Habitat fragmentation and adaptation: a reciprocal replant–transplant experiment among 15 populations of *Lychnis flos-cuculi*

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Summary

1. Habitat fragmentation and variation in habitat quality can both affect plant performance, but their effects have rarely been studied in combination. We thus examined plant performance in response to differences in habitat quality for a species subject to habitat fragmentation, the common but declining perennial herb *Lychnis flos-cuculi*.

2. We reciprocally transplanted plants between 15 fen grasslands in north-east Switzerland and recorded plant performance for 4 years.

3. Variation between the 15 target sites was the most important factor and affected all measures of plant performance in all years. This demonstrates the importance of plastic responses to habitat quality for plant performance.

4. Plants from smaller populations produced fewer rosettes than plants from larger populations in the first year of the replant–transplant experiment.

5. Plant performance decreased with increasing ecological difference between grassland of origin and target grassland, indicating adaptation to ecological conditions. In contrast, plant performance was not influenced by microsatellite distance and hardly by geographic distance between grassland of origin and target grassland.

6. Plants originating from larger populations were better able to cope with larger ecological differences between transplantation site and site of origin.

7. Synthesis: In addition to the direct effects of target grasslands, both habitat fragmentation, through reduced population size, and adaptation to habitats of different quality, contributed to the performance of *L. flos-cuculi*. This underlines that habitat fragmentation also affects species that are still common. Moreover, it suggests that restoration projects involving *L. flos-cuculi* should use plant material from large populations living in habitats similar to the restoration site. Finally, our results bring into question whether plants in small habitat remnants will be able to cope with future environmental change.

Key-words: allee effect, Caryophyllaceae, common species, environmental change, habitat quality, local adaptation, *Lychnis flos-cuculi*, population size, reciprocal transplantation experiment, *Silene flos-cuculi*

Introduction

Many formerly common species have been forced into smaller and more isolated habitat fragments due to land use changes (Saunders et al. 1991; Jennersten et al. 1992; Hooftman 2001; Lienert et al. 2002; Hooftman et al. 2003). Since habitat remnants are generally reduced in size, fragmented populations also frequently have fewer individuals compared to before fragmentation. Population genetic theory predicts that such populations will experience genetic erosion due to random genetic drift and inbreeding (Ellstrand & Elam 1993), and that isolation may prevent the alleviation of these effects by gene flow between populations (Barrett & Kohn 1991). Combined with inbreeding depression, decreased genetic variation

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may lead to reduced fitness of plants from smaller populations, that is, to an Allee effect (Stephens et al. 1999, Leimu et al. 2006).

Different plant populations experience different environmental conditions. Clearly, plants are likely to respond to environmental differences between habitats by phenotypic plasticity, where plant performance in different environments is due to a reaction norm. Moreover, differences in environmental conditions between populations may give rise to local adaptation. Plants are considered to be locally adapted if local plants perform better than foreign plants in reciprocal transplantation experiments (Kawecki & Ebert 2004). However, the degree to which such home-away differences are to be expected when studying pairs of populations depends on the actual environments and can also be masked by the founder effect and genetic drift (Jakobsson & Dinnetz 2005). Moreover, even if plants of different populations are adapted to their local environments, this may not lead to a significant overall home-away difference if the environments are similar for some pairs of populations but not for others in the same experiment. Therefore, examining the relationship of ecological differences between site of origin and target site and plant performance in a transplant experiment may be more instructive than simply examining a home-away contrast (Montalvo & Ellstrand 2000, Raabova et al. 2007). In some transplant studies between different countries geographical distance has been used as a proxy for climatic differences (Joshi et al. 2001, Becker et al. 2006). However, this is not appropriate in cases of transplant experiments between more near-by sites sharing the same climate but differing in other ecological conditions.

Clearly, plant performance in populations of different habitat quality depends on the interplay of genetic architecture of populations with interactions of genotypes with the environment (Schlichting & Pigliucci 1998) and adaptation to local conditions (Linhart & Grant 1996). It has been suggested that small genetically depauperate populations may be less able to adapt to changing conditions because of their generally reduced genetic variation (Willi et al. 2006). Therefore, plant performance in a changing landscape is best understood when adaptive responses to different habitat quality and responses to habitat fragmentation are considered simultaneously. However, to date these issues have scarcely been addressed in combination.

In Switzerland, wetland habitats such as fen grasslands have undergone large-scale destruction, fragmentation, and deterioration during the last century through land-use intensification. This includes high input of nutrients, abandonment of traditional management practices, and changes in ground water tables (Hintermann 1992). Our study species Lycnis flos-cuculi L. (Caryophyllaceae) is common in wet meadows (Landolt 1977). However, due to the decrease of wetland habitats, the species is declining, and its distribution is increasingly fragmented. The issue of local adaptation is also of applied relevance in L. flos-cuculi, whose seeds are used in seed mixtures for restoration projects in many cantons in Switzerland (Lehmann et al. 2000).

Genetic differences between populations can be demonstrated through greenhouse or common garden experiments. However, such experiments do not directly address the potential adaptive nature of such genetic variation (Rice & Mack 1991). Reciprocal replant–transplant experiments in natural populations allow for a more realistic assessment of genetic and environmental effects on plant performances. They also consider biotic factors such as competition or herbivory, which might be important for the development of local adaptations (Antonovics & Primack 1982). Therefore, reciprocal replant–transplant experiments have been used to assess the contributions of environmental and genetic variation (reviewed by Bradshaw 1984; Venable 1984; Linhart & Grant 1996; Van Andel 1998). Quantitative trait differences between populations have been documented for important features of plant structure and function (e.g. Waser & Price 1985; Sork et al. 1993; Miller & Fowler 1994; Biere 1995; Galloway & Fenster 2000; Joshi et al. 2001). However, because in most cases very few populations were studied, effects of population and habitat characteristics could not be tested at all, or not with sufficient statistical power (Kawecki & Ebert 2004).

To examine the influence of population and habitat characteristics on local adaptation, many populations need to be involved. Therefore, we performed a reciprocal replant–transplant experiment among 15 fen-grassland populations of L. flos-cuculi in north-east Switzerland differing in population size and abiotic characteristics. In each field site, we monitored transplanted plants of L. flos-cuculi surrounded by natural vegetation for four years. We ask the following specific questions: (i) Across all transplantation sites, does plant performance decrease with smaller size of the population of origin? (ii) Does plant performance differ between the different target sites? (iii) Does plant performance decrease with increasing geographic, genetic and ecological distances between populations? (iv) Are plants from larger populations better able to cope with the new conditions they encounter in the target site?

Methods

Study species

Lycnis flos-cuculi L. (Caryophyllaceae) is widespread in central Europe (Hulten & Fries 1986). The species is found in sunny, nutrient-rich and moist-to-wet grasslands from the plains to the montane level. In Switzerland, it occurs naturally in moist-to-wet hay meadows and in fen grasslands (Welten & Sutter 1982). Because of human activities, these habitats have been severely disturbed and fragmented in Switzerland during the last 150 years. As a consequence, populations of L. flos-cuculi have recently declined in size and number, which make them a good system to study habitat fragmentation.

Lycnis flos-cuculi is a perennial, rosette-forming herb. Seeds are able to germinate immediately after dissemination in autumn or spring (Biere 1991). During the first growing season, a primary rosette and usually several side rosettes are formed. One or more rosettes become reproductive and produce 20–90-cm tall flowering stalks. The inflorescence is a dichasium consisting of 20–50 flowers. The protandrous flowers are predominantly outcrossed, but selfing can occur. Mature fruit capsules split open at the top, and up to 200 seeds are dispersed by vibrations of the stiffened stalk (Hegi 1979).
S. mown annually in September and not supplied with fertilizer. From 1.2 to 68.9 km. All populations were situated in fen meadows of 850–1350 m (Table 1). Distances between populations ranged populations were situated in the north-east of Switzerland at altitudes 2005b). Thus we had a wide range of population sizes to evaluate effects of habitat fragmentation on plant performance. The 15 species of the Swiss flora with an indicator value for soil moisture, soil pH, soil nutrient level, soil humus content, soil aeration, soil acidity, light intensity, temperature, continentality of climate, and acidity (+ or –) and life form. A five-part scale from 1 (low) to 5 (high) is used except for acidity (+ or –) and life form. For this study we consider the indicator values describing the ecological gradients most relevant for Lychnis, that is, the light intensity (L), soil moisture (F), nutrient content (N) and temperature (T) indicator values (thereafter indicated only by their names, e.g. ‘light intensity’ for ‘light intensity indicator value’). Mean indicator values were not significantly correlated with population size cannot be due to confounding effects of habitat quality. To quantify pair-wise ecological differences between habitats we assessed absolute differences between habitat means of the F, N, L and T indicator values. Differences between pairs of populations ranged from 2.95 to 4.27 for F, 1.67 to 3.23 for N, 1.88 to 3.02 for L and 2.17 to 2.98 for T. Geographic and neutral genetic distances We described pair-wise distances between the 15 populations for geographic distance and genetic distance. We calculated geographic distances from our field recordings of site coordinates with a Global Positioning System (GPS, Garmin®, Olathe, KS). We obtained genetic distances between pairs of populations as $F_{ST}$ from a previous study of 8–18 plants per population with seven microsatellite markers (Galeuchet et al. 2005a). Pair-wise $F_{ST}$ was between 0.001 and 0.090, and the average $F_{ST}$ was low (0.022) but significant.

Habitat characteristics and ecological distances between habitats To characterise habitats we surveyed the fen vegetation of each study habitat in July 2002. We recorded the identity and ground cover of all higher plant species present in a 2 m$^2$-plot situated at a random position within the Lychnis population. We used species composition weighted by species abundance to calculate mean ecological indicator values after Landolt (1977). Landolt rated 3364 vascular plant species of the Swiss flora with an indicator value for soil moisture, soil pH, soil nutrient level, soil humus content, soil aeration, soil acidity, light intensity, temperature, continentality of climate, and life-form. A five-part scale from 1 (low) to 5 (high) is used except for acidity (+ or –) and life form. For this study we consider the indicator values describing the ecological gradients most relevant for Lychnis, as shown in Table 1. A five-part scale from 1 (low) to 5 (high) is used except for acidity (+ or –) and life form. For this study we consider the indicator values describing the ecological gradients most relevant for Lychnis, as shown in Table 1. Several small herbivores feed on L. flos-cuculi. Vegetative plant parts are frequently attacked by snails, leaf miners and larvae of Lepidoptera (Wirooks & Plassmann 1999).

**Table 1.** Characteristics of the 15 study sites and populations of *Lychnis flos-cuculi*

<table>
<thead>
<tr>
<th>Site</th>
<th>Number of flowering stem</th>
<th>Population size</th>
<th>Coordinates</th>
<th>Mean indicator value for</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Light (L)</td>
</tr>
<tr>
<td>Bühler (AR)</td>
<td>40</td>
<td>Small</td>
<td>940</td>
<td>751 865</td>
</tr>
<tr>
<td>Seilersee (SZ)</td>
<td>157</td>
<td>Small</td>
<td>1330</td>
<td>697 355</td>
</tr>
<tr>
<td>Gäbris Wald (AR)</td>
<td>192</td>
<td>Small</td>
<td>1175</td>
<td>753 430</td>
</tr>
<tr>
<td>Höchi (SG)</td>
<td>230</td>
<td>Small</td>
<td>970</td>
<td>725 865</td>
</tr>
<tr>
<td>Allmendingwald (SG)</td>
<td>330</td>
<td>Small</td>
<td>1080</td>
<td>732 220</td>
</tr>
<tr>
<td>Schlänggen (SG)</td>
<td>500</td>
<td>Small</td>
<td>900</td>
<td>705 586</td>
</tr>
<tr>
<td>Hasenried (SG)</td>
<td>800</td>
<td>Small</td>
<td>1171</td>
<td>740 520</td>
</tr>
<tr>
<td>Sulzei (SZ)</td>
<td>2744</td>
<td>Large</td>
<td>960</td>
<td>703 400</td>
</tr>
<tr>
<td>Bannholz (SZ)</td>
<td>11893</td>
<td>Large</td>
<td>950</td>
<td>704 130</td>
</tr>
<tr>
<td>Stein (SG)</td>
<td>14688</td>
<td>Large</td>
<td>950</td>
<td>733 655</td>
</tr>
<tr>
<td>Strandbad (SZ)</td>
<td>16502</td>
<td>Large</td>
<td>900</td>
<td>700 950</td>
</tr>
<tr>
<td>Wideralp (SG)</td>
<td>18046</td>
<td>Large</td>
<td>1350</td>
<td>741 465</td>
</tr>
<tr>
<td>Feusisberg (SZ)</td>
<td>19047</td>
<td>Large</td>
<td>875</td>
<td>697 570</td>
</tr>
<tr>
<td>Feldmoos (SG)</td>
<td>35000</td>
<td>Large</td>
<td>890</td>
<td>731 175</td>
</tr>
<tr>
<td>Munzenriet (SG)</td>
<td>51000</td>
<td>Large</td>
<td>1130</td>
<td>744 845</td>
</tr>
</tbody>
</table>

Municipality (Swiss canton in parentheses), name of fen, coordinates as per Swiss topographical maps, altitude, population size and mean indicator values are given. Populations were the seven smallest (S) and eight largest (L) of a larger set used for other demographic and genetic studies. Mean indicator values after Landolt (1977) are based on vegetation records taken in 2002 as explained in methods.
We transplanted the 1350 plantlets to the field in May 2001. At each of the 15 sites we planted one offspring of each of six families per population of origin. We established six 1 m$^2$-plots within a 2 × 3 m area marked with metal tubes. In each 1 m$^2$-plot, we planted 15 plantlets at 16 planting positions in four rows, each with four plants per row separated by a 20 cm interval. We marked all transplanted plantlets with plastic rings. Per 1 m$^2$-plot, the 15 plantlets represented one seed family of each of the 15 populations. As eight of the 90 families had fewer than 15 plantlets, we complemented the design with a few offspring of four more families of the appropriate populations of origin.

MEASUREMENTS

Plant performance was monitored during four years. In August 2001, and July 2002, 2003 and 2004, that is, 3, 14, 26 and 38 months after transplantation, we recorded plant survival and number of rosettes per plant. Also, we scored the presence or absence of damage by herbivores as any eaten or mined portion of the leaves or stems, because biotic factors such as herbivory might be important for local adaptation. Because of plant mortality, we measured 1309 plants in 2001, 1138 in 2002, 623 in 2003, and 206 in 2004. Therefore our analyses lost statistical power over time.

DATA ANALYSIS

We used mixed-model analyses of covariance (ANCOVA) for the normally distributed variables number of rosettes, and logistic regression for the binomially distributed variables survival from one year to the other, and presence/absence of herbivory. For significance tests in the mixed-model logistic regression we used ratios of mean deviance changes, quasi-F (Francis et al. 1993). We used the statistical software packages jmp (Version 4.0.1, SAS Institute Inc. 2000) and R (version 2.4.1).

The mixed model contained tests for plastic plant responses to the target population, for size of population of origin (Table 1), for genetic differentiation between populations of origin and between maternal families within populations of origin. Moreover, the model comprised tests for effects of geographic and genetic (microsatellite-$F_{ST}$) distances between populations. Furthermore, it comprised tests for effects of absolute differences between populations in four ecological conditions (moisture, nutrient, light and temperature) and their interaction with the size of the population of origin. The latter served to test for the potential effect of population size on the capacity of plants to cope with new environments. The interaction between population of origin and target population served as error term in the tests of effects of pair-wise population distances and their interactions with population size (see Table 2 for the full model, error terms and level of significance).

Out of 180 analyses 30 tests (17%) were significant at least at the 5% level (compared to nine expected by chance alone), 19 of these at least at the 1% level (compared to 1.8 expected by chance alone), and 13 of these at the 0.1% level (compared to 0.18 expected by chance alone). We did not apply the Bonferroni correction, because it is considered as overly conservative (Moran 2003; Garcia 2004).

For full summaries see Appendix S1. The model contains effects of the target site, size and identity of population of origin, maternal plant, and geographic, microsatellite $F_{ST}$, and ecological distances between populations. Population size is treated as a continuous variable and Log-transformed. ‘I’, ‘II’, ‘III’ and ‘IV’ denote the measurements 3, 14, 26, and 38 months after transplantation. We calculated delta | D | values as absolutes differences between means indicator values at target site and site of origin (light intensity (L), soil moisture (F), nutrient content (N), and temperature (T) indicator values). $T_{pop}$ = target population, $Pop_{o}$ = population of origin, $PS = size$ of population of origin, $ms = mean$ (for number of rosettes) or mean deviance (for survival and herbivory). $P$ values: $< 0.1; *$ $< 0.05; **$ $< 0.01; ***$ $< 0.001.$

Results

EFFECTS OF CHARACTERISTICS OF POPULATIONS OF ORIGIN OF TRANSPLANTS

Across all transplantation sites we tested whether plant performance decreases with smaller size of the population of
origin. By August 2001, plants originating from larger field populations had grown more rosettes \( (F_{1,11} = 4.9, P < 0.05) \) in the reciprocal re-plant–transplant experiment among 15 populations of *Lychnis flos-cuculi*. Significance levels were obtained with ANCOVA (see Appendix S1b). Symbols represent means of 90 plants from each of the 15 populations of origin.

**EFFECTS OF HABITAT QUALITY OF TARGET GRASSLANDS**

Target grasslands had a large effect on all measures of plant performance during all four years of the study (12 tests significant out of the 12 in Table 2). Therefore, differences between target grasslands were the single factor explaining most variation in plant performance in our study.

**EFFECTS OF GEOGRAPHIC, GENETIC AND ECOLOGICAL DIFFERENCES BETWEEN TARGET GRASSLANDS AND GRASSLANDS OF ORIGIN**

We tested whether plant performance decreased with increasing geographic, genetic and ecological distances between populations and found that transplants between pairs of grasslands with larger geographic inter-distance grew more rosettes in

their third year \( (F_{1,14} = 4.12, P < 0.01) \), one test significant out of 12 in Table 2). Transplant performance was independent of the pair-wise microsatellite \( F_{ST} \) distances between populations for all measurements and years.

Pair-wise absolute differences in indicator values between grasslands of origin and transplant grasslands explained significant variation for several fitness traits. Transplants between sites with more different light intensity had a lower survival to the second year \( (F_{1,160} = 8.91, P < 0.01) \) and grew fewer rosettes in the first year \( (F_{1,172} = 9.53, P < 0.01) \). Larger differences in temperature between sites increased transplant survival from 2003 to 2004 \( (F_{1,160} = 4.45, P < 0.05) \), and led to fewer rosettes in the second year \( (F_{1,160} = 6.21, P < 0.05) \). Larger differences in moisture decreased the transplant survival from 2003 to 2004 \( (F_{1,160} = 3.91, P < 0.05) \). Such a reduced performance of plants transplanted to ecologically more distant sites suggests adaptation of *L. flos-cuculi* to ecological gradients, although they were not apparent for all traits and all years (five significant tests out of 48 tests for effects of ecological distances between pairs of populations in Table 2).

**INTERACTING EFFECTS OF TARGET GRASSLANDS AND GRASSLANDS OF ORIGIN**

We tested whether plants from larger populations were better able to cope with the new conditions they encountered at the target sites than plants from smaller populations. We found that a lower proportion of plants originating from large populations was affected by herbivores in the second year than of plants from small populations, if they had been transplanted between sites with larger differences in nutrient indicator values \( (F_{1,160} = 5.21, P < 0.05) \) and also in the fourth year when transplanted to sites with larger differences in light \( (F_{1,60} = 10.25, P < 0.01) \). Transplants between sites with higher differences in light intensity had increased survival from 2002 to 2003 for plants from larger populations \( (F_{172} = 4.57, P < 0.05) \). Transplants between sites with more different moisture availability had decreased survival from 2003 to 2004 for small populations but not for large populations \( (F_{1,160} = 8.49, P < 0.01) \). These results indicate effects of habitat fragmentation on adaptation to ecological characteristics and on the ability to cope with new environments, although not for all traits and all years (four tests significant out of the 48 tests for interactions of population size of origin with ecological distances between pairs of populations in Table 2). Moreover, in the fourth year differences between target grasslands in herbivory depended on the population of origin (target grassland – by – grassland of origin interaction; \( F_{1,13} = 4.18, P < 0.001; \) one test significant out of 12 test in Table 2).

**Discussion**

**EFFECTS OF PLANT ORIGIN ON PLANT PERFORMANCE**

We found significant variation among populations of origin and maternal seed families indicating a pronounced genetic

component of plant performance. In 2 out of 4 years we observed differential offspring survival, growth and herbivore damage among maternal families. Our 15-population-study extends the results of Biere (1995) who also found part of the variation in autumn rosette biomass of *L. flos-cuculi* to be genetically based.

Larger population size of origin positively affected growth of vegetative plant parts (Fig. 1). We conclude that this represents a genetically-based Allee effect (Stephens et al. 1999), as it had previously been shown for our study species in a greenhouse experiment (Galeuchet et al. 2005b). In self-compatible plants, genetic Allee effects can be due to increased inbreeding depression in smaller populations and to increased fixed genetic load in smaller populations (Willi et al. 2005). Indeed, positive relationships between population size, genetic variation, and plant fitness are the general pattern emerging from a meta-analysis of many studies of plants of different life histories (Leimu et al. 2006).
However, to our knowledge, our study is the first to show a genetic Allee effect across many experimental transplant sites, which exactly represent the sites of origin. This is important because it excludes the problem of common environment studies that the common environment may happen to be more similar to the field environments of larger than of smaller populations.

**EFFECTS OF DIFFERENCES BETWEEN TARGET GRASSLANDS AND GRASSLANDS OF PLANT ORIGIN**

The target sites differed in ecological indicator values, were situated at inter-distances between 1.2 and 68.9 km, and microsatellites indicated differentiation between them (Galeuchet et al. 2005a). Most of the variation in plant performance in our study was due to differences caused by the different target grasslands indicating that the ecological differences between the sites really affect the performance of *L. flos-cuculi*.

The generally negative effects of higher ecological distances between sites of plant origin and target site on plant performance (Fig. 2) provided evidence for adaptation to these ecological conditions. In transplant experiments plants are often considered to be locally adapted if the local plants perform better than the foreign plants (Nagy & Rice 1997, Galloway & Fenster 2000, Kawecki & Ebert 2004). Our study was, however, explicitly designed to test the extent to which ecological differences between populations affect the degree of adaptation. Therefore, we analysed plant performance in relation to the ecological distance between populations rather than testing simple home-away contrasts. In a smaller transplantation study on *L. flos-cuculi* across four sites differing in nutrient supply, Biere (1995) found interacting effects of plant origin and transplant site on reproduction and survival rather than a clear home-away pattern. In another smaller transplantation study involving six populations of *Aster amellus* plant performance was also affected by ecological distances between sites (Raabova et al. 2007).

Between plants and herbivores there may be co-adaptation, and plants may evolve defences to adapt to herbivores (Crawley 1989). However, we only found indications for adaptation of herbivores to *Lychnis* plants or of plants to herbivores for 1 year out of four, indicated by the significant interaction between the population of origin and the target population. Rather, most of the variation in the occurrence of herbivory was explained by the target sites to which the plants had been transplanted, probably linked to the presence or absence of some herbivores.

Pair-wise geographic distances between populations were not very important in our transplant experiment and influenced only one of the measured traits in 1 year. This may be linked to the scale of the experiment with a maximum inter-distance between populations of about 70 km. Several transplantation experiments involving larger distances had reported stronger evidence for distance effects (e.g. Galloway & Fenster 2000, Joshi et al. 2001, Becker et al. 2006). In our study, genetic microsatellite distances between sites did not explain fitness variation among transplants, which is expected because microsatellite differentiation between populations is considered to be selectively neutral. In a smaller recent study with *Aster amellus*, Raabova et al. (2007) also concluded that ecological distances among populations predict adaptation better than did geographic or selectively neutral genetic distance. We conclude that between-population differences in habitat quality are more important predictors of plant performance after transplantation than geographic or selectively neutral genetic distance.

**EFFECT OF HABITAT FRAGMENTATION ON PERFORMANCE IN THE TRANSPLANTING ENVIRONMENTS**

Survival and reproduction in transplant sites with different ecological conditions varied significantly between *Lychnis* plants from different maternal families (data not shown), indicating genetic variation in response to the environment. In particular, plants originating from large populations generally maintained higher performance when transplanted to different environmental conditions than plants from small populations, suggesting a better capacity to cope with environmental changes. However, we did not find evidence for stronger local adaptation of plants in larger populations, which might have been expected as a result of the combination of higher genetic variation for selection to select upon with reduced importance of genetic drift and demographic stochasticity in large populations compared with small ones (Willi et al. 2006). A 12-population transplantation study with *Carlina vulgaris* even reported that small population size and high degree of population isolation increased local adaptation (Jakobsson & Dinnetz 2005), while in a cross-European transplant study also with *C. vulgaris* the strength of adaptation was independent of population size (Becker et al. 2006). As there are too few experimental studies on the interference of habitat fragmentation with adaptive evolution we strongly advocate addressing the interacting effects of adaptive evolution and of fragmentation-induced non-adaptive evolution for more species and for more habitat types.

**Conclusion**

Differences between the target habitats had the largest effects on plant performance. In addition, across 15 transplanting sites we demonstrated a negative genetic effect of small sizes of populations of plant origin of *Lychnis flos-cuculi*, that is, a genetically-based Allee effect. Although this impact of habitat fragmentation on plant fitness was much less important than variation explained by target habitat quality, it underlines that habitat fragmentation even affects plant species that are still very common, and is likely to contribute to their decline.

Moreover, we showed that plants of the common species *L. flos-cuculi* were doing best when transplanted to grassland sites with similar ecological characteristics to their home site, while geographic distances were not very important and selectively neutral genetic distance between grasslands of origin and target played no role. This implies that ecological
similarity is a more important criterion when selecting populations for mixing plant or seed material for ecological restoration or compensation programs than molecular genetic distance or geographic distance between populations, at least at the scale of 100 km and low Fs considered here. Moreover, plant material from large populations appears better suited for use in restoration. Finally, we conclude that habitat fragmentation can compromise the ability of plants to cope with new environments, which raises the question of whether plants in small habitat remnants will be able to cope with future environmental change.

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Galech et al. (2005a) Microsatellite variation and performance of Lychnis flos-cuculi, in a fragmented landscape. Evolution and Systematics, 14, 991–1000.


Appendix S1. Full summaries of analyses of (A) survival, (B) vegetative performance and (C) percentage of plant damage by herbivores of transplanted plants of *Lychnis flos-cuculi*.

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