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Habitat quality and population size as determinants of performance of two endangered hemiparasites

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Optimal understanding of biodiversity threats must consider the effects of population size and habitat quality on population viability. I examined the effects and relative importance of these factors for the performance of two endangered hemiparasitic plants, *Melampyrum cristatum* and *M. arvense* in Finland. I surveyed 18 *M. cristatum* and 14 *M. arvense* populations. Both habitat quality and population size influenced the performance of *M. cristatum*. By contrast, the performance of *M. arvense* was determined by habitat quality, but not influenced by population size. Habitat quality was improved in managed *M. cristatum* populations, which translated into greater hemiparasite performance in these populations. Degradation of suitable habitats has likely decreased the performance of the two endangered hemiparasites, resulting in reduced population sizes. The results highlight the importance of considering simultaneously population size effects and habitat quality. Habitat management seems to be the key to sustain or increase the viability of the hemiparasite populations, but the timing and intensity of management should be considered.

Key words: Habitat fragmentation, management, Melampyrum, parasitic plant, population size, plant fitness

Introduction

During recent decades the consequences of fragmentation and degradation of suitable habitats have received increasing attention and are considered as the major reasons for the worldwide decrease in biodiversity (Wilcox & Murphy 1985, Fahrig 2003, Ouborg *et al.* 2006). Due to changes in traditional land-use and management practices, large areas of semi-natural habitats are facing successional closure following abandonment. Moreover, habitat fragmentation has resulted in decreased population size and increased isolation of numerous formerly common plant species (Primack 1993, Fischer & Stöcklin 1997). Two paradigms, the “habitat quality” paradigm and the “conservation genetics” paradigm, have been launched to describe the elements of the major biodiversity threats (Ouborg *et al.* 2006). The “habitat quality” paradigm postulates that biodiversity reductions arise due to lack of ability of species and populations to adapt to changes in habitat quality (Ouborg *et al.* 2006). The "conservation genetics" paradigm, in turn, states that populations of species are endangered due to their small size and high degree of isolation (Ouborg *et.al.* 2006). Although providing alternative interpretations, the two paradigms are not mutually exclusive. In order to better understand biodiversity threats, they should be considered simultaneously despite the fact that it is often difficult to distinguish whether small population size *per se* leads to decreased plant fitness or whether the decrease is caused by confounding habitat differences. Environmental, demographic and genetic stochasticity increase the extinction risk of small and isolated populations (Lande 1993, Ellstrand & Elam 1993, Frankham *et al.* 2002, Boyce *et al.* 2006), but environmental trends, such as successional closure of habitats, can further decrease the viability of plant populations (Lehtilä *et al.* 2006, Kolb *et al.* 2007). The negative genetic and ecological consequences of small population size are widely studied and known to be common (reviewed in Leimu *et al.* 2006), but studies combining habitat quality and population size effects are still scarce (Ouborg *et al.* 2006, but *see* Vergeer *et al.* 2003).

In addition to direct effects on plants, fragmentation and habitat quality can also affect their interactions with other organisms (e.g. Kearns *et al.* 1998, Leimu *et al.* 2002, Tscharntke & Brandl 2004, Kolb *et al.* 2007). However, so far the effects of fragmentation and habitat quality on interactions between parasitic plants and their hosts have been largely neglected. Root hemiparasites form haustorial connections with the roots of their host plants and extract water and nutrients from the hosts (Musselman & Press 1995). Despite being partially photoautotrophic, these parasites largely depend on their host plants. Hence, hemiparasites function in a community as plants, but also on a higher trophic level using other plants as hosts, and are thus comparable to herbivores or consumers (Pennings & Callaway 2002). Hemiparasites are able to use a wide range of host plants, but their performance can vary significantly depending on the host species (Gibson & Watkinson 1989, Seel & Press 1993, Marvier 1998a) and some plant families are preferred while others are avoided (Matthies 1996). In the field individual hemiparasites often use several hosts simultaneously (Gibson & Watkinson 1989), which provides an ability to take up a more diverse mix of compounds and resources (Govier *et al.* 1967) and can improve their performance (Marvier 1998a, but *see* Matthies 1996). Thus, hemiparasites are predicted to perform best in species-rich communities (Joshi *et al.* 2000). On the other hand, because of the selective host-plant use and the host-dependent variation in performance, parasitic plants can alter the competitive interactions between different plant species and may thus, in turn, influence the structure and diversity of the plant community (Anderson & May 1986, Marvier 1998b, Pennings & Callaway 1996, 2002, Press & Phoenix 2005). Because of this, in addition to the negative genetic and ecological consequences of fragmentation, hemiparasitic plants likely suffer from changed habitat quality caused e.g. by successional closure.

Here, I examined the associations between habitat quality (vegetation structure, species diversity), population size, and the performance of two endangered hemiparasites; *Melampyrum cristatum* and *M. arvense* (Orobranchaceae). These species have declined in Europe due to fragmentation and the successional closure of suitable habitats, and are considered endangered (Rassi *et al.* 2001). In addition to direct damage on plants, management by mowing and/or grazing is likely to influence plant performance by changing the competition for light and nutrients, litter accumulation and disturbance frequency (Ehrlén *et al.* 2005). Such effects can be especially important for hemiparasitic plants, because management may have additional influence on them via its impact on their host plants. I collected data from 18 *M. cristatum* and 14 *M. arvense* populations at the northern boarder of their distribution range in Finland. A subset of the surveyed *M. cristatum* populations were situated in areas where the habitat had been managed by grazing and/or mowing, which allowed me to further examine differences in the performance of this hemiparasite between managed and unmanaged populations. I asked the following specific questions: (1) Is there among-population variation (a) in hemiparasite performance and (b) in habitat quality in terms of successional closure (vegetation height and density), species richness or the abundance of different functional host plant groups (grasses, legumes, and other herbs)? (2) Does habitat quality, population size and the performance of *M. cristatum* differ between managed and unmanaged populations? (3) Is population size associated with habitat quality in *M. arvense* and *M. cristatum*? (4) What are the relative roles of population size and measures of habitat quality in determining the performance of the two hemiparasites?

Methods

Study species and populations

Melampyrum cristatum and *M. arvense* (Orobranchaceae) are annual root hemiparasites. They occur in open semi-natural dry meadows and grasslands, and woodland margins preferring calcium rich calcareous soils. Individuals can use many host species simultaneously (Horrill 1972, Matthies 1996). The cotyledons develop in spring and haustorial connections are made with the roots of species in the surrounding soil. Plants grown without hosts often die at a young stage. Flowering starts in June and the flowers are mainly pollinated by bumblebees. The fruits usually contain four seeds, but the total number of seeds per plant can be variable. Seeds are dispersed by ants and seed dispersal range is considered to be very limited (Horrill 1972). Seeds start to germinate in autumn. Seeds can stay dormant in the soil for at least two years (Horrill 1972). Germination of dormant seeds is the likely reason for the reappearance of these hemiparasites following disturbance (Horrill 1972).

In Finland, both *M. cristatum* and *M. arvense* occur at the northern border of their distribution range and the localities are restricted to southwestern Finland. *Melampyrum cristatum* still occur relatively frequently in the southwestern archipelago of Finland and on the Åland islands, whereas the existing populations of *M. arvense*, which is locally considerably rarer, are restricted only to three nearby islands. According to the IUCN threat classification, both *M. cristatum* and *M. arvense* are considered as vulnerable (VU) in Finland (Rassi *et al*. 2001). The major threats to these species are degradation and overgrowing of suitable habitats followed by changes in traditional land use, which have lead to declining population sizes (Rassi *et al*. 2001). Many of the populations have declined dramatically, and many populations of *M. cristatum* and *M. arvense* have gone extinct. On the other hand, in some localities restoration and management of formerly open habitats have increased the viability of the *M. cristatum* populations (L. Lindgren pers. comm.). In some areas, the plants occur in intensively farmed regions and are vulnerable to effects of modern farming and woodland management, although a certain amount of mechanical disturbance of the habitat can be favourable (Horrill 1972, Rassi *et al*. 2001).

I collected data from 18 *Melampyrum cristatum* populations and 14 *M. arvense* populations. Sixteen of the *M. cristatum* populations were situated in the southwestern archipelago of Finland or on the Åland islands and two remnant populations were situated at the coastal areas of the southwestern mainland. The surveyed *M. arvense* populations were situated in the southwestern archipelago of Finland on the three nearby islands and included all the existing Finnish populations or sub-populations. Ten of the *M. cristatum* populations are situated in managed areas where the habitats have been kept open by grazing or regular mowing (L. Lindgren pers. comm.).

Data collection

I marked twenty randomly chosen individuals in each population or all individuals in populations with fewer than 20 individuals. I measured the length of the main stem and counted the number of leaves, branches (flowering and non-flowering), and the number of flowers, buds and capsules of each individual in mid-June 2003. I surveyed the populations again in late July, when the capsules and seeds had matured. From the *M. arvense* individuals, I additionally counted the seeds from a subset of fruits and collected and weighted a sample of the seeds on a microbalance. Unfortunately, I was not able to determine reliably the seed number and mass for the *M.*

cristatum individuals since most seeds had dispersed before the survey.

To estimate the population size, I counted the total number of flowering individuals in all populations during the first survey in June. The size of the *M. cristatum* populations ranged from 15 to 6100 individuals and the *M. arvense* populations from 5 to 344 individuals. To determine the diversity of the neighbouring plant community and the structure of the vegetation, I placed a 50 × 50-cm frame around each marked individual and measured the height of the vegetation, identified plant species, recorded the number of species, and estimated the proportional cover of three functional groups (legumes, grasses and herbs).

Statistical analyses

I used a multivariate analysis of variance (MANOVA) to examine the effects of management (mowing and/or grazing) and the among-population variation in, first, plant performance and second, in habitat characteristics. In the first MANOVA, stem length, the number of leaf pairs, the total number of branches and flowering branches, flower number, fruit set, and for *M. arvense* also seed number and seed mass were used to estimate plant performance. The habitat characteristics included in the second MANOVA were the height of the vegetation and the mean vegetation cover (%), and the mean number of neighbouring species (diversity) and the proportion of legumes, grasses and other herbs of the total vegetation cover to describe species richness and the different functional groups of potential host plants. Populations were nested within the management category (managed or unmanaged) in the analyses for *M. cristatum*. Roy's greatest root statistics was used to test for the differences among the groups (Scheiner & Gurevitch 2001).

I conducted a one-way ANOVA to test if management (managed or unmanaged) influenced population size of *M. cristatum*. I used population mean values in the analyses. Population size was log-transformed to meet the assumptions of normal distribution.

I used a multiple regression analysis to first examine the associations of the habitat characteristics and the size of the hemiparasite populations. To find the best fit model, I used the CP model selection option of PROC REG, which finds a specified number of models with the lowest C_p within a range of model sizes (SAS Institute 2003). Second, I examined the associations of the habitat characteristics and the performance of *M. arvense* conducting the model selection procedure in a similar manner. The analyses were conducted using the means of the response variables for each population.

To investigate the associations of the habitat characteristics and the performance traits of *M. cristatum* in managed and unmanaged populations, I conducted an analysis of covariance (ANCOVA) with management (managed or unmanaged) and the habitat characteristics and their interactions as explanatory variables. ANCOVA allows for comparing series of regression models and thus to analyze data with both categorical and continuous explanatory variables and their interactions (Littell *et al*. 2006). I first ran the model with all possible interactions and then excluded the non-significant ones starting from the highest order interaction (Littell *et al*. 2006). To further investigate cases of significant interactions between the habitat characteristics and management (cases of heterogeneity of the slopes), I calculated the covariate-adjusted least square mean estimates for both managed and unmanaged populations for different levels (minimum, 25%, 50%, 75%, and maximum) of each of the continuous variables that interacted significantly with management (Littell *et al*. 2006). I also used these covariate-adjusted LS-mean values for graphs illustrating significant habitat characteristic by management interactions.

Results

Effects of management and population on hemiparasite performance and habitat structure

Managed *M. cristatum* populations were found to be larger in terms of number of flowering individuals than the unmanaged populations ($F = 10.38$, df = 1, $P = 0.0053$). Overall, management had a significant effect on the performance

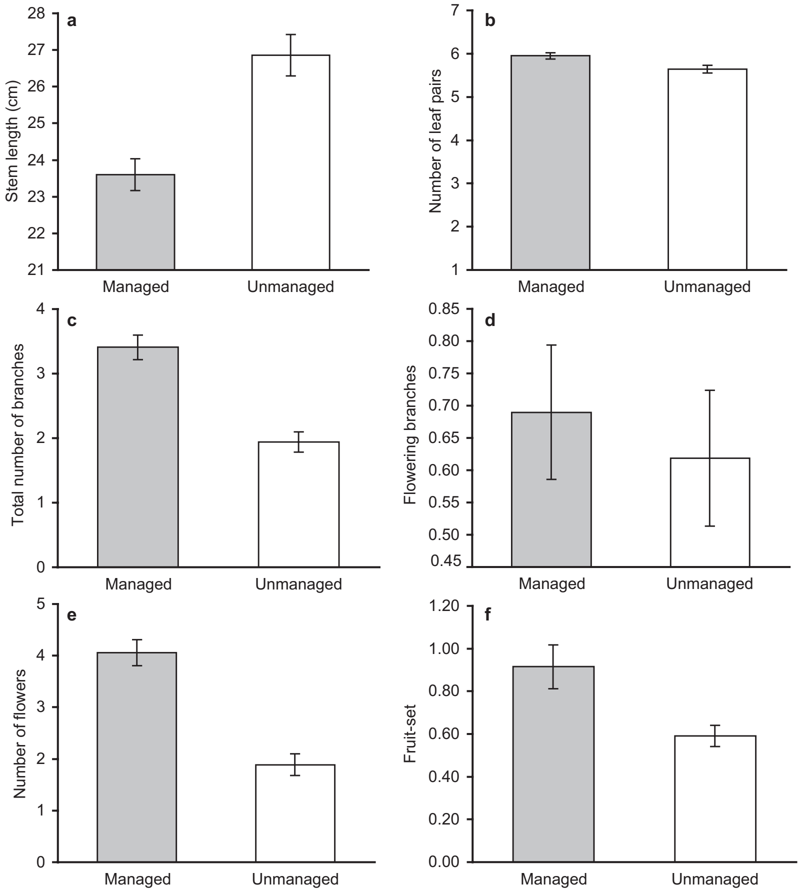

Fig. 1. Differences in plant performance between unmanaged and managed *Melampyrum cristatum* populations. Means ± SE are presented.

of *M. cristatum* (Roy's Greatest Root: $F = 4.64$, ndf = 6, ddf = 11, $P = 0.0137$), but significant among-population variation was also found within managed and unmanaged populations (Roy's Greatest Root: $F = 61.56$, ndf = 16, ddf = 325, $P = 0.0001$). Plants in managed populations produced significantly more flowers, had more branches and leaves, and a greater fruit-set than plants in unmanaged populations (Table 1 and Fig. 1). Plants grew taller in unmanaged populations (Table 1 and Fig. 1).

Significant overall differences were found in

Table 1. Effects of management and among population variation in the performance of *M. cristatum*.

	Source	df	*F*	*P*
Stem length	Management	1	50.99	0.0001
	Population(Management)	16	18.65	0.0001
Number of leaf pairs	Management	1	5.34	0.0215
	Population(Management)	16	19.23	0.0001
Number of flowering branches	Management	1	0.76	0.3843
	Population(Management)	16	3.58	0.0001
Total number of branches	Management	1	36.02	0.0001
	Population(Management)	16	10.27	0.0001
Number of flowers	Management	1	52.00	0.0001
	Population(Management)	16	16.51	0.0001
Fruit-set	Management	1	11.57	0.0008
	Population(Management)	16	27.07	0.0001

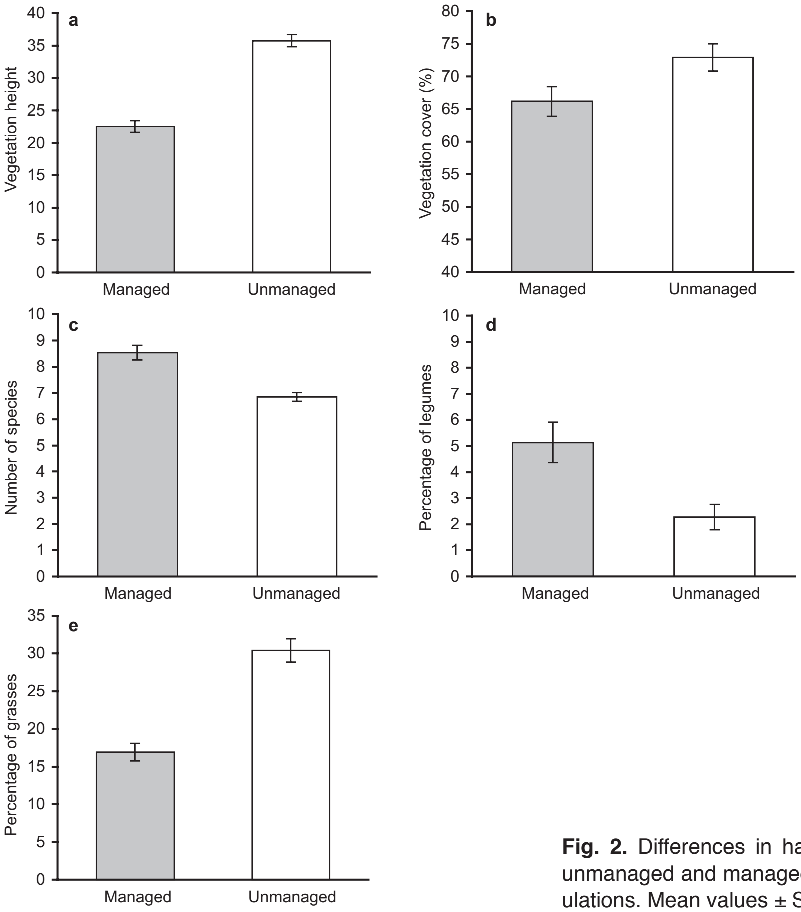

Fig. 2. Differences in habitat characteristics between unmanaged and managed *Melampyrum cristatum* populations. Mean values ± SE are presented.

habitat structure of managed and unmanaged *M. cristatum* populations (Roy's Greatest Root: $F = 3.38$, ndf = 5, ddf = 9, $P = 0.0540$), although significant variation was also found among managed and unmanaged populations (Roy's Greatest Root: $F = 35.43$, ndf = 13, ddf = 279, $P = 0.0001$). Species richness and the proportion of legumes were larger at managed sites (Table 2 and Fig. 2), whereas vegetation was taller and the mean cover of vegetation greater at unmanaged sites where also grasses were more dominant than in managed sites (Table 2 and Fig. 2).

Table 2. Effects of management and among population variation in the habitat characteristics of the *M. cristatum* sites.

	Source	df	*F*	*p*
Vegetation height	Management	1	307.09	0.0001
	Population(Management)	13	16.92	0.0001
Number of species	Management	1	22.35	0.0001
	Population(Management)	13	29.89	0.0001
Vegetation cover	Management	1	32.82	0.0001
	Population(Management)	13	13.44	0.0001
Percentage of grasses	Management	1	77.24	0.0001
	Population(Management)	13	10.81	0.0001
Percentage of legumes	Management	1	7.51	0.0065
	Population(Management)	13	15.52	0.0001

Plant performance and habitat structure varied overall also among the examined *M. arvense* populations (Roy's Greatest Root: F = 8.11, ndf = 11, ddf = 99, P = 0.0001; and F = 17.36, ndf = 12, ddf = 213, P = 0.0001, respectively). Significant among-population differences were found in plant height (F =3.08, df = 11, P = 0.0014), the number of flowering branches (F = 3.17, df = 11, P = 0.001), the number of flowers (F = 2.46, df = 11, P = 0.0091), seed mass (F = 4.30, df = 11, P = 0.0001) and the number of seeds produced (F = 2.88, df = 11, P = 0.0025). No significant differences were found in the number of leaf pairs (F = 0.46, df = 11, P = 0.9245), the total number of branches (F = 0.67, df = 11, P = 0.7620) or in fruit-set (F = 1.08, df = 11, P = 0.3874). The mean vegetation height and cover, the number of species and the proportion of legumes also varied significantly among the *M. arvense* populations (F = 2.41, df = 12, P = 0.0059; F = 2.63, df = 12, P = 0.0027; F = 16.97, df = 12, P = 0.0001; F = 3.31, df = 12, P = 0.0002, respectively). No significant among-population differences were found in the proportion of grasses (F = 0.89, df = 12, P = 0.5560).

Habitat characteristics and population size

Although managed populations were found to be larger in terms of number of flowering individuals, none of the examined habitat characteristics were significantly associated with population size of *M. cristatum* (data not shown). A positive association was found between *M. arvense* population size and the mean height of the vegetation ($y = 0.65\ (\pm\ 0.85) + 0.21\ (\pm\ 0.06) \times$ vegetation height, df = 1, F = 14.18, P = 0.0027, Adj. R^2 = 0.50). The other habitat characteristics were not significantly associated with population size of *M. arvense* (data not shown).

Habitat characteristics, population size and hemiparasite performance

When considered together with habitat quality, population size was positively associated with the number of flowering branches in *M. arvense* (Table 3). Moreover, vegetation height was positively associated with the number of branches and seed mass, and vegetation cover negatively associated with flower production of *M. arvense* (Table 3). The average fruit set of *M. arvense* increased with increasing mean number of surrounding species. Finally, the mean proportion of grasses in the surrounding vegetation was negatively associated with the number of branches but positively with the number of flowers in (Table 3).

In general, population size was positively associated with the total number of branches, but negatively with stem length and the number of flowers in *M. cristatum* (Table 4). Individuals produced on average significantly more flowers, and leaves, and grew taller in *M. cristatum* population with higher vegetation as indicated by the significant positive associations between vegetation height and these plant traits (Table 4). Moreover, vegetation cover and the mean proportion of grasses in the surrounding vegetation were positively associated with plant height (Table 4). The proportion of legumes in the surrounding vegetation was, in turn, positively associated with the average total number

Table 3. Effects of population size and habitat characteristics on the performance of *Melampyrum arvense*. Significant estimates of regression slopes (± SE) presented in the table.

	Variable	df	Estimate	SE	t	p	Adj. R^2
Total branches	Vegetation height	1	0.085	0.027	3.10	0.0112	0.53
	Grasses (%)	1	0.280	0.090	3.10	0.0113	
Flowering branches	Log population size	1	0.261	0.094	2.77	0.0269	0.34
Flowers	Vegetation cover (%)	1	–0.480	0.138	–3.47	0.0061	0.57
	Grasses (%)	1	0.820	0.372	2.20	0.0522	
Fruit set	Number of species	1	0.679	0.138	4.94	0.0004	0.66
Seed mass	Vegetation height	1	0.419	0.094	4.46	0.0010	0.61

Table 4. ANCOVA summary of effects of habitat characteristics and population size on *Melampyrum cristatum* performance in managed and unmanaged populations. The + and – denote the direction of significant main effects. Directions for significant interactions are illustrated in Fig. 3.

	Source of variation	df	*F*	*p*	
Stem length	Management	1	1.35	0.3093	
	Log population size	1	21.25	0.0100	–
	Vegetation height	1	28.51	0.0155	+
	Vegetation cover (%)	1	16.38	0.0059	+
	Grasses (%)	1	22.37	0.0091	+
	Legumes (%)	1	49.93	0.0145	
	Number of species	1	17.08	0.0021	
	Management × Log population size	1	17.09	0.0228	
	Management × Legumes (%)	1	12.95	0.0144	
	Management × Number of Species	1	25.86	0.0071	
	Error	4			
Leaf pairs	Management	1	18.41	0.0078	
	Log population size	1	1.07	0.3481	
	Vegetation height	1	6.93	0.0464	+
	Vegetation cover (%)	1	2.04	0.2124	
	Grasses (%)	1	0.01	0.9431	
	Legumes (%)	1	0.84	0.4015	
	Number of species	1	9.94	0.0253	
	Management × Legumes (%)	1	10.62	0.0225	
	Management × Number of Species	1	32.09	0.0024	
	Error	5			
Total branches	Management	1	1.36	0.2959	
	Log population size	1	14.22	0.0130	+
	Vegetation height	1	0.54	0.4973	
	Vegetation cover (%)	1	0.42	0.5471	
	Grasses (%)	1	0.65	0.4570	
	Legumes (%)	1	52.02	0.0008	+
	Number of species	1	0.47	0.5225	
	Management × Vegetation height	1	34.31	0.0021	
	Management × Number of Species	1	62.71	0.0005	
	Error	5			
Flowering branches	Management	1	0.17	0.6972	
	Log population size	1	0.04	0.8550	
	Vegetation height	1	1.74	0.2445	
	Vegetation cover (%)	1	17.24	0.0089	
	Grasses (%)	1	5.40	0.0677	
	Legumes (%)	1	8.18	0.0354	–
	Number of species	1	11.40	0.0198	–
	Management × Vegetation height	1	6.01	0.0597	
	Management × Vegetation cover (%)	1	9.50	0.0274	
	Error	5			
Flowers	Management	1	113.41	0.0004	
	Log population size	1	301.45	0.0001	–
	Vegetation height	1	189.60	0.0002	+
	Vegetation cover (%)	1	657.85	0.0001	
	Grasses (%)	1	45.62	0.0025	
	Legumes (%)	1	262.81	0.0001	+
	Number of species	1	23.13	0.0086	
	Management × Vegetation cover (%)	1	250.14	0.0001	
	Management × Grasses (%)	1	13.89	0.0204	
	Management × Number of Species	1	165.13	0.0002	
	Error	4			

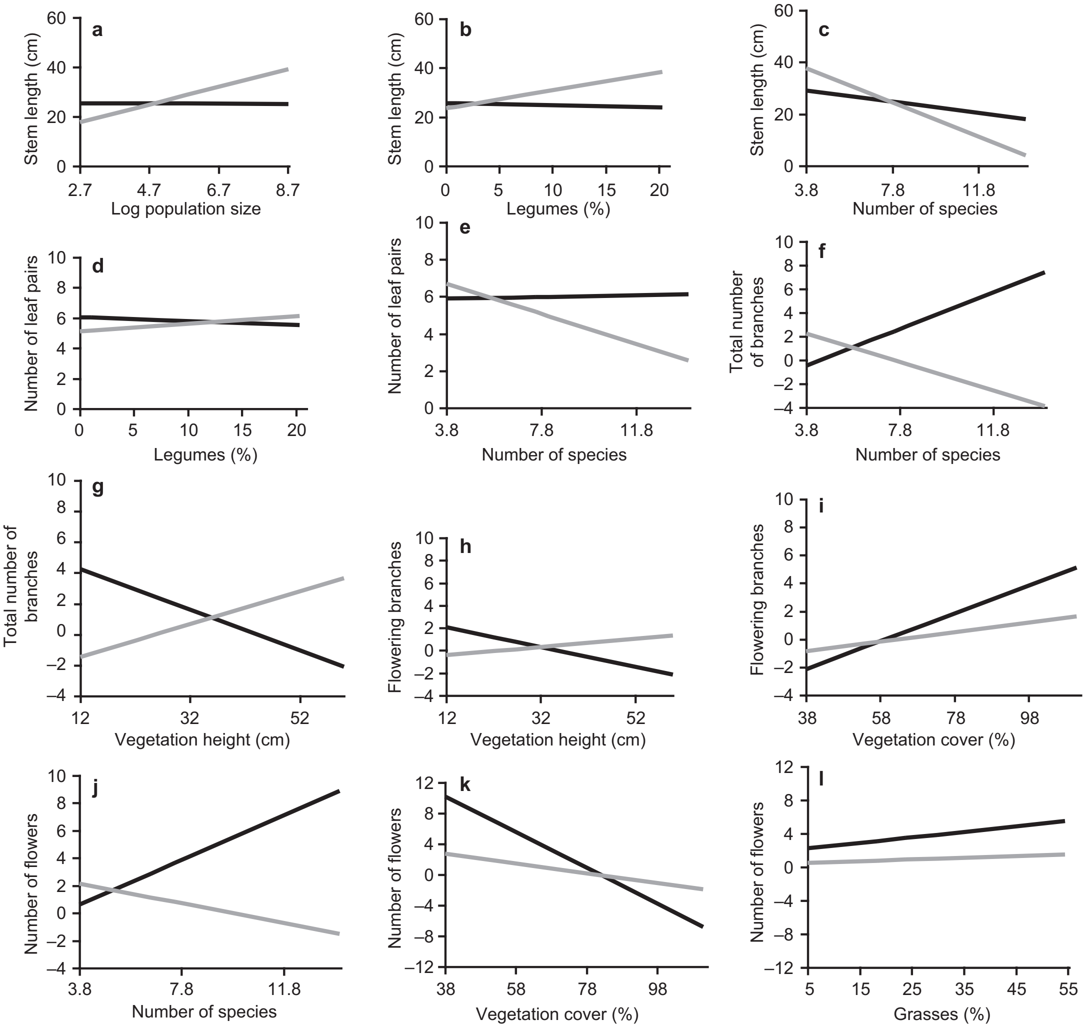

Fig. 3. Associations of habitat characteristics on *Melampyrum cristatum* performance in managed and unmanaged populations. Covariate adjusted LS-means for managed (black line) and unmanaged (grey line) populations at different levels (minimum, 25%, 50%, 75%, and maximum) of each of the continuous variables that interacted significantly with management.

of branches and number of flowers produced, but negatively with the number of flowering branches (Table 4). These results demonstrate how population size and some of the habitat characteristics influenced the performance of *M. cristatum* irrespective of whether the populations were managed or not. By contrast, as indicated by significant interactions between management (managed or unmanaged) and population size or the habitat characteristics, these factors influenced *M. cristatum* performance differently depending on management (Table 4 and Fig. 3). Stem length was positively associated with the size of unmanaged populations, whereas stem length was independent of the size of managed populations (Table 4 and Fig. 3). The proportion of legumes in the surrounding vegetation was positively associated and the total number of species negatively associated with stem length and number of leaf pairs in unmanaged populations, whereas legumes or number of species had no effect on plant height or number of leafs in managed populations (Table 4 and Fig. 3). The total number of branches increased with increasing number of species for managed populations, but decreased for unmanaged populations (Table

4 and Fig. 3). Vegetation height was positively associated with total number of branches for unmanaged populations, but negatively so for managed populations (Table 4 and Fig. 3). Moreover, the number of flowering branches increased with increasing vegetation cover for managed populations, whereas for unmanaged populations vegetation cover had no significant impact on the number of flowering branches (Table 4 and Fig. 3). Finally, the number of flowers produced increased with the number of species and proportion of grasses, but decreased with vegetation cover in managed populations (Table 4 and Fig. 3). By contrast, number of flowers tended to decrease with increasing number of species and was independent of vegetation cover and proportion of grasses in unmanaged populations (Table 4 and Fig. 3).

Discussion

In general, the results suggest that habitat quality has a strong impact on the performance of the two hemiparasites, and that fitness can be further reduced in small populations due to poor habitat quality. However, habitat quality and population size together influenced the performance of *Melampyrum cristatum*: the effects were diverse ranging from positive to negative. By contrast, variation in performance between *M. arvense* populations seems to arise mainly due to differences in habitat quality. The relatively small size of the examined *M. arvense* populations could explain the lack of significant population size effects on the performance of this hemiparasite. Fitness can be reduced in small populations due to reduced genetic diversity, mutation accumulation, increased inbreeding, and Allee effects (Young *et al*. 1996). Reduced fitness and genetic variation in small plant populations is indeed known to be common (Jennersten & Nilsson 1993, Fritz & Nilsson 1994, Ågren 1996, Oostermeijer *et al*. 1998, Fischer & Matthies 1998, Kéry *et al*. 2000, Leimu *et al*. 2006). However, the actual impact of small population size and associated changes in habitat quality *per se* and their relative importance in determining population viability and plant performance is less well studied (but *see* Vergeer *et al*. 2003). Moreover, the relative importance of the two is likely to differ between autotrophic plants and hemiparasitic plants. Because of their dependence on other plant species, hemiparasites can be expected to be more sensitive to changes in habitat quality than autotrophic plants. The results of this study further suggest that reduced habitat quality is the main reason for reduced performance of the two hemiparasites resulting in reduced population sizes, and ultimately reduced viability.

High and dense vegetation can increase competition for space and light, and increase the allocation of resources into growth instead of reproduction. In this study, high surrounding vegetation resulted in internode elongation and leaf biomass in *M. cristatum*, but had no effect on reproductive output. By contrast, vegetation height had positive overall impact on branching and seed mass of *M. arvense*. Vegetation cover, which likely indicates overall vegetation density, had negative impact on the reproductive output of both hemiparasites. It has been suggested that in communities with dense vegetation hemiparasites may be better able to connect to suitable hosts and to several hosts simultaneously (Gibson & Watkinson 1989, Joshi *et al*. 2000, Press & Phoenix 2005). Indeed, a greater biomass and density of the surrounding vegetation increased the fecundity of the hemiparasitic *Rhinathus* species (Van Hulst *et al*. 1987). However, this association was non-linear, indicating that increased vegetation biomass and density increases the effectiveness of root parasitism, but after reaching a threshold a further increase in the biomass and density of the vegetation the hemiparasites are likely to be outcompeted for light (Van Hulst *et al*. 1987). Moreover, the effects of vegetation density are likely to depend on the composition and diversity of the species in the community, rather than density *per se*.

Changes in species diversity may affect individual plant species by influencing competition, resource availability, plant-pollinator interactions or plant-herbivore interactions. The diversity of plant community may influence the performance of parasitic plants (Joshi *et al*. 2000). In the current study, species richness had a positive impact on reproductive success of *M. arvense*, whereas the overall effects of number of species on the performance of *M. cristatum* varied from positive to negative. In an earlier experimental study, the performance of *M. arvense* did not differ between individuals grown with one host species as compared with those with two species (Mathies 1996). However, another study on natural populations of semi-natural grasslands found that the presence of hemiparasitic *Rhinanthus* species increased with species richness (Pywell *et al*. 2004). The reason why no clear effects of species richness were found could be because the direction of the effects of species richness in the community may depend on the quality of the species as hosts, their competitive abilities or on other associated habitat characteristics.

In addition to the overall species diversity, the abundance of different functional host-plant groups may influence hemiparasite performance. Legumes are preferred hosts, and may increase the growth and fitness of the attacking parasites (Govier *et al*. 1967, Seel & Press 1993). Here, the abundance of the different functional groups had relatively minor effects on the performance of the two *Melampyrum* species. On average, higher proportion of legumes in the community increased the height, total number of branches and number of flowers in *M. cristatum* individuals, whereas the number of flowering branches was decreased. Moreover, stem length of *M. cristatum* increased and flowering of *M. arvense* was reduced in grass-dominated communities. Host selectivity and host-dependent variation in parasite performance can vary within and among populations, and can be influenced by the composition of the species in the community and their relative abundance. Furthermore, the parasitic plants may adapt to use the most abundant hosts in the community (Gibson & Watkinson 1991), and thus parasite performance might not vary between populations with contrasting host communities. Since the current study was on endangered plants, it was not possible to examine which species were infected and used as hosts, and thus to accurately determine how well the community diversity represents the actual host diversity.

Managing habitats by grazing or mowing can increase plant performance and population viability if these practices increase habitat quality and suitability for the given species. Although intensive natural or simulated herbivory often has a negative impact on the plant performance, the effects of mowing or grazing are not necessarily negative if plants are able to compensate or even over-compensate the damage (e.g. Lennartsson *et al*. 1997, Juenger & Bergelsson 2000). In general, management had a positive impact on *M. cristatum*, but the effect depended on the intensity of mowing or grazing. In two of the managed *M. cristatum* populations, grazing was so intensive that the majority of the individuals was completely eaten and produced no seeds. In a previous study on other *Melampyrum* species (*M. pratense* and *M. sylvaticum*) experimental defoliation decreased growth and seed set (Lehtilä & Syrjänen 1995). Main stem clipping, on the other hand, resulted in a higher number of branches and greater fruit and seed production in *M. sylvaticum*, whereas the responses were opposite in *M. pratense* (Lehtilä & Syrjänen 1995). The greater observed performance and larger population sizes at managed sites, suggest that the positive effect of management on *M. cristatum* is due to improved habitat quality. This is further supported by the observed differences in the effects of the habitat characteristics on *M. cristatum* performance between managed and unmanaged populations (Table 4 and Fig. 3). Increase in number of species in managed populations translates into increased number of branches and flowers in these populations. By contrast, number of surrounding species was negatively associated with stem length and number of flowers in unmanaged populations where the overall number of species was lower. This indicates that in addition to influencing the actual number of species, management may affect the identity of the species and the composition of the community, which likely influences hemiparasite performance. The effects of the different functional groups on *M. cristatum* performance varied to some degree between managed and unmanaged populations: stem length and the number of leafs increased with increasing proportion of legumes in unmanaged populations whereas in managed populations, where the proportion of legumes was in general higher, an increase in the proportion of legumes had no effect on *M. cristatum* performance. Finally, the variation in performance and habitat traits among managed and unmanaged

M. cristatum populations, and the fact that both habitat quality and population size influenced performance, suggests that in addition to habitat quality the genetic structure of the populations is likely to play a role. This is further supported by the finding that population size was not clearly associated with the individual habitat characteristics. Even though the two paradigms dealing with biodiversity threats also provide different solutions to solve the problems, they do not deny the importance of both habitat quality and population size. The "habitat quality" paradigm highlights the importance of preserving high quality habitats and restoring those that have been deteriorated (Ouborg *et al*. 2006). Within the "conservation genetics" paradigm the solution lies, in turn, in population reinforcement and/or in reduction of isolation (Ouborg *et al*. 2006). However, even if habitat quality is optimal, populations can go extinct if they are small and isolated and have low genetic diversity. Moreover, small populations may lack the ability to adapt to "new" habitats following restoration or management practises, although the quality of the habitat is improved.

To conclude, the findings of this study suggest that degradation of suitable habitats have likely decreased the performance of the two endangered hemiparasites, resulting in reduced population sizes, and that these species are also likely to be threatened by the negative genetic and ecological consequences of small population size. This highlights the importance of integrating the "habitat quality" and "conservation genetics" paradigms when trying to understand the threats to viability of species and/or populations. This can be particularly important for species interactions where the quality of the habitat plays a central role, such as plant–hemiparasite interactions. Management and restoration of habitats seem to be the key solution to sustain or increase the viability of populations of these hemiparasites, but the timing and intensity of the management should be carefully considered. Nonetheless, small and isolated populations are likely to be more prone to extinction due to environmental and demographic stochasticity. Thus, to ensure the long-term viability, the genetic variation and adaptive potential of the populations should not be neglected.

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