plant reproduction. *Ecological Monographs*, **74**, 281-308.

Veldman, J. W. & Putz, F. E. (2010) Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. *Biotropica*, **42**, 697-703.

Verdú, M. & Traveset, A. (2005) Early emergence enhances plant fitness: A phylogenetically controlled meta-analysis. *Ecology*, **86**, 1385-1394.

Verkaar, H. J. (1987) Population dynamics - the influence of herbivory. *New Phytologist*, **106**, 49-60.

Vieira, E. M. & Port, D. (2007) Niche overlap and resource partitioning between two sympatric fox species in southern Brazil. *Journal of Zoology*, **272**, 57-63.

Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) Human Domination of Earth's Ecosystems. *Science*, **277**, 494-499.

Walker, D. A. & Everett, K. R. (1987) Road dust and its environmental impact on Alaskan taiga and tundra. *Arctic & Alpine Research*, **19**, 479-489.

Wandrag, E. M., Sheppard, A., Duncan, R. P. & Hulme, P. E. (2013) Mutualism vs. antagonism in introduced and native ranges: Can seed dispersal and predation determine *Acacia* invasion success? *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 171-179.

Wang, B. C. & Smith, T. B. (2002) Closing the seed dispersal loop. *Trends in Ecology and Evolution*, **17**, 379-385.

Watkins, R. Z., Chen, J., Pickens, J. & Brosnoks, K. D. (2003) Effects of forest roads on understory plants in a managed hardwood landscape. *Conservation Biology*, **17**, 411-419.

Webb, S. L. & Willson, M. F. (1985) Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. *Oecologia*, **67**, 150-153.

Wehling, S. & Diekmann, M. (2009) Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biological Conservation*, **142**, 2522-2530.

Wenny, D. G. (2001) Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research*, **3**, 51-74.

- Western, D. & Pearl, M. C. (1989) *Conservation for the Twenty-first Century*. Oxford University Press.
- Wieland, L. M., Mesquita, R. C. G., Bobrowiec, P. E. D., Bentos, T. V. & Williamson, G. B. (2011) Seed rain and advance regeneration in secondary succession in the Brazilian Amazon. *Tropical Conservation Science*, **4**, 300-316.
- Wilcock, C. & Neiland, R. (2002) Pollination failure in plants: Why it happens and when it matters. *Trends in Plant Science*, **7**, 270-277.
- Williams, P., Hannah, L. E. E., Andelman, S., Midgley, G. U. Y., AraÚJo, M., Hughes, G., Manne, L., Martinez-Meyer, E. & Pearson, R. (2005) Planning for Climate Change: Identifying Minimum-Dispersal Corridors for the Cape Proteaceae. *Conservation Biology*, **19**, 1063-1074.
- Willis, K. J., Araújo, M. B., Bennett, K. D., Figueroa-Rangel, B., Froyd, C. A. & Myers, N. (2007) How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 175-186.
- Wilson, P. & Thomson, J. D. (1991) Heterogeneity Among Floral Visitors Leads to Discordance Between Removal and Deposition of Pollen. *Ecology*, **72**, 1503-1507.
- Wratten, S. D., Gillespie, M., Decourtye, A., Mader, E. & Desneux, N. (2012) Pollinator habitat enhancement: Benefits to other ecosystem services. *Agriculture, Ecosystems & Environment*, **159**, 112-122.

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Algunos animales como los herbívoros o los dispersores de semillas tienen una gran capacidad para modificar la configuración de las comunidades vegetales, y por ello se les conoce como *ingenieros del paisaje*.

Las interacciones entre animales y plantas pueden verse alteradas por la presencia de estructuras lineales humanas, tales como caminos y cortafuegos.

Esta tesis pretende aportar información sobre esta ignorada triple interacción entre estructuras lineales, plantas y animales desde un punto de vista aplicado a la gestión de los espacios naturales.

