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Susceptibility of Common and Rare Plant Species to the Genetic Consequences of Habitat Fragmentation

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Abstract: *Small plant populations are more prone to extinction due to the loss of genetic variation through random genetic drift, increased selfing, and mating among related individuals. To date, most researchers dealing with genetic erosion in fragmented plant populations have focused on threatened or rare species. We raise the question whether common plant species are as susceptible to habitat fragmentation as rare species. We conducted a formal meta-analysis of habitat fragmentation studies that reported both population size and population genetic diversity. We estimated the overall weighted mean and variance of the correlation coefficients among four different measures of genetic diversity and plant population size. We then tested whether rarity, mating system, and plant longevity are potential moderators of the relationship between population size and genetic diversity. Mean gene diversity, percent polymorphic loci, and allelic richness across studies were positively and highly significantly correlated with population size, whereas no significant relationship was found between population size and the inbreeding coefficient. Genetic diversity of self-compatible species was less affected by decreasing population size than that of obligate outcrossing and self-compatible but mainly outcrossing species. Longevity did not affect the population genetic response to fragmentation. Our most important finding, however, was that common species were as, or more, susceptible to the population genetic consequences of habitat fragmentation than rare species, even when historically or naturally rare species were excluded from the analysis. These results are dramatic in that many more plant species than previously assumed may be vulnerable to genetic erosion and loss of genetic diversity as a result of ongoing fragmentation processes. This implies that many fragmented habitats have become unable to support plant populations that are large enough to maintain a mutation-drift balance and that occupied habitat fragments have become too isolated to allow sufficient gene flow to enable replenishment of lost alleles.*

Keywords: genetic diversity, habitat fragmentation, inbreeding, mating system, population size

Susceptibilidad de Especies de Plantas Comunes y Raras a las Consecuencias Genéticas de la Fragmentación del Hábitat

Resumen: *Las poblaciones pequeñas de plantas son más propensas a la extinción debido a la pérdida de variación genética por medio de la deriva génica aleatoria, el incremento de autogamia y la reproducción entre individuos emparentados. A la fecha, la mayoría de los investigadores que trabajan con erosión genética en poblaciones fragmentadas de plantas se han enfocado en las especies amenazadas o raras. Cuestionamos si las especies de plantas comunes son tan susceptibles a la fragmentación del hábitat como las especies raras. Realizamos un meta análisis formal de estudios de fragmentación que reportaron tanto tamaño poblacional como diversidad genética. Estimamos la media general ponderada y la varianza de los coeficientes de correlación entre cuatro medidas de diversidad genética y de tamaño poblacional de las plantas. Posteriormente probamos si la rareza, el sistema reproductivo y la longevidad de la planta son moderadores potenciales de la relación entre el tamaño poblacional y la diversidad genética. La diversidad genética promedio, el porcentaje de loci polimórficos y la riqueza alélica en los estudios tuvieron una correlación positiva y altamente significativa*

con el tamaño poblacional, mientras que no encontramos relación significativa entre el tamaño poblacional y el coeficiente de endogamia. La diversidad genética de especies auto compatibles fue menos afectada por la reducción en el tamaño poblacional que la de especies exogámicas obligadas y especies auto compatibles, pero principalmente exogámicas. La longevidad no afectó la respuesta genética de la población a la fragmentación. Sin embargo, nuestro hallazgo más importante fue que las especies comunes fueron tan, o más, susceptibles a las consecuencias genéticas de la fragmentación del hábitat que las especies raras, aun cuando las especies histórica o naturalmente raras fueron excluidas del análisis. Estos resultados son dramáticos porque muchas especies más pueden ser vulnerables a la erosión genética y a la pérdida de diversidad genética como conse-cuencia de los procesos de fragmentación que lo se asumía previamente. Esto implica que muchos hábitats fragmentados han perdido la capacidad para soportar poblaciones de plantas lo suficientemente grandes para mantener un equilibrio mutación-deriva y que los fragmentos de hábitat ocupados están tan aislados que el flujo génico es insuficiente para permitir la reposición de alelos perdidos.

Palabras Clave: diversidad genética, endogamia, fragmentación de hábitat, sistema reproductivo, tamaño pobla-cional

Introduction

Next to decreasing habitat quality and the introduction of exotic species, habitat fragmentation is one of the main drivers behind the present biodiversity crisis (Young & Clarke 2000). Habitat fragmentation includes three components (Andren 1994): (1) pure loss of habitat, (2) reduced fragment size, and (3) increased spatial isolation of remnant fragments. Small habitat fragments contain small populations, which are more vulnerable to extinction due to environmental and demographic stochasticity (Shaffer 1981; Lande 1988). In addition, small populations may be more prone to extinction due to the loss of genetic variation (Frankham 1996). A decreasing population size may result in erosion of genetic variation through the loss of alleles by random genetic drift. In addition, increased selfing (in plants) and mating among closely related individuals in small populations may result in inbreeding and a reduction of the number of heterozygotes (Schaal & Leverich 1996; Young et al. 1996). Over the short term decreasing heterozygosity and the expression of deleterious alleles may result in reduced fitness (Keller & Waller 2002; Reed & Frankham 2003). In the long term lower levels of genetic variation may limit a species' ability to respond to changing environmental conditions through adaptation and selection (Booy et al. 2000).

To date, most studies dealing with genetic erosion in fragmented plant populations have focused on threatened or rare species (e.g., Raijman et al. 1994; Cruzan 2001; Gonzales & Hamrick 2005). The few available studies that explicitly looked for a relationship between habitat fragmentation and genetic erosion in common species, however, have demonstrated that commonness does not protect a species from loss of genetic variation (e.g., Lienert et al. 2002; Hooftman et al. 2004; Galeuchet et al. 2005). These findings are unexpected because common species are by definition characterized by higher fragment occupancy and/or higher local abundance than rare species (Gaston et al. 2000). These spatial population character-

istics can be expected to mitigate the loss of genetic diversity in common species, for example, by allowing genetic rescue (i.e., the replenishment of lost alleles through gene flow between habitat fragments) (Richards 2000; Tallmon et al. 2004). On the other hand, rare species include both species that are historically or naturally rare (e.g., Wolf et al. 2000*a*) and those that are rare due to recent population declines. The effects of habitat fragmentation are expected to be more severe in recently fragmented populations (Huenneke 1991; Gitzendanner & Soltis 2000).

If the loss of genetic diversity in common species appears to be a universal phenomenon, then this may have major consequences for plant community composition and species richness of fragmented habitats. In turn, changing community composition and decreasing species richness may negatively affect ecosystem functioning (Loreau et al. 2001; Leps 2005).

Along with rarity, mating system and longevity may also affect the genetic response of plants to habitat fragmentation. Plants display a wide variety of mating systems that differ in their influence on population genetic structure (Barrett & Kohn 1991; Richards 1997). Nevertheless, it is currently not known whether the effects of habitat fragmentation on the degree of inbreeding and genetic drift systematically differ for species with different mating systems and, more specifically, between self-compatible and self-incompatible species (Galeuchet et al. 2005). Longevity (and especially prolonged clonal growth) may also mitigate the loss of genetic diversity because it extends the time between generations and therefore moderates the loss of alleles through genetic drift (Young et al. 1996; Honnay & Bossuyt 2005).

Some authors have compared overall genetic diversity between rare and common (congeneric) species (Hamrick & Godt 1996; Gitzendanner & Soltis 2000) although summary of the available habitat fragmentation studies and comparison of the relationship between genetic diversity and population size between common and rare plant species has not been conducted. Thus, we

conducted a formal meta-analysis of habitat fragmentation studies that report the relationship between population size and genetic diversity. Meta-analysis focuses on the size and direction of effects across studies, examining the consistency of effects and the relationship between study features (i.e., moderator variables) and observed effects. We estimated the overall mean and the variance of the correlation coefficients among different measures of genetic diversity and plant population size and tested for rarity, mating system, and longevity as potential moderators of the relation between population size and genetic diversity.

Specifically, we addressed whether small, fragmented plant populations are genetically impoverished compared with larger populations; whether rare species are more vulnerable to habitat-fragmentation-mediated loss of genetic diversity than common species; and how moderator variables mating system and longevity affect the relationship between population size and genetic diversity.

Methods

Study Selection and Coding

In January 2006 we used the keywords *habitat fragmentation AND genetic** in a search of Thomson's on line Web of Science. From this query all papers dealing with plant species and applying codominant markers (allozyme or microsatellite markers) to quantify genetic diversity were selected. Amplified fragment length polymorphism (AFLP) and random amplified polymorphic DNA (RAPD) studies were omitted because we were mainly interested in the effects of habitat fragmentation on the inbreeding coefficient (i.e., on the divergence of observed from expected heterozygosity), which is impossible to infer from dominant DNA markers (Mueller & Wolfenbarger 1999). We supplemented the selected papers with studies we found in the papers' cited literature. We examined the full-text version of all selected studies. Studies that did not report population sizes, the number of samples used for genetic analysis, and genetic diversity measures at the level of the individual population were excluded. Studies dealing with fewer than five populations were also omitted. In two studies we used population density as a surrogate of population size (Neel & Ellstrand 2001, 2003)

In each study we recorded the following measures of genetic diversity for all surveyed populations: inbreeding coefficient (F_{IS}), expected heterozygosity or gene diversity (H_e), percentage of polymorphic loci (P), and the number of alleles per locus (A). Not all studies reported all diversity measures, and in some cases it was possible to calculate the inbreeding coefficient from the reported expected and observed heterozygosity. We recorded the Pearson correlation coefficient (r) between each of the four measures of genetic diversity and population size (number of individuals). In most cases we had to calculate r ourselves. Because the Pearson correlation coefficient quantifies linear fits only, we log transformed population sizes in some cases. This log transformation was not applied more frequently for species defined as common than for species defined as rare. In some studies population sizes were reported as categories. For these cases we calculated the Spearman rank correlation coefficient instead of the Pearson correlation coefficient. The correlation coefficients r between population size and the four genetic diversity measures were used as the effect sizes (ES) of the meta-analysis.

Plant species that were explicitly mentioned by authors as "widespread," "common," or "quite common" were coded as common. Other species, referred to as "threatened," "endangered," "relatively rare," or "rare" were coded as rare. A species could be common in one study and rare in another (e.g., Van Rossum et al. 1997 vs. Van Rossum et al. 2003) or both common and rare in one study. In the latter case the same species was studied in two different regions where it differed in abundance and patch occupancy (e.g., Mandak et al. 2005). We believe that relying on the expert knowledge of the authors on the status of a certain species in a certain region is far more accurate in this context than defining rarity and commonness based on reported population sizes and patch occupancies. Moreover, patch occupancies of the species were rarely reported, and we found no indication that the range in size of the studied populations was different for common versus rare species. This makes a quantitative approach of rarity and commonness extremely difficult. We also coded whether a rare study species was subjected to recent fragmentation events (e.g., Luijten et al. 2000) or whether it was naturally or historically rare (e.g., Wolf et al. 2000*a*).

Almost all studies provided information on the mating system of the study species. This information was always reported as "obligate outcrossing," "self-compatible but mainly outcrossing," or "self-compatible" and was coded accordingly. None of the surveyed species was reported as being a complete selfer. Finally, we recorded whether a species was perennial or annual, and if it was perennial, whether it was reported as being clonal.

Statistical Analyses

The weight of each study was calculated according to Reed and Frankham (2003) as follows: $[(K - 2)N]^{1/2}$, where K is the number of populations in the study and N is the mean number of individuals per population sampled for genetic analysis. The applied weight is, strictly speaking, not equal to the inverse variance of the Spearman rank correlation ($K - 3$), which is commonly used in meta-analysis (Lipsey & Wilson 2001), but allowed accounting of the number of individuals sampled.

We explored the possibility of a publication bias by examining funnel plots and weighted histograms. Funnel plots were constructed by plotting the ES of each study against study weight. We also calculated the significance of the Spearman rank correlation coefficient between ES and study weight (Light & Pillemer 1984). When authors do not submit studies or editors reject submissions with small treatment effects or nonsignificant results, the literature becomes biased (Thornton & Lee 2000). A publication bias against nonsignificant results implies that only large effects are reported by small sample size studies because only large effects reach statistical significance in small samples. This may result in a positive correlation between ES and study weight.

We performed the meta-analysis according to Lipsey and Wilson's (2001) methods and with SPSS (SPSS, Chicago, Illinois) macros written by these authors. We did not, however, apply the Fisher transformation to the correlation coefficients, because it may lead to overestimation of the ES (Hunter & Schmidt 1990). We preferred to use a more conservative, but more realistic, mixed model with maximum likelihood estimation above a fixed model for calculation of the mean ES (Lipsey & Wilson 2001). Heterogeneity of the ES across studies was examined with the Q statistic (Hedges & Olkin 1985). We tested the role of the moderator variables (commonness, mating system, and longevity) in explaining heterogeneity across studies by performing a one-way analysis of variance (ANOVA) analog mixed model and by examining the resulting Q statistic between groups (Lipsey & Wilson 2001). To test for potential confounding interactions between the moderator variables we measured their pairwise degree of association with a chi-square test. All calculations were performed with SPSS (version 12.0).

Results

The final database contained 57 records, including 52 different plant species covered in 53 publications (Table 1). Twenty-one records applied to common species and 36 to rare species. Nine of these 36 rare species could be defined as historically rare. For two species, no information regarding the mating system could be retrieved. Allozymes were used in all but three studies, and the median number of polymorphic loci was 7 (range 2–21). There was no Spearman rank correlation between any of the four ES and the number of polymorphic loci ($p > 0.1$).

There was no evidence of a publication bias. All four funnel plots were symmetrical around the mean weighted ES (results not shown), and none of the rank correlations between study weight and F_{IS} (0.15), H_e (–0.08), A (−0.13), and P (–0.26) were significant ($p > 0.05$). The mean weighted ES (±SE) for H_e (0.23 ± 0.04), P (0.35 ± 0.05), and A (0.36 ± 0.04) were positive and highly sig-

nificant ($p < 0.001$), whereas no significant ES was found for F_{IS} (-0.04 ± 0.05).

There were no significant pairwise associations between the three moderator variables ($p > 0.1$). Mean weighted ES for F_{IS}, P, and A were not significantly lower for common than for rare species (Table 2). There was, on the contrary, a trend for a stronger correlation between H_e and population size for common than for rare species (Table 2, Fig. 1). The difference in strength of the ES for F_{IS}, P, and A between common and rare species remained insignificant when the nine historically rare species were omitted from the analysis (results not shown). Mating system did not affect the strength of the correlation between population size and F_{IS}. Self-compatible species, however, showed a lower ES for P, H_e, and A than obligate outcrossers and self-compatible but mainly outcrossing species (Table 3, Fig. 1). Self-compatible species exhibited no significant ES at all (Table 3).

Because only two species were reported to be annuals, we did not conduct a statistical comparison between annuals and perennials. Ten species were considered clonal, but they were not significantly less affected by declining population size than nonclonal species (results not shown).

Discussion

Based on the results obtained for 52 plant species, small populations consistently contained significantly less genetic variation (measured by H_e, A, and P) than large populations. Population size had a lower effect on H_e than on P and A, suggesting that alleles lost through habitat fragmentation and population size reduction were mainly those initially present at low densities (Nei et al. 1975; Sun 1996). Our results support the conclusions of Young et al. (1996) and suggest that loss of alleles through population bottlenecks and random genetic drift play an important role in the genetic impoverishment of plant populations.

Overall, the homozygosity excess, as measured by F_{IS}, was not affected by population size. Heterozygosity can be lost as a direct result of decreasing gene diversity and, more importantly, through increased inbreeding arising from increased self-pollination or mating between related individuals (Barrett & Kohn 1991; Young et al. 1996). Several not mutually exclusive explanations are possible for the absence of an overall relationship between F_{IS} and population size. The F_{IS} in small populations may be biased downward because homozygotes for rare alleles are absent (Kirby 1975; Young et al. 1999), whereas F_{IS} in large populations may be frequently biased upward because of population substructuring (the Wahlund effect) (e.g., Lowe et al. 2004). Moreover, Lesica and Allendorf (1992) suggest that selection against homozygotes occurs during early stages of growth in plant populations.

Table 1. Studies used for the meta-analysis on the relation between genetic diversity and population size.

| Species | Study | Moderator variables[a] | | | |
		status	n	mating system	clonal
Acacia anomala	Coates 1988	1[b]	10	SC/MO	1
Acer saccharum	Young et al. 1993	0	8	SC/MO	0
Aconitum noveboracense	Dixon & May 1990	1	38	SC	0
Anacamptis palustris	Cozzolino et al. 2003	1	5	SC/MO	0
Antherosperma moschatum	Shapcott 1994	0	22	SC	1
Armeria maritima	Weidema et al. 1996	0	17	OO	0
Arnica montana	Kahmen & Poschlod 2000	1	11	OO	1
Arnica montana	Luijten et al. 2000	1	26	OO	1
Atriplex tatarica	Mandak et al. 2005	0	14	SC	0
Atriplex tatarica	Mandak et al. 2005	1[b]	11	SC	0
Begonia dregei	Matolweni et al. 2000	1	12	SC	0
Begonia homonyma	Matolweni et al. 2000	1	7	SC	0
Brassica insularis	Hutrez-Bousses 1996	1	7	SC/MO	0
Calypso bulbosa	Alexandersson & Ågren 2000	1[b]	21	SC/MO	0
Calystegia collina	Wolf et al. 2000a, 2000b	1[b]	32	OO	1
Castilleja levisecta	Godt et al. 2005	1	11	OO	0
Centaurea corymbosa	Colas et al. 1997	1[b]	6	OO	0
Clematis acerifolia	Lopez-Pujol 2005	1	9	no data	0
Cochlearia bavarica	Paschke et al. 2002	1[b]	24	OO	0
Erigeron parishii	Neel & Ellstrand 2001	1	31	SC	0
Eriogonum ovalifolium	Neel & Ellstrand 2003	1	31	SC/MO	1
Eucalyptus albens	Prober & Brown 1994	0	25	SC/MO	0
Festuca ovina	Berge et al. 1998	0	34	OO	1
Filipendula vulgaris	Weidema et al. 2000	0	17	SC/MO	0
Gentiana pneumonanthe	Raijmann et al. 1994	1	25	SC/MO	0
Geum urbanum	Vandepitte et al., unpublished	0	18	SC	0
Gymnadenia conopsea	Gustafsson 2000	1	10	SC	0
Gypsophila fastigiata	Lönn & Prentice 2002	0	16	SC/MO	0
Juniperus communis	Oostermeijer & De Knegt 2004	1	12	OO	0
Leontice microrhyncha	Chang et al. 2004	1	6	SC	0
Lychnis flos-cuculi	Galeuchet et al. 2005	0	28	SC	0
Lychnis viscaria	Berge et al. 1998	0	28	SC/MO	0
Lychnis viscaria	Lammi et al. 1999	1	8	SC/MO	0
Megaleranthis saniculifolia	Chang et al. 2005	1[b]	8	OO	0
Microseris lanceolata	Prober et al. 1998	1	16	OO	0
Primula elatior	Van Rossum et al. 2002	0	9	OO	0
Primula veris	Van Rossum et al. 2004	0	24	OO	0
Primula vulgaris	Van Rossum et al. 2004	1	41	OO	0
Rutidosis leptorrhynchoides	Young et al. 1999	1	16	OO	1
Salvia pratensis	Van Treuren et al. 1991	1	14	SC/MO	0
Scabiosa columbaria	Van Treuren et al. 1991	1	12	SC/MO	0
Scuttelaria montana	Cruzan 2001	1[b]	31	SC	0
Silene dioica	Giles & Goudet 1997	0	52	OO	0
Silene nutans	Van Rossum et al. 2003	0	21	SC/MO	0
Silene nutans	Van Rossum & Prentice 2004	0	34	SC/MO	0
Silene nutans	Van Rossum et al. 1997	1	34	SC/MO	0
Silene regia	Dolan 1994	0	18	SC/MO	0
Sorbus aucuparia	Bacles et al. 2004	1	8	OO	0
Spiranthes sinensis	Sun 1996	1	6	OO	0
Stachys maritima	Lopez-Pujol 2003	1	5	SC/MO	1
Succisa pratensis	Vergeer et al. 2003	0	17	SC	0
Swainsona recta	Buza et al. 2000	1	18	SC	0
Trillium camchatcense	Tomimatsu & Ohara 2003	0	12	OO	0
Trillium reliquum	Gonzales & Hamrick 2006	1	21	OO	1
Vincetoxicum hirundinaria	Leimu & Mutikainen 2005	0	12	SC	0
Viola pubescens	Culley & Grub 2003	0	9	SC	0
Washingtonia filifera	McClenaghan & Beauchamp 1986	1[b]	16	no data	0

[a] *Key: status: 1, rare; 0, common;* n, *population size; SC, self-compatible; SC/MO, self-compatible but mainly outcrossing; OO, obligate outcrossing; 1, clonal; 0, not clonal.*
[b] *Naturally or historically rare.*

Table 2. Difference in effect size (ES) between common and rare species (Q statistic).

Genetic diversity measure[a]	n	Q between groups[b]	Mean weighted ES by group[b]	SE
F_{IS}	48	0.02		
H_e	51	3.58*		
common	19		0.32***	0.06
rare	32		0.17**	0.05
P	42	0.13		
A	39	0.36		

[a]*Key:* F_{IS}, *inbreeding coefficient;* H_e, *expected heterozygosity;* P, *percent polymorphic loci;* A, *number of alleles per locus;* n, *number of records.*
[b]**0.05 ≤ p < 0.1; **0.001 ≤ p < 0.01, ***p < 0.001.*

Because in most plant species only a small proportion of the offspring survives into the adult stage, selection against homozygotes may occur without affecting recruitment. Especially under harsh environmental conditions with high selection pressures against homozygotes, heterozygosity may be lost very slowly. For example, in grassland species, highly heterozygous individuals have better survival chances during the gradual process of spontaneous afforestation and subsequent habitat fragmentation (Kahmen & Poschlod 2000). Therefore, the smallest and most fragmented populations do not contain a random sample from previously larger populations; rather they exhibit a significant heterozygosity excess (Raijman et
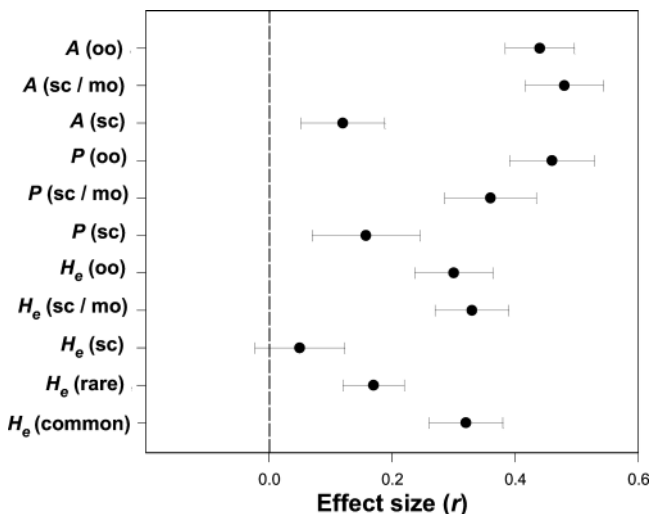

Figure 1. Effect size (correlation between genetic diversity and population size) for 52 plant species considered in 53 publications for the moderator variables with a significant Q statistic. Bars are standard errors (H_e*, expected heterozygosity; A, number of alleles per locus; P, percent polymorphic loci; sc, self-compatible; sc/mo, self-compatible but mainly outcrossing; oo, obligate outcrossing).*

al. 1994; Kahmen & Poschlod 2000). In any case further research regarding the uncertain relation between homozygote excess and plant population size remains necessary, especially because a homozygote excess affects short-term fitness (Reed & Frankham 2003).

Our most important finding was that population genetic diversity (H_e, A, and P) was also eroded in species that were considered common. Even when historically or naturally fragmented populations of rare species were omitted from the analysis, no difference between rare and common species in population genetic response to habitat fragmentation was found. These results are dramatic in that many more plant species than previously assumed may be vulnerable to genetic erosion and loss of genetic diversity as a result of ongoing fragmentation processes. It seems that many fragmented habitats have become unable to support plant populations that are large enough to maintain a mutation-drift balance and that habitat fragments have become too isolated to allow sufficient gene flow to enable replenishment of lost alleles.

Although genetic impoverishment may not result in a short-term loss of fitness in all species, given the absence of a general relationship between population size and F_{IS} (Young et al. 1999; Matolweni et al. 2000), the fragmentation-mediated loss of alleles will at least affect the evolutionary adaptation potential of even common species (Ellstrand & Elam 1993). In the global context of rapid climate change, the latter is alarming because many plant species lack the colonization ability to track the shifting climate northward (Honnay et al. 2002).

Our results also indicated that obligate or mainly outcrossing species are more vulnerable to the loss of genetic variation through habitat fragmentation than self-compatible species. This may be an indication that the role of gene flow is very important in conserving genetic diversity in outbreeding species. Obligate outcrossing or mainly outcrossing species can maintain high population genetic diversity through frequent exchange of genes with other populations and even a very few migrants per generation are sufficient to counter genetic differentiation (Wright 1931). Indeed, these species are generally characterized by low between-population genetic differentiation (Hamrick & Godt 1996). With increasing habitat destruction and decreasing local population size and patch occupancy, the exchange of alleles becomes less likely, and the smallest populations may loose genetic diversity without the possibility of replenishing the alleles lost through drift. Almost all surveyed plant species rely on insects for pollination, and changing pollinator behavior may play an important role in this process (Wilcock & Neiland 2002). Small plant populations may become too inconspicuous or too isolated to attract pollinating insects (Kwak et al. 1998; Steffan-Dewenter & Tscharntke 1999). Increasing fragmentation may therefore directly translate into reduced pollinator activity, reduced gene flow, and loss of genetic diversity. Mainly selfing species

Table 3. Difference in effect size (ES) between different mating systems (Q statistic).

Genetic diversity measure[a]	n	Q between groups[b]	Mean weighted ES by group[b]	SE
F_{IS}	46	1.11		
H_e	49	9.97**		
self-compatible	16		0.05	0.07
self-compatible, mainly outcrossing	15		0.33***	0.07
obligate outcrossing	18		0.30***	0.06
P	40	7.62*		
self-compatible	11		0.16	0.09
self-compatible, mainly outcrossing	14		0.36***	0.07
obligate outcrossing	15		0.46***	0.07
A	41	15.84***		
self-compatible	12		0.12	0.07
self-compatible, mainly outcrossing	13		0.48***	0.07
obligate outcrossing	16		0.44***	0.06

[a]*Key:* F_{IS}, inbreeding coefficient; H_e, expected heterozygosity; P, percent polymorphic loci; A, number of alleles per locus; n, number of records.
[b]*$0.01 < p \leq 0.05$; **$0.001 \leq p < 0.01$, ***$p < 0.001$.

on the other hand, naturally contain most of their genetic diversity within populations, and their level of population genetic diversity will be less affected by reduced gene flow.

Our inability to find an effect of clonality on population genetic response to habitat fragmentation is likely partly due to the unequal sample sizes between clonal and nonclonal plants. Our results point to a serious bias of plant fragmentation studies toward perennial, nonclonal species. Inclusion of annuals and strongly clonal species in future studies will allow a more accurate assessment of the impact of degree of longevity on the population genetic response to habitat fragmentation.

Some authors suggest that different taxa cannot be treated as independent samples because of their phylogenetic relatedness and that in the absence of a phylogeny only congeneric comparisons can be made (Felsenstein 1985; Gitzendanner & Soltis 2000). We are not aware, however, of any method that includes phylogenetically independent contrasts in a meta-analytical approach, and we found the required habitat fragmentation data for only five congeneric species pairs. Moreover, possible nonindependence of our data increased the probability of a Type I error, making it unlikely that applying a correction for phylogenetic relatedness will reveal significant differences between the response of common and rare species to habitat fragmentation (Gitzendanner & Soltis 2000).

We found a highly significant effect of population size on population genetic diversity, with the exception of the inbreeding coefficient. The population size effect was much more pronounced in self-compatible but mainly outcrossing species and in obligate outcrossing species. Most important, our results revealed that the effect of population size on genetic diversity is as pronounced in common as in rare species. This means that in our fragmented landscapes, even common species may have reached a critical threshold in population size and patch occupancy; thus, measures mitigating habitat fragmentation are strongly needed.

Acknowledgments

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