Effects of microsite disturbances and herbivory on seedling performance in the perennial herb *Helleborus foetidus* (Ranunculaceae)

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Abstract

The impact of small scale disturbances on the early seedling performance components of *Helleborus foetidus* (Ranunculaceae) was studied through a transplant experiment. The aims of this study were: (i) to determine if the herbivory pattern depends on microsite disturbance, by the analysis of two of its components, seedling encounter (the probability of at least one seedling being harmed) and seedling exploitation (the proportion of seedling tissue removed once encountered); (ii) to test if seedlings of *H. foetidus* in disturbed microsites will survive in a greater proportion than seedlings in undisturbed microsites; (iii) to investigate if seedling survival is correlated with the degree of herbivory. Microsite disturbances had a large effect on the herbivory pattern. Seedlings growing in undisturbed vegetation had a 2-fold higher likelihood of being grazed and suffered 1.38-fold higher damage than those growing in disturbed plots. At the end of this experiment, after fourteen months, only 10.4% of the seedlings transplanted were still alive due to seedling desiccation, but no differences on seedling survival were found between disturbed and undisturbed plots. The effect of herbivory and the interactive effect of herbivory and disturbance on seedling survival only reached statistical significance dependent upon site. We concluded that although small scale disturbances had a large impact on herbivory patterns; they had only a minor role in the early seedling survival of *H. foetidus*. Only locally, small scale disturbances showed an effect on seedling survival through herbivory. Abiotic factors like summer drought and spatial variations determined the early survival of *H. foetidus* seedlings to a major extent.

Introduction

A common requirement for seedling recruitment is the absence of competition with other species within the immediate vicinity (Kitajima and Fenner 2000). Absence of competition is commonly found in gaps and/or after microsite disturbance, which generates a competitor-free space for a period of time (Bullock 2000; Cahill and Casper 2002). The study of gap dynamics and the ecological processes occurring within are a central theme in understanding plant natural regeneration and in explaining plant community structure (Pickett and White 1985; Silvertown and Smith 1988; Laska 2001; Silvertown and Bullock 2003). The occurrence of microsite disturbances often

represents the only chance for colonization by plants (Denslow 1987; Silvertown and Smith 1988; Bullock et al. 1995). Thus, many studies have dealt with the influence of microsite disturbances on the structure and dynamics of many perennial plant communities, seeking also to determine the gap-colonization ability of the different species within a plant community (see Bullock 2000 for a thorough review).

Overall, seedling survival is enhanced in gaps compared with intact vegetation (Aguilera and Lauenroth 1993, 1995; Hanley et al. 1996); however, in some instances, neutral or lower survival in gaps compared with intact vegetation has been related to water-limited plant communities or under water stress conditions (Ryser 1993; O'Connor 1996). In particular, in the Mediterranean-climate areas, the presence of a dry period, with low or no rainfall during part of the growing season, has a large negative effect on seedling survival. In fact, such dry periods cause remarkable water stress situations, which constitute the main abiotic constraint for seedlings (Herrera et al. 1994; Thébaud et al. 1996; Rey and Alcántara 2000). Contrary to large-scale disturbances (fires, extreme droughts, grazing, etc.), whose historical effects on the relationship with Mediterranean vegetation are relatively well known (Mills 1983; Thébaud et al. 1996; Lavorel 1999; Zavala et al. 2000), the importance of small scale disturbances on plant regeneration has received little attention in Mediterranean ecosystems. Thus, the impact of microsite disturbances on establishment has been sparsely studied (but see Lavorel et al. 1994; Herrera 1997), in spite of the fact that such small scale disturbances, (e.g. diggings, wallowing or intensive trampling, derived from the activity of small mammals and ungulates) are the rule in Mediterranean old fields (Lavorel et al. 1994), sclerophyllous shrublands and well-preserved mountain forests (Herrera 1997).

Seedling herbivory is other major factor affecting seedling performance and survival (Kitajima and Fenner 2000). The amount of herbivory suffered by seedlings may be strongly affected by the competitive scenario in which they are embedded (Cipollini and Bergelson 2001, 2002; Hambäck and Beckerman 2003; but see Maron 1997). For example, Cipollini and Bergelson (2001) showed that the expression of chemical defences in *Brassica napus* L. seedlings is constrained under competitive conditions and nutrient depletion, leading to higher levels of herbivore damage. It is also well known that plants under competitive stress are less able to compensate for a given level of herbivory than plants growing in a free-competitors scenario (Edwards et al. 1992; Hjalten et al. 1993). These and other studies (e.g. Rees and Brown 1992) suggest that the effect of herbivory and competition on seedlings are not merely additive, and thus that releasing a seedling from competition through disturbance may influence how herbivory affects its establishment. However, the effect of microsite disturbances on the herbivory pattern remains almost unknown (but see Rice 1987; Hanley et al. 1996).

Here, we investigate, through a transplant experiment, whether microsite disturbances and herbivory have any influence on the early seedling performance components of *Helleborus foetidus* (Ranunculaceae). More specifically, the aims of this study are: first, to determine if the herbivory pattern depends on microsite disturbance, through the analysis of two of its components (Hulme 1994): seedling encounter (the probability of at least one seedling being harmed) and seedling exploitation (the proportion of seedling tissue removed once encountered); second, to test if seedlings of *H. foetidus* in disturbed microsites will survive in a greater proportion than seedlings in undisturbed microsites; and third to investigate if seedling survival is correlated with the degree of herbivory.

Methods

Study system and sites

Helleborus foetidus L. (Ranunculaceae) is a perennial herb distributed across Western Europe (Werner and Ebel 1994). In the Iberian Peninsula, it is abundant in montane areas, especially in the north, but is also locally common in the south, being infrequent in the west (Fernández Casas and Gamarra 1991). It grows in the understorey of deciduous and mixed forest, in patchy scrub and ruderal habitats. Detailed aspects concerning its floral biology, seed ecology and evolutionary ecology in the Iberian Peninsula can be found in Herrera et al. (2001, 2002a, b), Herrera (2002a),

Garrido et al. (2002) and Fedriani et al. (2004). Seeds are often dispersed by ants due to the presence of an elaiosome. After a period of dormancy, the vast majority of seeds germinate (average percentage of seed germination after 3 years ≈21%, $n = 3600$; Garrido 2003) during the second spring after entering the seed bank (Herrera et al. 2002b). Cotyledons start to grow after releasing from the seed-coat, becoming green immediately and remain attached to the seedling axis for several months (normally, up to the dry period). True leaves appear after 3–5 cm of shoot growth. Seedlings are not eaten by vertebrates. However, lepidoptera larvae (*Noctua* spp. and *Trigonophora flammea*), which frequently consume flowers and developing fruits (Herrera et al. 2002b), feed on seedlings (C.M. Herrera pers. comm.; authors obs. pers.). Feeding activity by lepidoptera larvae in our study area starts in April and reaches a distinct peak during the first half of June, declining abruptly afterwards (Yela and Herrera 1993). Thus, seedling herbivory is mainly concentrated on cotyledons, although is also possible to find signs of herbivory in the first pair of true leaves (authors obs. pers.).

This study was conducted between March 2000 and May 2001 at five sites within Reserva Natural Navahondona-Guadahornillos, Parque Natural de la Sierra de Cazorla, Segura y las Villas, Jaén Province (south-eastern Spain). Three of the sites, Roblehondo 1 (RH1), Roblehondo 2 (RH2) and Roblehondo 3 (RH3), are within a radius of 500 m at 1300 m elevation, and located in an old evergreen oak–pine (*Quercus rotundifolia* and *Pinus nigra ssp. salzmanii*) mixed forest, with a northeast exposure. The fourth site, Barranco de la Hiedra (BH), is located 10 km NNW from the other sites, at 1200 m elevation in an evergreen oak–pine mixed forest with a northern exposure. The last site, Roblehermoso Alto (RA), is located at least 15 km from the other study sites, at 1300 m elevation, in an open pine forest with a north-western exposition (see Herrera 2000, 2002b, for further details on localities). In these sites, the density of small mammals and ungulates like Red deer (*Cervus elaphus* L.), Fallow deer (*Dama dama* L.) and Wild boar (*Sus scrofa* L.) is exceptionally high which cause widespread disturbances on the topsoil as consequence of their behaviour. The natural appearance rate of such disturbances in our study sites is high, 6.75 dis-

turbances/100 m^2, and their extent ranges 675–16 936 cm^2, 5–10 cm depth ($n = 54$).

The climate is Mediterranean, with a dry period typically extending from June to October. Rainfall in the study area during the dry period (June 2000–October 2000) was 49 mm (5.64% of total 2000-rainfall), and the mean of the maximum temperatures for this dry period was 25.5 °C (data for 2000; Consejería de Medio Ambiente 2001). From the beginning of the experiment (March 2000) to June, the total amount of rainfall was 314 mm (36.13% of total annual rainfall) and the mean of the maximum temperatures was 11 °C. Finally, from November to May 2001, the total amount of rainfall was 702 mm (58.21% of total annual rainfall) and the mean of the maximum temperatures was 15.7 °C (data for 2000 and 2001; Consejería de Medio Ambiente 2001, 2002).

Transplant experiment

In March 2000, we collected from a single site one thousand newly emerged seedlings, with similar cotyledon and root size, before the first pair of true leaves had developed. Seedlings were carefully extracted from the soil without damaging the root-system, and were shaken until all the roots were clean. Then, seedlings were transplanted according to the following design. At each of the five study sites, we set ten 0.5×0.5 m (simulating the average extent of these type of disturbances yielded by ungulates and small mammals in our study sites, see above) transplant plots separated 0.5–4 m from each other. Five transplant plots were randomly assigned to a disturbance treatment and the other five were left as control ('undisturbed' hereafter). In the disturbance treatment, the aboveground and part of the below-ground vegetation, mainly grass and forbs (*Poa annua*, *Trifolium repens*, *Erodium* spp., *Plantago* spp.) which constituted a continuous and dense turf (5–15 cm height), were removed (stem, roots and canopy). The soil was turned to a depth of 5–10 cm. To avoid an undesired border effect, the removal process was extended on disturbance treatment beyond the border of the transplant plot (≈10 cm around the perimeter). Undisturbed treatments (controls) consisted in notional areas (0.5×0.5 m) of vegetation (also grass and forbs) marked in each

corner with four nails labeled. Twenty seedlings were transplanted (using the extreme of a spade, an incision in the ground was made just to insert the root, 7–10 × 1.5 and 10 cm depth) into each 0.5 × 0.5 m transplant plot and, within each plot, seedlings were spaced ≈10 cm from each other. Although sites differed in tree cover conditions (mean percent of tree cover ranged from 55.2% in RA site to 87.3% in RH1 site, A.J. Manzaneda unpublished data) all the transplant plots were shaded by trees. Seedlings were watered twice during the first two weeks of the experiment (5 l per transplant plot) to minimize mortality due to transfer stress. The first week after transplantation, 8.5% of seedlings did not survive and neither were replaced nor included in the analysis. Afterwards, seedling survival and herbivory levels were recorded in the beginning of June, July, September and November 2000 and in May 2001. Here, we stopped the experiment since the probability of seedling survival in *H. foetidus* once overcome the first year is quite constant (Garrido 2003). A simple scale was used to estimate visually the levels of herbivory on cotyledons for each seedling, 0: no herbivory; 1: <25%; 2: 26–50%; 3: 51–75%; 4: >76% of tissue removed.

Data analysis

To test the effect of microsite disturbance on herbivore encounter, we used as dependent variable the proportion of seedlings with any sign of damage on cotyledons per transplant plot, treated as a binary variable (harmed or not harmed). We used Generalized Linear Mixed Model with binomial distribution and logit link function. The treatment (disturbance) was included as a fixed factor with two levels. In order to test the consistency of potential effects of the treatment among study sites, Site was considered as a fixed factor effect (Benninington and Thayne 1994). To analyse the effect of microsite disturbance on cotyledons damage (intensity of exploitation), we used the accumulated proportion of cotyledon removed per seedling once encountered and fitted a Generalized Linear Mixed Model with binomial distribution (4 as binomial denominator) and logit link function. In both analyses, transplant plot nested within site was incorporated in the models as a random factor. Analyses were conducted with SAS macro GLIMMIX implemented in the SAS MIXED Procedure (SAS Institute 1999). LSMEANS statement in the MIXED procedure was used to get mean ± 1 SE model-adjusted values (back-transformed from logit scale). Since the data were corrected for overdispersion, we used *F*-statistics values instead of χ^2 values (Littell et al. 1996).

Potential biases due to spatial autocorrelation on both seedling encounter and seedling exploitation were previously accounted for by expressing the spatial structure of both variables as a linear combination of the Cartesian coordinates of seedlings within the transplant plots (x and y coordinates allowed to explore the bi-dimensional component of spatial structure, $x * y$, x^2, y^2 and $x^2 * y^2$ to explore the surface component of spatial structure). Thus, a partial logistic regression analysis (Legendre 1993; Legendre and Legendre 1998) between this Cartesian coordinates and both variables was conducted to evaluate spatial autocorrelation patterns within each study sites. We used Generalized Linear Models with binomial distribution and logit link function in both cases. These analyses were conducted with SAS GENMOD Procedure (SAS Institute 1999). No evidence of spatial autocorrelation effects on both seedling encounter and seedling exploitation was found within site (for all components of spatial structure, see above, $p > 0.05$). Thus, raw variables were eventually analysed.

To analyse the effect of microsite disturbance on seedling establishment, we used the proportion of seedlings remaining per transplantation plot as a dependent variable. We performed a Generalized Linear Mixed Model with binomial distribution and logit link function. The treatment (disturbance) was included as a fixed factor with two levels and Site were considered as a fixed factor effect. To test whether the herbivory levels found on cotyledons (assessed as the total proportion of damage accumulated on cotyledons for each individual seedling) had some influence on seedling recruitment, were incorporated as covariate in the analysis. Furthermore, transplant plot nested within site was incorporated as random factor. This analysis was conducted with SAS macro GLIMMIX implemented in the SAS MIXED Procedure (SAS Institute 1999).
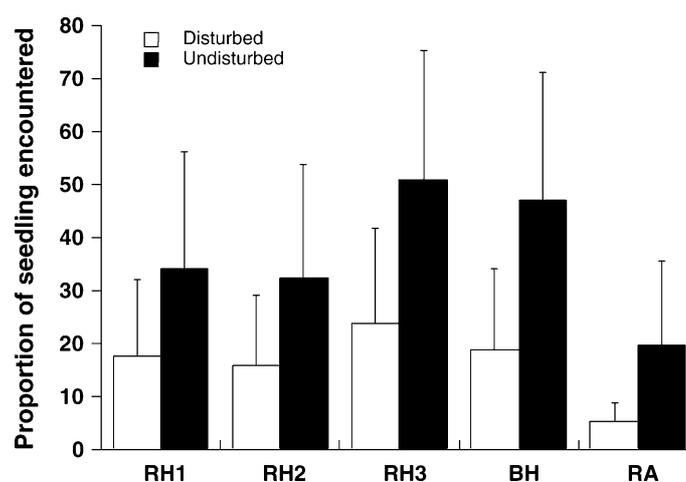
Figure 1. Mean proportion of seedlings encountered (%) per transplant plot, treatment and sites (mean and 1 SE model-adjusted values). Solid bars denote undisturbed treatment and open bars denote disturbed treatment. The disturbance treatment effect on the seedling encounter was constant in all the study sites.

Table 1. Summary of mixed model Deviance analysis to test microsite disturbance effects on the proportion of seedling encountered and seedling damage.

Effects	Seedling encounter			Seedling damage		
	d.f.	F	p	d.f.	F	p
Disturbance	1.20	19.71	**0.0003**	1.196	12.55	**0.0005**
Site	4.20	2.92	**0.047**	4.35	0.42	0.790
Disturbance × Site	4.20	0.19	0.942	4.196	1.34	0.256
		Z	p		Z	p
Random effect						
Transplant plot (Site)		0.23	0.409		0.76	0.222

Results

Effect of microsite disturbance on herbivory

The total proportion of seedlings with any sign of herbivory during the period of study was 26.33% (n = 915). Overall seedling encounter differed significantly between Disturbance treatments (Table 1). The proportion of seedlings harmed under disturbance treatment was significantly smaller than seedlings growing in undisturbed plots (mean ± 1 SE model-adjusted values) 15.00 ± 23.69%, 36.07 ± 39.82% for disturbed and undisturbed plots respectively. Thus, the likelihood to be grazed was 2-fold higher for seedlings growing in intact vegetation than those

growing in disturbed plots. The proportion of seedlings encountered varied among study sites (Table 1), furthermore, there was consistency among sites in the effects of disturbance on herbivory as shown by the non-significance of Disturbance × Site interaction term (Table 1; Figure 1). However, there was no significant effect of transplant plot on seedling encounter by herbivores (Table 1).

The mean proportion of cumulative cotyledons damage per seedling was significantly affected by the disturbance treatment (Table 1), being larger in undisturbed (49.65 ± 53.29%) than in disturbed plots (36.09 ± 42.26%). Seedlings growing in undisturbed vegetation suffered 1.38-fold higher damage than seedlings living in disturbed plots. This result was constant for all study sites as showed the non-significance of Disturbance × Site interaction term (Table 1). However, the mean proportion of cumulative cotyledons damage per seedling did not vary significantly either sites (Figure 2) or at micro-scale level within site (Table 1), suggesting no spatial variation in the levels of seedling damage.

Microsite disturbance and seedling survival. Herbivory correlates

At the end of this experiment, after 14 months, only 10.4% of the seedlings transplanted were still
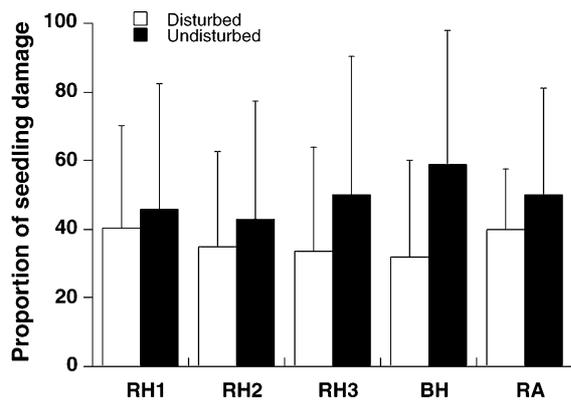
Figure 2. Mean proportion of cumulative damage on cotyledons (%) per transplant plot, treatment and sites (mean and 1 SE model-adjusted values). Solid bars denote undisturbed treatment and open bars denote disturbed treatment. For all sites, seedlings growing in undisturbed plots suffered more damage on cotyledons than seedlings growing in disturbed ones. No differences in the proportion of damage were found among sites.

Table 2. Summary of mixed model Deviance analysis to test the effect of microsite disturbance on the proportion of seedling remaining per transplantation plot and site during the experiment.

	d.f.	F	p
Fixed effects			
Disturbance	1.855	0.09	0.764
Site	4.40	14.33	**< 0.0001**
Covariate			
Herbivory	1.855	2.43	0.119
Interactions			
Disturbance × Site	4.855	0.56	0.692
Herbivory × Disturbance	1.855	0.38	0.536
Herbivory × Site	4.855	3.24	**0.012**
Herbivory × Site × Disturbance	4.855	4.14	**0.002**
		Z	p
Random effect			
Transplant plot (Site)		20.74	**< 0.0001**

alive. The highest seedling mortality occurred during the dry period due to seedling desiccation. Overall, the proportion of seedlings remaining per transplant plot was not significantly affected by disturbance treatment (Table 2). Surviving seedlings (mean ± 1 SE model-adjusted values) in undisturbed and disturbed plots were respectively, 8.08 ± 12.39%, 7.95 ± 14.51%. Site affected significantly the proportion of seedling remaining per transplantation plot (Table 2), suggesting a spatial variation on the proportion of seedling recruited (Figure 3). Neither the Disturbance × Site interaction or Disturbance × Herbivory covariate interaction, had any effect on the proportion of seedling remaining per plot (Table 2), suggesting both that the non-effect of disturbance treatment on the proportion of seedlings recruited was consistent among sites, and that, overall, both levels of the disturbance treatment were similarly affected by herbivory.

Herbivory, as a main effect, were not correlated to the proportion of seedling recruited per plot; however, both Herbivory × Site and Herbivory × Site × Disturbance interaction terms had significant effects on the proportion of seedling remaining per plot (Table 2), indicating that the sign and or/magnitude of the Herbivory effect was not consistent among sites. In fact, the analysis of the coefficients from Herbivory × Site interaction term showed that, it was in BH site the only place where the sign of the Herbivory effect varied (estimate ± 1 SE, back-transformed from the logit scale, = −0.47 ± 0.27). Finally, transplant plot effect was significant (Table 2), suggesting micro-scale variability on seedling recruitment within site.

Discussion

Microsite disturbances and herbivory patterns

Herbivory, both seedling encounter and seedling damage was highly affected by microsite disturbances. This effect of microsite disturbance on herbivory patterns was strongly consistent in all study sites. Several mechanisms are possible to explain this pattern of herbivory. Firstly, the removal of vegetation conducted in the disturbed treatment probably involved the removal of herbivores living in those plots (in our system of study, mainly lepidoptera larvae, see Methods). Consequently, a reduction of the density of herbivores is expected, which could affect the likelihood of seedling encounter in disturbed plots compared to intact vegetation. Secondly, intact vegetation may provide shelter from predators and parasitoids of herbivores (Reader 1992; Cipollini and Bergelson 2002), and this could increase seedling herbivory in undisturbed vegetation compared to disturbed plots. Finally, neighbourhood
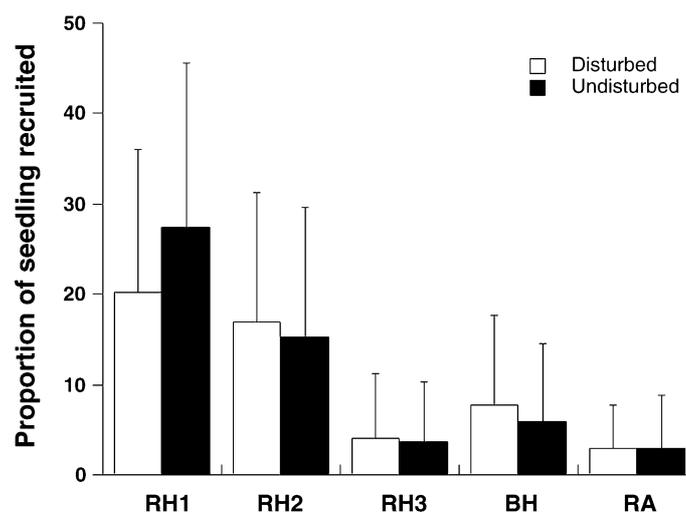
Figure 3. Mean proportion of seedlings recruited (%) per transplant plot and sites (mean and 1 SE model-adjusted values). Solid bars denote undisturbed treatment and open bars denote disturbed treatment. Overall, no differences were found between the two treatments. However, Site affected the proportion of seedling recruited per transplant plot (see Table 2 for details).

effects may play an important role on the risk of being grazed (Fenner 1987; Rousset and Lepart 2002) given the probability of being grazed not only depends of life history traits of seedlings but also on the quality of its neighbours (Rousset and Lepart 2002). Therefore, seedlings of relatively unpalatable species (for *H. foetidus*, the presence of phytoecdysteroids, defensive compounds against invertebrates herbivores, has been reported, see Dinan et al. 2002) growing within a mixture of palatable species (grasses and forbs in our study) are probably more likely to be grazed than seedlings growing alone (Fenner 1987).

Seedling survival and microsite disturbances.
Influence of herbivory

Although the death rate of seedlings could be higher than normal due to root disturbance associated with transplantation, seedling survival of *H. foetidus* was unaffected by small scale disturbances. The main cause of mortality was seedling desiccation during the dry period, and the disturbance treatment did not affect to the proportion of seedlings remaining alive. Gaps frequently present a release from competition for one or more resources and therefore could enhance seedling survival (Aguilera and Lauenroth 1995; Bullock 2000). Besides, some advantages have been

demonstrated for seedlings in gaps when facing a seasonal dry period: they become larger than those established under canopy and could face the dry period better; seedlings growing in disturbed places present a lower root:shoot ratio; soil water potentials are often more favourable in gaps (Howe 1990; Huante et al. 1992; Veenendaal et al. 1996, respectively). Our results, however, do not support the hypothesis that seedlings growing in disturbed microsites survive in greater proportion than seedlings growing in undisturbed ones. A plausible explanation for this neutral effect of microsite disturbances on seedling survival could be related to gap size. Environmental conditions of gaps and undisturbed vegetation may not be different when the gap is not large enough (Bullock 2000). Although our experiment mimicked the average size of microsite disturbances yielded by animals (ungulates and small mammals) in our study sites, perhaps, the size of microsite disturbances were not large enough and disturbed plots had a very similar environment than those under intact vegetation. Hence, the amount of reduction in competition for resources (in our latitude, mainly water and/or nutrients rather than light, Rey Benayas et al. 2002) might not be sufficient to affect seedling survival, yielding a similar seedling response on both treatments. Neutral seedling survival in gaps compared with intact vegetation has been described previously in water-limited

communities (Ryser 1993; García-Fayos and Verdú 1998). Thus, Ryser (1993) found for seedlings of some species in nutrient-poor limestone grassland, that physical hazards such drought and frost controlled seedling survival to a larger extent than competition from vegetation, suggesting that in relatively non-productive communities abiotic factors become most important. Our results support this idea strongly, as factors like summer drought, were more important for survival of *H. foetidus* seedlings than microsite disturbance effects.

Both the effect of herbivory and the interactive effect of herbivory and disturbance on seedling survival only reached statistical significance dependent upon site. It means that there were some sites where the herbivory could affect seedling survival, either directly and/or indirectly through the disturbance treatment. Which were the sites where the herbivory could influence seedling survival? Differences in seedling encounter among sites rather than differences in seedling damage could explain this influence of herbivory site-dependent. Seedling encounter varied among study sites, while seedling damage did not (Table 1). BH site was one of the places with major proportion of seedling harmed (Figure 1) as this site was one where the herbivory played a significant role. This is reinforced by the fact that was in BH site where the sign of the herbivory effect varied (see Results). On other hand, the total removal of cotyledons was rare (0.87%, $n = 915$), suggesting that the negative effect of herbivory on seedling survival in this site was not straightforward. For example, cotyledon removal may reduce the seedling's ability to compete, and/or diminish its capability to face the dry period. The more plausible explanation for these results may be found in the hierarchy which the different factors controlling the recruitment process, i.e. abiotic constrains (water stress) rather than small scale disturbances effects (release from competition and/or increasing of herbivory levels), seemed to govern seedling survival. Future studies would be necessary to corroborate this lack of correlational evidence of the interactive effects of herbivory and competition, besides, since our study was conducted with just one transplant date, they might contemplate the possible year to year variability, which is frequent in the majority of the systems of recruitment.

Spatial variation on early seedling survival

The location of seedlings has revealed a main factor affecting seedling survival. Spatial variation both at large scale (site, i.e kilometres) and small scale (transplant plot, i.e. metres) determined the proportion of seedling remaining. Some sites were particularly unfavourable for seedling survival, like the RA site, where none of the seedlings survived the summer drought, while 20–30% of the seedlings were still alive after the dry period in other two places (Figure 3). Even though these sites where in general favourable for seedling survival, there was a within-site effect as some transplant plots were more favourable for seedling survival than others. One possible explanation for these spatial differences can be micro-scale variability in availability of water and/or nutrients in the soil. Herrera (2002b) found such micro-scale differences in conditions for survival in *Lavandula latifolia* in the same study area. He found that important soil properties for seedling emergence and survival, like soil texture and nutrients, varied both in a large scale (kilometres) and a small scale (metres). This means that a very fine scale variation in soil properties had a large effect on the spatial distribution of adult plants. The same effect on spatial distribution in the landscape might be happening for *H. foetidus* plants, since our study shows that seedling survival in *H. foetidus* is very much dependant on the specific location (site and transplant plot, corresponding to a large and a small scale in our study), where the seedling is. On the other hand, the origin of the seedlings used in our transplant experiment can account for the explanation of spatial differences, at least at large-scale level. All the seedlings came from one unique site very close to RH1 and RH2 sites, where seedling survival was highest too. This could suggest the presence of spatial dependence on seedling survival and perhaps the existence of local adaptation processes on seedling survival for *H. foetidus*. However, a complete and fully reciprocate design of seedlings transplant would be necessary to test this hypothesis.

In conclusion, this study has shown that small scale disturbances had a large impact on herbivory patterns. However, small scale disturbances had a minor role on the early seedling survival of *H. foetidus*. Only locally, small scale disturbances showed an effect on seedling survival through

herbivory rather than directly. Others factors like summer drought and spatial variation determined to a major extent the early survival of *H. foetidus* seedlings.

Acknowledgements

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