

## **Unpaved roads disrupt the effect of herbivores and pollinators on the reproduction of a dominant shrub.**

Alberto Suárez-Esteban <sup>\*a,b</sup>, Miguel Delibes<sup>b</sup> and José M. Fedriani<sup>b,c</sup>

<sup>a</sup>Department of Renewable Resources. University of Alberta. 116 St. and 85 Ave.,  
Edmonton, AB, T6G 2R3 Canada;

<sup>b</sup>Departamento de Biología de la Conservación. Estación Biológica de Doñana (CSIC).  
Américo Vespucio s/n, 41092, Sevilla, Spain.

<sup>c</sup>Department of Ecological Modelling. Helmholtz Centre for Environmental Research  
GmbH-UFZ. Permoserstrasse 15, 04318 Leipzig, Germany.

\*Correspondin author. Tel: 1-780-492-0552; fax: 1- 780-492-4323; E-mail address:

[suarez@ualberta.ca](mailto:suarez@ualberta.ca)

## 1 **Abstract**

2 Anthropogenic linear developments, such as trails and firebreaks, also called soft linear  
3 developments (SLD), can influence animal behavior, altering the ecological interactions in  
4 which animals are involved. For example, SLD can affect the behavior of pollinators and  
5 herbivores, but little is known about the combined effect of these three elements on plant  
6 reproduction.

7 We evaluated the combined effect of SLD, insect pollinators and herbivores (ungulates)  
8 on three reproductive output variables (fruit set, seed set, and seed mass) of a Mediterranean  
9 shrub (*Halimium halimifolium*). We considered two different habitats (SLD verges vs. adjacent  
10 scrublands), two scenarios of herbivory (with and without ungulates), and three scenarios of  
11 pollinator activity (without pollinators, with manual pollination and with natural pollination).

12 SLD had contrasting effects on *H. halimifolium* reproduction. In the absence of  
13 herbivores, overall fruit set was lower in the verges of SLD than in adjacent scrublands,  
14 probably due to lower flower pollination rates. Where herbivores were present, overall fruit set  
15 was similar between habitats, because ungulate browsing was lower in SLD verges than in  
16 adjacent scrublands. The quantity and weight of seeds per fruit was similar in both habitats,  
17 probably because all fertilized flowers received similar amounts of pollen.

18 SLD can alter the interaction among pollinators, herbivores and plants, leading to  
19 changes in the reproductive performance of the latter. These changes can have strong negative  
20 impacts on endangered plants that rely on fruit and seed production to persist. However, SLD  
21 verges could be safe places for plants particularly sensitive to herbivory by ungulates.

## 22 **Zusammenfassung**

23 Anthropogene lineare Landschaftselemente wie Wanderwege oder Feuerschneisen  
24 können das Verhalten von Tieren beeinflussen und damit die ökologischen Interaktionen, an  
25 denen die Arten beteiligt sind, verändern. Diese grünen linearen Strukturen (GLS) können  
26 beispielsweise das Verhalten von Bestäubern und Herbivoren beeinflussen, aber wenig ist über  
27 den gemeinsamen Effekt dieser drei Elemente auf die Reproduktion von Pflanzen bekannt.

28 Wir untersuchten den gemeinsamen Effekt von GLS, bestäubenden Insekten und  
29 Herbivoren (freilaufende Nutz- und Wildtiere) auf drei die reproduktive Leistung  
30 beschreibenden Variablen (Fruchtansatz, Samenansatz und Samengewicht) bei einem  
31 mediterranen Strauch (*Halimium halimifolium*). Wir untersuchten zwei Habitattypen (Ränder  
32 von GLS und benachbartes Buschland), zwei Herbivorievarianten (mit und ohne Huftiere) und  
33 drei Bestäubungsszenarien (ohne Bestäuber, manuelle Bestäubung und natürliche Bestäubung).

34 GLS hatten unterschiedliche Auswirkungen auf die Reproduktion von *H. halimifolium*.  
35 Bei Herbivorenausschluss war der Gesamtfruchtansatz an den Rändern der GLS geringer als im  
36 Buschland, möglicherweise aufgrund von geringerer Bestäubung. Bei Anwesenheit von  
37 Herbivoren war der Gesamtfruchtansatz in beiden Habitattypen ungefähr gleich, weil die  
38 Huftiere an den GLS-Rändern weniger weideten als im Buschland. Die Menge und das Gewicht  
39 der Samen pro Frucht waren in beiden Habitattypen ähnlich, vermutlich weil alle befruchteten  
40 Blüten ähnliche Mengen von Pollen erhielten.

41 GLS können die Interaktionen zwischen Bestäubern, Herbivoren und Pflanzen  
42 verändern, was zu veränderter reproduktiver Leistung bei den Pflanzen führt. Diese  
43 Veränderungen können stark negative Auswirkungen auf gefährdete Pflanzenarten haben, die  
44 auf Frucht- und Samenproduktion angewiesen sind, um zu persistieren. Indessen können GLS-  
45 Ränder sichere Orte für Pflanzen sein, die gegen Pflanzenfraß durch Huftiere empfindlich sind.

46 **Keywords:** ecosystem services, fruit set, *Halimium halimifolium*, herbivory,  
47 pollination, trails.

## 48 **Introduction**

49           Human-induced changes in plant and/or pollinator populations often lead to the  
50 disruption of pollination mutualisms and consequently to pollen limitation (Ashman,  
51 Knight, Steets, Amarasekare, Burd et al. 2004; Gómez, Abdelaziz, Lorite, Muñoz-  
52 Pajares & Perfectti 2010; González-Varo, Arroyo & Aparicio 2009). Pollen limitation  
53 leads to decreased fruit and seed production in countless crops and wild plants, which  
54 negatively affects agricultural yields (Garibaldi, Aizen, Klein, Cunningham & Harder  
55 2011) as well as the colonization ability and the persistence of wild plants (Biesmeijer,  
56 Roberts, Reemer, Ohlemüller, Edwards et al. 2006; Bond 1994; Burd 1994).  
57 Understanding how and to what extent human activities affect plant-pollinator  
58 interactions and, ultimately, plant reproductive performance, is therefore a priority for  
59 conserving the supply of goods and services that plants provide (Biesmeijer et al. 2006;  
60 Bond 1994; Isbell, Calcagno, Hector, Connolly, Harpole et al. 2011).

61           At a global scale, human activities have led to the so-called “pollination crisis”  
62 (Kearns, Inouye & Waser 1998). More specifically, pollinators are declining due to  
63 habitat loss and fragmentation (i.e. reduced availability of feeding and nesting  
64 resources), agriculture intensification (which usually involves pesticide and herbicide  
65 application), and climate change, in addition to the spread of pests, pathogens and alien  
66 species (Potts, Biesmeijer, Kremen, Neumann, Schweiger et al. 2010). At smaller  
67 scales, pollinator abundance and behavior can be negatively influenced by local  
68 anthropogenic habitat transformation (Elliott, Lindenmayer, Cunningham & Young  
69 2012; Kennedy, Lonsdorf, Neel, Williams, Ricketts et al. 2013; Winfree, Aguilar,  
70 Vázquez, LeBuhn & Aizen 2009).

71           One of the most pervasive human-mediated habitat transformations is the  
72 construction of paved roads (e.g. highways), as well as similar structures that involve

73 minor habitat transformation such as trails and firebreaks (also known as “Soft Linear  
74 Developments”, SLD; Suárez-Esteban, Delibes & Fedriani 2013a). Paved roads can  
75 have contrasting effects on plant pollination. For example, they can reduce the  
76 frequency of pollinating birds visiting flowers (Geerts & Pauw 2011; but see Francis,  
77 Kleist, Ortega & Cruz 2012; Magrach, Guitián & Larrinaga 2011). On the other hand,  
78 roadsides often host flourishing grasslands that provide suitable habitats for diverse and  
79 abundant populations of pollinators (Hopwood 2008; Noordijk, Delille, Schaffers &  
80 Sýkora 2009).

81         SLD are as pervasive as paved roads (e.g. Pasher, Seed & Duffe 2013).  
82 However, very few studies have assessed their effects on plant reproduction. For  
83 example, SLD can result in increased habitat fragmentation and edge effects, such as  
84 dust deposition on flowers, extreme climate conditions and pollinator mortality  
85 (Cunningham 2000; Huang, Sun, Yu, Luo, Hutchings et al. 2009; Jules & Rathcke  
86 1999; Kolb 2008; but see Magrach, Santamaría & Larrinaga 2013), that can reduce the  
87 abundance of plants and pollinators, and also affect the behavior of the latter. On the  
88 other hand, shrub hedgerows may exist in the verges of SLD, either because they were  
89 planted (Karim & Mallik 2008) or because they established naturally (Suárez-Esteban,  
90 Delibes & Fedriani 2013b). In such cases, SLD might assist pollination, as hedgerows  
91 are known to provide food resources and shelter for pollinators (Morandin & Kremen  
92 2013; Schmucki & De Blois 2009). Interestingly, SLD can also modify the behavior of  
93 large herbivores such as ungulates. Wild ungulates usually avoid SLD and other similar  
94 habitat edges (Cadenasso & Pickett 2000; Suárez-Esteban et al. 2013a). Therefore, SLD  
95 could buffer herbivore damage on plant reproduction (e.g. predation of leaves, flowers,  
96 unripe fruits or whole plants), limiting the loss of plant attractiveness for pollinators  
97 (Gómez 2003).

98           Although both pollinators and ungulates can be affected by SLD (Huang et al.  
99   2009; James & Stuart-Smith 2000), and all these three elements pervasively co-occur in  
100 the wild, no prior study has assessed their combined effect on plant reproduction. A  
101 better understanding on the potential of SLD to disrupt key plant-animal interactions  
102 (e.g. pollination, herbivory) will allow us to better predict the effects of SLD and  
103 increase our efficiency when planning SLD networks. We specifically chose to evaluate  
104 the combined effect of SLD, ungulate herbivores (e.g. deer, cattle) and pollinators on  
105 the reproductive output of the common shrub *Halimium halimifolium* L. (Cistaceae) in  
106 several patches of Mediterranean scrubland. We compare three measures of  
107 reproductive output (fruit set, seed set, and seed mass) in naturally-pollinated flowers  
108 between two habitats (SLD verges and scrubland) under two scenarios of herbivory  
109 (with and without ungulates). In order to link reproductive output and pollination  
110 (Cunningham 2000), we compared flowers exposed to different pollination scenarios  
111 (without pollinators, with manual pollination and with natural pollination).

112           With this experimental design, we aimed to answer the following questions: does  
113 herbivory by ungulates limit the reproductive output of *H. halimifolium*? Are the effects  
114 of ungulates conditioned by the presence of SLD? Is the reproductive output of *H.*  
115 *halimifolium* dependent upon pollination? Is this species' reproductive output affected  
116 by SLD? Based on the literature, the net effect of SLD on *H. halimifolium* predispersal  
117 reproductive performance is difficult to anticipate.

118

## 119 **Materials and methods**

### 120 **Study system**

121           This study was carried out during April-August of 2010 and 2011 in Doñana  
122 National Park (SW Spain; 37° 9' N, 6° 26' W; 510 km<sup>2</sup>; elevation 0-80 m). The climate

123 is Mediterranean sub-humid, characterized by dry, warm summers (June–September)  
124 and mild, wet winters (December–March). Annual rainfall is irregular, averaging 577  
125 mm  $\pm$  39 SE, with 88.4% of rain falling between October and April (data from Natural  
126 Processes Monitoring Group, Doñana Biological Station, [http://www-](http://www-rbd.ebd.csic.es/Seguimiento/seguimiento.htm)  
127 [rbd.ebd.csic.es/Seguimiento/seguimiento.htm](http://www-rbd.ebd.csic.es/Seguimiento/seguimiento.htm)).

128 The Doñana area contains several habitats (e.g. marshland, scrubland, dunes)  
129 and a vast SLD system (over 2,000 km) composed mainly of dirt trails (62.5%) and  
130 firebreaks (35.5%). The scrubland patches harbor a diverse community of native  
131 Mediterranean shrubs. This community of shrubs includes our model species, *Halimium*  
132 *halimifolium* L., an abundant Cistaceae shrub that grows in a wide range of  
133 environmental conditions in the Western Mediterranean. At Doñana, it dominates  
134 extensive scrubland patches from the edges of marshlands to mobile dunes (Díaz  
135 Barradas, Zunzunegui & García Novo 1999). Throughout the study area, it reaches  
136 similarly high densities in both SLD verges ( $10.14 \pm 1.33$  mean number of  
137 individuals/m<sup>2</sup>  $\pm$  SE) and in adjacent scrublands ( $9.79 \pm 1.13$ ; Suárez-Esteban et al.  
138 2013b).

139 *H. halimifolium* has large (up to 62 mm in diameter) hermaphrodite yellow  
140 flowers that bloom mainly in late-spring and early-summer (May-June; Herrera 1988).  
141 Flowers emerge as apical inflorescences and are pollinated mainly by pollen-eating  
142 beetles, such as *Heliotaurus ruficollis* Fabricius (Tenebrionidae), and less frequently by  
143 some bees (Halictidae; (Herrera 1986). Both beetles and bees are usually observed  
144 feeding on *H. halimifolium* flowers both near and far from SLD in our study area  
145 (*Authors personal observation*). Fertilized flowers lead to small dry fruits, containing 25  
146 seeds on average (Herrera 1987a). After the fruiting period, fruits dry up and usually  
147 drop their seeds on the ground. Although no evident specialized dispersal mechanism is

148 observed, this species seems to have a great colonization ability, as documented in other  
149 Cistaceae species (Bastida & Talavera 2002).

150         Within our study area, browsing ungulates such as red deer (*Cervus elaphus* L.),  
151 fallow deer (*Dama dama* L.), and livestock (e.g. cattle, horses) reach high densities,  
152 because of the absence of both hunting pressure and natural predators. These ungulates  
153 can severely damage *H. halimifolium* (Silva, Barradas & Zunzunegui 1996).

#### 154         **Experimental design**

155         Because reproductive output can vary in time and space, we surveyed three  
156 different study sites separated from each other by 2.5 – 14 km that are called “Reserva”,  
157 “Rocina” and “Matasgordas” (described in detail in Suárez-Esteban et al. 2013a), during  
158 two consecutive years (2010 and 2011). At each site, we set up two independent  
159 experimental blocks separated by a minimum of 1 km (Fig. 1). Within each  
160 experimental block we set up four plots (~ 36 m<sup>2</sup> each). Two of the plots were located  
161 along SLD verges and the other two were located in the scrubland, 60 meters away from  
162 SLD (since most edge effects cease to be significant within 50 m; Murcia 1995; Fig. 1).  
163 Of the two plots established in each habitat, one was fenced to exclude large herbivores  
164 (i.e. ungulates such as deer and cattle), while another was left completely open (Fig. 1).  
165 Open and fenced plots within each habitat were adjacent, ensuring that they were  
166 subjected to the same environmental conditions. In total, we established 24 plots (12 in  
167 SLD verges, 12 in the scrubland), all of them containing at least ten reproductive *H.*  
168 *halimifolium* individuals.

169         To evaluate whether herbivory by ungulates affected the reproductive output of  
170 *H. halimifolium* both near and far from SLD verges, we compared fruit set, seed set, and  
171 seed mass between open and fenced plots in SLD verges and in the scrubland. To assess  
172 whether SLD alone affected the reproductive output of *H. halimifolium*, we also



173 compared the same three reproductive measures between fenced plots (i.e. controlling  
174 for the effect of herbivory) in SLD verges and in the scrubland.

175         Linking habitat differences in reproductive output with differential pollination  
176 requires confirmation that pollen reception limits the reproductive output (Cunningham  
177 2000). To do this, in each plot we simulated three scenarios of pollinator activity:

178         a)       Without pollinators:

179               After counting the flower-buds, we tagged and bagged a number of  
180 inflorescences (five in 2010 and two in 2011) of each of five randomly selected *H.*  
181 *halimifolium* plants within each plot to preclude pollinator access (Parker 1997).  
182 Overall, we tagged and bagged 779 inflorescences with 53152 flowers. After the  
183 flowering period (July-August), we counted the resulting fruits and randomly sampled  
184 three of them from each bagged inflorescence. All collected fruits were stored in paper  
185 bags, then dissected in the lab to count the number of seeds produced per fruit and to  
186 measure their mass (using a precision scale).

187         b)       Manually supplemented cross-pollination:

188               Using the same five *H. halimifolium* plants mentioned above, we randomly  
189 selected five open inflorescences that were different from those that had been bagged to  
190 exclude pollinators. For each of these open inflorescences, we added supplemental  
191 pollen to one randomly selected flower per inflorescence (hereafter “supplemented  
192 flower”), by rubbing its stigma with collected anthers from distant (20-30 m)  
193 conspecifics until it was completely covered with pollen.

194         Pollen addition may overestimate the magnitude of pollen limitation if plants  
195 reallocate resources from non-manipulated flowers to supplemented flowers (Haig &  
196 Westoby 1988; Knight, Steets & Ashman 2006). To assess whether such resource  
197 reallocation occurs (thereby potentially affecting our results), for each supplemented

198 flower we labeled three control flowers: one within the same inflorescence as the  
199 supplemented flower (hereafter “intra-inflorescence control”), one within another  
200 inflorescence on the same plant (hereafter “inter-inflorescence control”), and the last  
201 one on another adjacent individual, outside the plot (hereafter “external control”). All  
202 control flowers were exposed to natural pollination (no pollen was added). For this, we  
203 tagged and monitored 1034 flowers for each of the four treatments (i.e. supplemented  
204 cross-pollination and three controls). After the flowering period, we counted all  
205 resulting fruits set by supplemented and control flowers, harvesting and processing all  
206 of them as above.

207 c) Natural pollination

208 To estimate *H. halimifolium* natural fruit set, we tagged five inflorescences  
209 (when possible) of each of five additional *H. halimifolium* plants (different from the five  
210 plants used to simulate the absence of pollinators and the effect of supplemented cross-  
211 pollination) within each plot and counted their flowers, which were exposed to natural  
212 pollination (hereafter “naturally-pollinated flowers”). Overall, we tagged 1149  
213 inflorescences with 80038 flowers. As above, we counted the number of fruits set by all  
214 tagged inflorescences and randomly sampled three fruits from each. In the 2011  
215 surveys, we selected the same individuals used in 2010 when possible.

## 216 **Statistical analyses**

217 Fruit set of bagged flowers (i.e. those that were not exposed to pollinators) was  
218 ~2% in both habitats, confirming that *H. halimifolium* reproductive output relies on  
219 animal pollination. Because of its small sample size, we excluded this treatment from  
220 the analyses.

221 Using data on the supplemented flowers, we evaluated whether habitat,  
222 herbivory or their interaction altered the importance of pollination for *H. halimifolium*

223 reproductive output. To address the effect of habitat, we compared plots in SLD verges  
224 vs. plots in the scrubland. To address the effect of herbivory by ungulates, we compared  
225 open vs. fenced plots. Finally, to quantify a potential interaction between habitat and  
226 herbivory, we compared SLD verges with the scrubland in terms of any differences  
227 between open and fenced plots.

228         We fitted three generalized linear mixed models (GLMMs) with three different  
229 response variables: (1) the proportion of flowers that set fruits, i.e. fruit set, per plant  
230 (using a binomial error-distribution and logit-link function), (2) the number of seeds  
231 produced per fruit, i.e. seed set (using a negative binomial distribution and log-link  
232 function), and (3) the overall seed mass per fruit (using a Gaussian distribution and  
233 identity-link function). In these models, we also included data on control flowers to  
234 assess the potential occurrence of resource reallocation.

235         Using data on natural pollination, we evaluated the effect of habitat, herbivory  
236 and their interaction on the reproductive output of naturally-pollinated flowers. To do  
237 so, we fitted three additional GLMMs with the same response variables as above (i.e.  
238 fruit set per plant, seed set per fruit and seed mass per fruit).

239         All GLMMs were implemented using the SAS 9.2 GLIMMIX procedure (Littell,  
240 Milliken, Stroup, Wolfinger & Schabenberger 2006) and adjusted using maximum  
241 likelihood (Bolker, Brooks, Clark, Geange, Poulsen et al. 2009). In all models we  
242 considered the habitat (SLD verges vs. scrubland), herbivory by ungulates (open vs.  
243 fenced plots), and their interaction as fixed factors. When analyzing whether pollen  
244 reception and resource reallocation varied among factor combinations, we also included  
245 the pollination treatment (i.e. supplemented vs. control flowers; referred to as  
246 “Supplement” in Table 1) and its interactions with habitat and herbivory as fixed  
247 factors. When any interaction was significant, we performed tests for the effect of a

248 factor at the different levels of the other factor (“tests of simple main effects”) using the  
249 SLICE option in the LSMEANS statement (Littell et al. 2006).

250 The use of GLMMs allowed us to model non-normal variables as well as to  
251 introduce random factors in order to account for temporal and spatial heterogeneity, in  
252 addition to potential individual effects that might influence our results. Specifically, we  
253 included the year, the study site, the plot (nested within site), and the plant (nested  
254 within plot) as random factors. For every model concerning seed set and seed mass, we  
255 removed from the dataset all fruits that presented some fault (e.g. with depredated,  
256 unripe or rotten seeds), which happened rarely.

## 257 **Results**

### 258 **Supplemented cross-pollination**

259 Pollen supplementation increased fruit set by 114.6%, seed set by 35.0% and  
260 seed mass by 29.0%, as compared with control (naturally-pollinated) flowers (see  
261 “Supplement” in Table 1; Fig. 3). This suggests that the reproductive output of *H.*  
262 *halimifolium* (all three variables) is generally limited under natural conditions. As found  
263 for naturally-pollinated flowers, fruit set of both supplemented and control flowers was  
264 slightly higher in fenced plots than in open plots in the scrubland, although these  
265 differences were only marginally significant (Table 1).

266 With respect to the possibility of resource reallocation, control flowers showed  
267 similar ( $P > 0.05$ ) fruit set (Fig. 2), seed set (Fig. 3) and seed mass. This indicates the  
268 lack of resource reallocation in *H. halimifolium* at any scale, reinforcing the strength of  
269 our inference on the link between pollen reception and reproductive output in our study  
270 system.

271 The effect of pollen supplementation on fruit set was consistent in both habitats,  
272 and in both fenced and open plots (i.e. habitat, herbivory and their interactions with the

273 pollination treatment were not statistically different between either habitats or plots;  
274 Table 1). However, when analyzing seed set and seed mass, we found marginally  
275 significant differences between habitats (see “Habitat” in Table 1). These marginal  
276 differences were the result of a higher seed set and seed mass of pollen-supplemented  
277 flowers in the scrubland than in SLD verges (see Fig. 3). We did not find any other  
278 significant effect of habitat or herbivory on seed set or seed mass (Table 1).

### 279 **Natural pollination**

280 Naturally-pollinated flowers set 27689 fruits (overall fruit set 34.6%; n =  
281 80038). Habitat and herbivory did not significantly affect fruit set (Table 1). However,  
282 the interaction between habitat and herbivory was significant (Table 1), suggesting that  
283 the effect of ungulates differed between habitats. Indeed, the exclusion of ungulates had  
284 a significant effect in the scrubland, but not in SLD verges. In SLD verges we found no  
285 differences in the fruit set between open and fenced plots. In the scrubland, however,  
286 fruit set was 33.0% higher in fenced than in open plots (Fig. 4). Considering exclusively  
287 the differences between fenced plots in both habitats (i.e. controlling for the effect of  
288 herbivory), the fruit set per plant was a 33.1% higher in the scrubland than in SLD  
289 verges (test of slices:  $F_{1,113} = 6.90$  ;  $P < 0.01$ ; Fig. 4). Thus, SLD negatively affected *H.*  
290 *halimifolium* fruit set in absence of ungulates.

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

298           The overall seed mass per fruit ranged between 0.1 and 31.4 mg. As was true for  
299 the average seed set, seed mass was similar between SLD verges ( $8.97 \pm 0.59$  mg; mean  
300  $\pm$  SE) and adjacent scrublands ( $9.80 \pm 0.59$  mg). We did not detect any significant effect  
301 of habitat, herbivory, or their interaction on seed mass (Table 1). These results for both  
302 seed set and seed mass suggest that SLD did not affect seed production.

## 303 **Discussion**

### 304 **Effects of SLD on pollination**

305           As found by Herrera (1987a), bagged *H. halimifolium* barely produced fruits in  
306 either habitat. Furthermore, Herrera (1987b) found that self-pollinated flowers of a  
307 closely related species (*H. calycinum*) did not set any fruit. This evidence suggests that  
308 *H. halimifolium* is highly dependent on cross-pollination mediated by insects regardless  
309 of the presence of SLD. *H. halimifolium* did not reallocate resources in response to  
310 pollen supplementation. This confirms that the more pollen a plant receives, the more  
311 fruits and seeds it produces, i.e. *H. halimifolium* is pollen-limited, as found for other  
312 species (Burd 1994; Parker 1997). This pollen-reception dependence was consistent in  
313 both habitats.

314           We found that, in the absence of herbivores, plants in SLD verges produced  
315 relatively fewer fruits despite having a similar seed yield (i.e. seed number and mass)  
316 per fruit than plants in the scrubland. Given that pollen-reception is positively correlated  
317 with both fruit and seed production, our results suggest that the proportion of pollinated  
318 flowers was lower in SLD verges than in the scrubland (which resulted in a lower fruit  
319 set), but all pollinated flowers received similar amounts of pollen, regardless of the  
320 habitat (which explains the consistency of seed set and seed mass between habitats).

321           Lower flower pollination rates in SLD verges relative to adjacent scrubland in  
322 the absence of herbivores can be related to the reception of fewer or poorer quality

323 pollen grains (Aizen & Harder 2007). Lower pollen arrival is usually associated with  
324 either lower visitation rates by pollinators (Kolb 2008; Parker 1997) or with lower  
325 pollinator efficiency when removing and transporting pollen, e.g. due to briefer visits  
326 (Aizen et al. 2007; Wilson & Thomson 1991). As our results suggest that all pollinated  
327 flowers received a similar amount of pollen, we assume that pollinator efficiency did  
328 not vary between habitats. Thus, we propose that this pattern is largely explained by  
329 lower visitation rates.

330 Flower visitation rates by pollinators can be affected by abiotic conditions (Jules  
331 et al. 1999). As a matter of fact, we observed that *H. halimifolium* flowers tended to  
332 close with windy weather. Wind turbulence and exposure is probably much higher at  
333 SLD verges, given the lack of surrounding, protective vegetation. This probably  
334 decreased the period of time during which *H. halimifolium* flowers along SLD were  
335 available relative to those within the scrubland. Reduced availability of open flowers  
336 could have reduced the likelihood of pollen reception and fecundation in SLD due to  
337 both a reduced time of exposure for each flower, as well as an overall reduction in  
338 attractiveness for pollinators. Furthermore, wind intensity and turbulence can hinder  
339 pollinator activity (Sayre, Kelty, Simmons, Clayton, Kassam et al. 2013), which could  
340 act in synergy with the reduced availability of flowers.

341 Considering that in the absence of herbivores, naturally-pollinated flowers set  
342 more fruits in the scrubland than along SLD verges, the overall production of seeds in  
343 the scrubland was higher than in SLD verges. Although the number of seeds per fruit set  
344 by naturally-pollinated flowers was similar in both habitats, we found that pollen-  
345 supplemented flowers set a significantly higher number of seeds per fruit in the  
346 scrubland than along SLD verges (see “Suppl” in Fig. 3). This suggests the existence of

347 other effects of SLD (e.g. dust deposition and interference with pollen, Lewis, Schupp  
348 & Monaco 2012) that would affect negatively the seed set when pollen is unlimited.

### 349 **Combined effect of SLD and ungulates on plant reproduction**

350 Large ungulates such as red deer and caribou (*Rangifer tarandus*) usually avoid  
351 linear structures such as SLD (James et al. 2000; Suárez-Esteban et al. 2013a).  
352 Accordingly, we only found a negative effect of ungulates on *H. halimifolium* fruit set  
353 in the scrubland (Fig. 4). Thus, SLD had a partly beneficial effect on *H. halimifolium*  
354 reproductive output. We did not detect any significant effect of herbivory by ungulates  
355 on the number of seeds produced per fruit. This suggests that ungulates mainly disrupt  
356 fruit set, probably by removing flowers and entire inflorescences (Vázquez &  
357 Simberloff 2004). By reducing the fruit set in the scrubland, ungulates diminished in  
358 turn the overall production of seeds in that habitat, but not at SLD verges. However, this  
359 potentially positive effect of SLD was counterbalanced by other negative effects on  
360 pollination (see above). We expect this reduction in herbivory mediated by SLD will be  
361 rather advantageous in other plant ontogenetic stages, such as the seedling and the  
362 sapling stage (Cadenasso et al. 2000).

### 363 **Conclusions and implications**

364 Effective management of plant populations in anthropic ecosystems requires an  
365 understanding of the ecological drivers of plant reproduction and how they interact with  
366 pervasive human features. Our results suggest that SLD can have negative effects on  
367 local pollination and thereby on the reproductive output of *H. halimifolium*, a dominant  
368 Mediterranean shrub. However, limited fruit or seed production do not necessarily mean  
369 a negative effect on plant populations (Herrera, Medrano, Rey, Sánchez-Lafuente,  
370 García et al. 2002). Negative effects of SLD on pollination might be overcome by  
371 positive effects at other stages such as seed dispersal (Suárez-Esteban et al. 2013a),



372 while the resulting net effect will ultimately determine plant fitness (Magrath et al.  
373 2013). Despite the importance of considering all ontogenetic stages as a whole, very  
374 little is known about whether SLD affect seed predation, germination, and seedling  
375 establishment (Ogden, Heynen, Oslender, West, Kassam et al. 2013; but see Suárez-  
376 Esteban 2013). Thus, further research is clearly needed.

377         Given that *H. halimifolium* readily colonizes SLD after one year without  
378 perturbations (*Authors personal observation*), fruit and seed set do not seem to be the  
379 most limiting factors for population size. Rather, the availability of empty sites without  
380 competitors is more likely to influence *H. halimifolium* dynamics. However, the fact  
381 that we detected a negative effect of SLD on the reproductive output of such locally  
382 widespread and abundant species suggests that SLD disturbances could have a deeper  
383 impact on other taxa (Cunningham 2000). For instance, those plants with small  
384 populations, depending upon specialist pollinators sensitive to SLD derived effects (e.g.  
385 wind, dust), and those whose fitness relies mainly on sexual reproduction, will likely be  
386 significantly deterred by SLD. On the other hand, SLD could have a positive effect on  
387 plant populations whose viability is negatively affected by ungulates. Therefore, careful  
388 SLD development in conjunction with further research is desirable to effectively  
389 manage sensitive plant populations.

390         SLD effects are likely heterogeneous among different species (i.e. SLD effects  
391 are context-dependent; Suárez-Esteban et al. 2013b). This highlights the importance of  
392 local scale studies that can be translated into management practices. In order to reduce  
393 the negative effects of SLD on pollination, we propose the conservation of roadside  
394 native vegetation. SLD verges have the potential to host shrubby hedgerows (Suárez-  
395 Esteban et al. 2013b) that can act as wind and dust screens, as well as provide  
396 pollinators with habitat for both foraging or nesting (Morandin et al. 2013; Mwangi,

397 Kasina, Nderitu, Hagen, Gikungu et al. 2012). Natural hedgerows along roadsides can  
398 be achieved by conserving endozoochorous seed dispersal vectors that positively select  
399 SLD verges for defecation (Suárez-Esteban et al. 2013a) and by promoting shrub  
400 establishment along SLD verges (Karim et al. 2008; Suárez-Esteban et al. 2013b).

401 **Acknowledgements**

402           We are grateful to Gemma Calvo, Sarah Ayangma, M. Carmen Ramírez, Sofía  
403 Conradi, and the staff of Doñana's Biological Station and Reserve for their assistance.  
404 Dr. Pedro Jordano, Dr. Daniel García and especially Dr. José M<sup>a</sup> Gómez, helped with  
405 the experimental design and provided useful feedback. Two anonymous reviewers  
406 provided useful comments. We thank Joanna Jack for language review. The research  
407 was financed by the Spanish Ministerio de Medio Ambiente, Rural y Marino  
408 (070/2009), Ministerio de Ciencia e Innovación (CGL2010-21926/BOS) and Ministerio  
409 de Educación (FPU grant to A.S.E.; AP2008-01874).

410

411 **References**

- 412 Aizen, M.A., & Harder, L.D. (2007). Expanding the limits of the pollen-limitation  
413 concept: Effects of pollen quantity and quality. *Ecology*, 88, 271-281.
- 414 Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R.,  
415 Dudash, M.R., Johnston, M.O., Mazer, S.J., Mitchell, R.J., Morgan, M.T., & Wilson,  
416 W.G. (2004). Pollen limitation of plant reproduction: Ecological and evolutionary  
417 causes and consequences. *Ecology*, 85, 2408-2421.
- 418 Bastida, F., & Talavera, S. (2002). Temporal and spatial patterns of seed dispersal in  
419 two *Cistus* species (Cistaceae). *Annals of Botany*, 89, 427-434.
- 420 Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters,  
421 T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., & Kunin, W.E.  
422 (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the  
423 Netherlands. *Science*, 313, 351-354.
- 424 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H.,  
425 & White, J.S.S. (2009). Generalized linear mixed models: a practical guide for ecology  
426 and evolution. *Trends in Ecology and Evolution*, 24, 127-135.
- 427 Bond, W.J. (1994). Do mutualisms matter? Assessing the impact of pollinator and  
428 disperser disruption on plant extinction. *Philosophical Transactions - Royal Society of*  
429 *London, B*, 344, 83-90.
- 430 Burd, M. (1994). Bateman's principle and plant reproduction: the role of pollen  
431 limitation in fruit and seed set. *Botanical Review*, 60, 83-139.
- 432 Cadenasso, M.L., & Pickett, S.T.A. (2000). Linking forest edge structure to edge  
433 function: Mediation of herbivore damage. *Journal of Ecology*, 88, 31-44.
- 434 Cunningham, S.A. (2000). Depressed pollination in habitat fragments causes low fruit  
435 set. *Proceedings of the Royal Society B: Biological Sciences*, 267, 1149-1152.

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

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

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

445 Garibaldi, L.A., Aizen, M.A., Klein, A.M., Cunningham, S.A., & Harder, L.D. (2011).  
446 Global growth and stability of agricultural yield decrease with pollinator dependence.  
447 *Proceedings of the National Academy of Sciences of the United States of America*, 108,  
448 5909-5914.

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

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

455 Gómez, J.M., Abdelaziz, M., Lorite, J., Muñoz-Pajares, A.J., & Perfectti, F. (2010).  
456 Changes in pollinator fauna cause spatial variation in pollen limitation. *Journal of*  
457 *Ecology*, 98, 1243-1252.

458 González-Varo, J.P., Arroyo, J., & Aparicio, A. (2009). Effects of fragmentation on  
459 pollinator assemblage, pollen limitation and seed production of Mediterranean myrtle  
460 (*Myrtus communis*). *Biological Conservation*, 142, 1058-1065.

461 Haig, D., & Westoby, M. (1988). On limits to seed production. *American Naturalist*,  
462 *131*, 757-759.

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

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

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

471 Herrera, J. (1987b). Reproductive biology of some species of Donana scrub. *Anales del*  
472 *Jardín Botánico de Madrid*, *44*, 483-497.

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

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

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

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

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

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

488 Karim, M.N., & Mallik, A.U. (2008). Roadside revegetation by native plants. I.  
489 Roadside microhabitats, floristic zonation and species traits. *Ecological Engineering*,  
490 32, 222-237.

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

494 Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R.,  
495 Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff,  
496 N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R.,  
497 Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein,  
498 A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A.,  
499 Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H.,  
500 Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., & Kremen, C. (2013). A global  
501 quantitative synthesis of local and landscape effects on wild bee pollinators in  
502 agroecosystems. *Ecology Letters*, 16, 584-599.

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

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

508 Lewis, M.B., Schupp, E.W., & Monaco, T.A. (2012). Dust deposition from unpaved  
509 roads is correlated with decreased reproduction of an endangered Utah endemic shrub.  
510 *Restoring the West conference. Balancing energy, development and biodiversity*. Utah.

511 Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., & Schabenberger, O.  
512 (2006). *SAS for mixed models*. (Second ed.): Cary NC: SAS Institute Inc.

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

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

519 Morandin, L.A., & Kremen, C. (2013). Hedgerow restoration promotes pollinator  
520 populations and exports native bees to adjacent fields. *Ecological Applications*, 23, 829-  
521 839.

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

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

527 Noordijk, J., Delille, K., Schaffers, A.P., & Sýkora, K.V. (2009). Optimizing grassland  
528 management for flower-visiting insects in roadside verges. *Biological Conservation*,  
529 142, 2097-2103.

530 Ogden, L., Heynen, N., Oslender, U., West, P., Kassam, K.-A., & Robbins, P. (2013).  
531 Global assemblages, resilience, and Earth Stewardship in the Anthropocene. *Frontiers*  
532 *in Ecology and the Environment*, 11, 341-347.

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



535 Pasher, J., Seed, E., & Duffe, J. (2013). Development of boreal ecosystem  
536 anthropogenic disturbance layers for Canada based on 2008 to 2010 Landsat imagery.  
537 *Canadian Journal of Remote Sensing*, 39, 42-58.

538 Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W.E.  
539 (2010). Global pollinator declines: trends, impacts and drivers. *Trends in ecology &*  
540 *evolution (Personal edition)*, 25, 345-353.

541 Sayre, N.F., Kelty, R., Simmons, M., Clayton, S., Kassam, K.-A., Pickett, S.T.A., &  
542 Chapin, F.S. (2013). Invitation to Earth Stewardship. *Frontiers in Ecology and the*  
543 *Environment*, 11, 339-339.

544 Schmucki, R., & De Blois, S. (2009). Pollination and reproduction of a self-  
545 incompatible forest herb in hedgerow corridors and forest patches. *Oecologia*, 160, 721-  
546 733.

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

550 Suárez-Esteban, A. (2013). Ecological engineers in Doñana: combined effect of linear  
551 structures and plant- animal interactions on the Mediterranean scrubland. (p. 154).  
552 Oviedo: University of Oviedo.

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

556 Suárez-Esteban, A., Delibes, M., & Fedriani, J.M. (2013b). Unpaved road verges as  
557 hotspots of fleshy-fruited shrub recruitment and establishment. *Biological Conservation*,  
558 167, 50-56.

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

561 Wilson, P., & Thomson, J.D. (1991). Heterogeneity Among Floral Visitors Leads to  
562 Discordance Between Removal and Deposition of Pollen. *Ecology*, 72, 1503-1507.

563 Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., & Aizen, M.A. (2009). A meta-  
564 analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90, 2068-2076.

565

566

567 **TABLES**

568 **Table 1.** Results of the GLMMs fitted for testing the effects of habitat, herbivory, pollen-supplementation (Supplement) and their interactions on  
 569 the fruit set, seed set and seed mass. *P*-values are represented by asterisks (m.s.  $P < 0.07$ ; \*  $P < 0.05$ ; \*\*\*  $P < 0.0001$ ).

Factor	Supplemented cross-pollination						Natural pollination					
	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	1,763	0.16	1,1369	3.73 <sup>m.s.</sup>	1,1369	3.73 <sup>m.s.</sup>	1,113	2.72	1,2491	1.90	1,2491	1.61
Herbivory	1,763	0.23	1,1369	2.27	1,1369	2.04	1,113	2.71	1,2491	0.002	1,2491	0.08
Supplement	3,763	127.89***	3,1369	39.04***	3,1369	34.86***	-	-	-	-	-	-
Hab*Suppl	3,763	2.19	3,1369	0.63	3,1369	1.57	-	-	-	-	-	-
Herb* Suppl	3,763	1.74	3,1369	1.62	3,1369	1.01	-	-	-	-	-	-
Hab*Herb	1,763	3.29 <sup>m.s.</sup>	1,1369	0.00	1,1369	0.34	1,113	4.34*	1,2491	0.13	1,2491	0.04
Hab*Herb*Suppl	3,763	0.45	3,1369	1.35	3,1369	0.88	-	-	-	-	-	-

570

## Figure captions

**Fig. 1.** Spatial distribution of our three study sites inside Doñana National Park (SW Spain). In each of the three sites, we set up two experimental blocks, with open and fenced plots both along SLD (dark grey stripe) verges and in the scrubland, as shown by the diagram in the top-right.

**Fig. 2.** Model-adjusted means ( $\pm$  SE) of fruit set by pollen-supplemented (“Suppl”) and control flowers (from left to right: intra-inflorescence, inter-inflorescence and external controls) along SLD verges (black bars) and in the scrubland (white bars). We only found significant differences between supplemented (a) and all types of control flowers (b). No significant differences were found between habitats (n.s. = non significant,  $P > 0.05$ ).

**Fig. 3.** Model-adjusted means ( $\pm$  SE) of seed set by pollen-supplemented (“Suppl”) and control flowers (from left to right: intra-inflorescence, inter-inflorescence and external controls) along SLD verges (black bars) and in the scrubland (white bars). We only found significant differences between supplemented and control flowers. No significant variations were found between habitats, though the overall seed set was slightly higher in the scrubland as compared with SLD verges (\*\*  $P < 0.01$ ; m.s.  $P = 0.054$ ; n.s. = non significant,  $P > 0.054$ ).

**Fig. 4.** 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 show whether differences between least-square means were significant (n.s. = non significant).

FIGURE 1

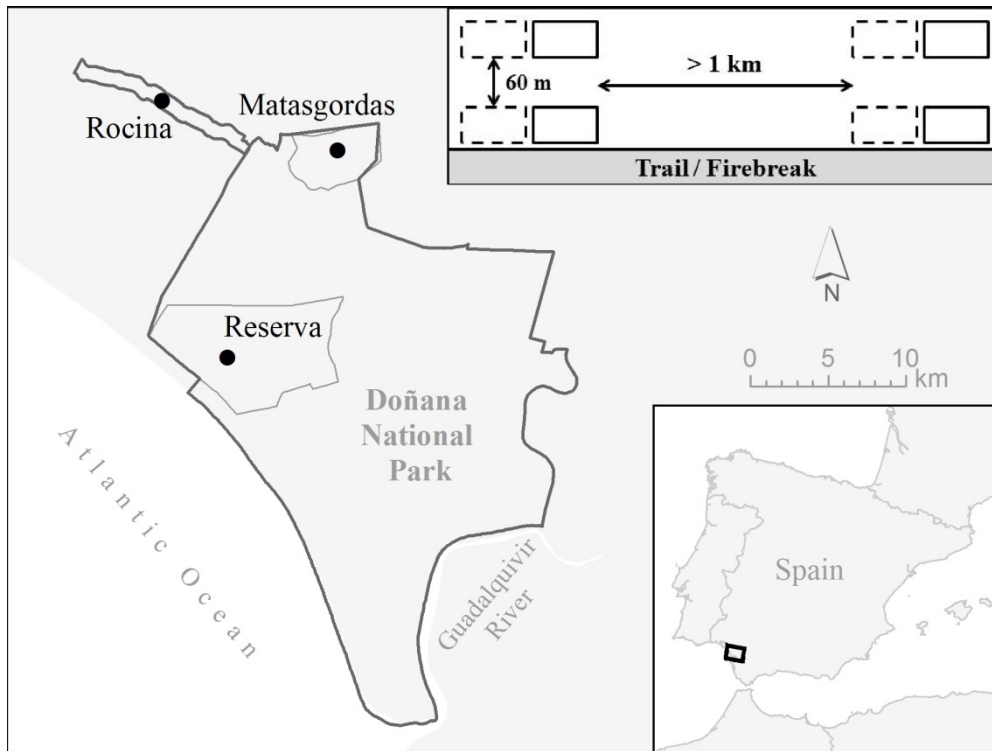


FIGURE 2

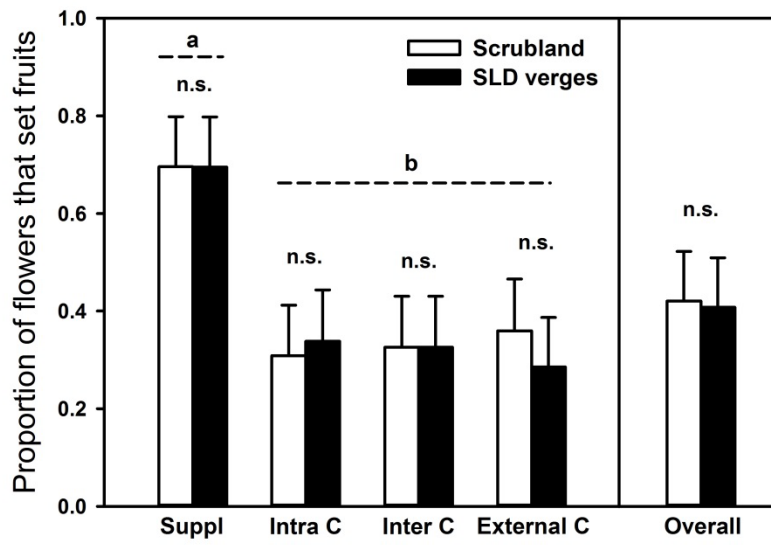


FIGURE 3

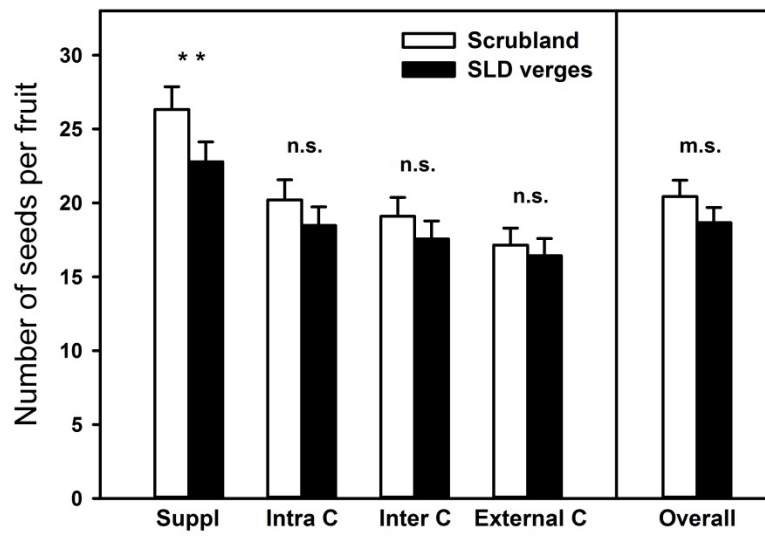


FIGURE 4

