Evolutionary changes in plant reproductive traits following habitat fragmentation and their consequences for population fitness

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Summary

1. The effects of habitat fragmentation on plant population genetic structure and diversity are relatively well studied. Yet, most of these studies used molecular tools focusing on neutral genetic markers, and much less is known about the potential evolutionary consequences of habitat fragmentation on ecologically relevant plant traits.

2. It can be expected that the altered biotic and abiotic conditions and limited gene flow following habitat fragmentation may impose strong selection pressures on traits important for plant fitness. Responses to these selection pressures may, however, be hampered by reduced genetic diversity through genetic drift. Conversely, evolutionary changes in flower or dispersal traits may itself impact the strength of inbreeding and genetic drift.

3. In this review, we highlight different reproductive plant traits that may be under selection following habitat fragmentation, and we examine studies that have shown indications for rapid evolutionary responses.

4. There are still relatively few studies that have convincingly shown that habitat fragmentation generates rapid evolutionary responses. Separating genetic from plastic trait responses and quantifying the long-term fitness consequences of evolutionary changes in plant traits also remain major challenges.

5. Synthesis. Many plant traits may be subject to selection following habitat fragmentation, but, until now, studies that quantified evolutionary responses to habitat fragmentation are limited. To study the consequences of changing plant traits for population fitness, we advocate applying population models that link demographic vital rates, the responding plant traits and their heritability.

Key-words: dispersal, habitat fragmentation, mating system, nectar, phenotypic variation, population dynamics, selection

Introduction

Habitat loss and fragmentation, together with climate change, environmental degradation through pollution, the invasion of exotic species and overexploitation, are considered to be the most important threats to biodiversity world-wide (Diamond 1989; Pimm & Raven 2000). The disintegration of large tracts of natural habitat into many small and spatially isolated fragments has major and well-documented consequences for the population biology, genetics and long-term viability of the residing plant species (Honnay et al. 2005; Broadhurst & Young 2007).

The population biological consequences of habitat fragmentation are driven by both direct and indirect effects of changes in population size and isolation. In a direct way, decreased population size may lead to the loss of alleles through genetic drift, and to increased homozygosity through inbreeding (Wright 1931, Young, Boyle & Brown 1996) (Fig. 1, arrow 1). The increased spatial isolation may hamper gene flow between plant populations and may therefore prevent the replenishment of alleles lost through drift, thereby increasing genetic differentiation between populations (Wright 1931; Franklin 1980). The impact of habitat fragmentation on population
habitats become fragmented, resulting in concomitant loss of quantitative genetic variation together with neutral genetic variation (Hoffmann & Willi 2008). Recent meta-analyses of this population genetic work have clearly shown that habitat fragmentation lowers within-population genetic diversity through genetic drift (Leimu et al. 2006; Honnay & Jacquemyn 2007; Aguilar et al. 2008) and inbreeding (Angeloni, Ouborg & Leimu 2011). However, not all plant species are equally susceptible to loss of genetic diversity resulting from habitat fragmentation, and the extent of changes in local genetic variation is strongly mediated by plant traits such as pollination mode and mating system (Aguilar et al. 2008), or the presence of a persistent seed bank (Honnay et al. 2008).

Indirect effects of changes in population size and isolation are mediated by changes in interspecific interactions (Fig. 1, arrow 2). Small and isolated plant populations have been shown to experience problems with pollination and sexual reproduction due to pollinator shortage, or to altered pollinator behaviour and flight patterns (Aguilar et al. 2006). Especially in self-incompatible, dioecious or heterostylous species, the disruption of plant–pollinator mutualisms may result in significantly lower reproductive success (Jacquemyn, Brys & Hermy 2002; Tewksbury et al. 2002; Kolb 2005; Leimu et al. 2006). Similar effects can be expected for wind-pollinated species as severe reductions in population density, which are likely to occur after habitats have become fragmented, have been shown to lead to substantial reductions in seed production (e.g. Jacquemyn & Brys, 2008; Hesse & Pannell 2011). Habitat fragmentation may also affect the interaction of plants with their animal seed dispersers (Levey et al. 2005; Grünwald, Breitbach & Böhning-Gaese 2010; Herrera & García 2010), mycorrhizal fungi (Peay, Garbelotto & Bruns 2010), insect herbivores (Cagnolo et al. 2009) and parasites (Valladares, Salvo & Cagnolo 2006), all of which may affect the dynamics and long-term viability of plant populations.

Habitat fragmentation has a direct impact on a population and often alters ecological interactions. Therefore, it is reasonable to expect that fragmentation exerts strong selection pressures that could potentially drive the evolution of ecologically relevant plant traits in small and isolated populations (Fig. 1, arrow 3). Moreover, the absence of gene flow between fragmented populations may facilitate such an evolutionary response (Merilä & Crnokrak 2001). The high genetic drift typically observed in fragmented populations can facilitate a two-phase process of adaptation in subdivided populations, as proposed in the shifting balance theory of evolution (Wright 1931). In the first phase, genetic drift causes each subpopulation to undergo a random walk in allele frequencies to explore new combinations of alleles. In the second phase, a new favourable combination of alleles can become fixed by natural selection and exported to other populations through migration. Evidence for the shifting balance theory of evolution affecting mating system evolution was given by Barrett, Ness & Vallejo-Marín (2009), who showed that the transition from outcrossing to selfing in the tristylos Eichhornia paniculata was triggered by genetic drift and founder events, followed by selective loss of outcrossing morphs and fixation of self-pollinating variants.

On the other hand, evolutionary responses to habitat fragmentation may be hampered by a lack of sufficient genetic diversity, resulting from drift and inbreeding (Fig 1, arrow 4). If the genetic variation that is lost codes for phenotypic variation, habitat fragmentation may impede adaptive responses (Stockwell, Hendry & Kinnison 2003; Leimu & Fischer 2008). Moreover, decreases in population genetic diversity or changes
in genotype composition through drift may also have ecological effects, which may in turn affect the direction of the evolution of plant traits (Fig. 1, arrow 5). Ecological consequences of genetic diversity in plants have been demonstrated at different levels of organization, from the population to the community to the ecosystem (Antonovics 1992; Hughes et al. 2008; Bailey et al. 2009). For example, decreasing plant genotypic diversity in fragmented plant populations may negatively affect biomass production or increase community invasibility (Booth & Grime 2003; Vellend, Drummond & Tomimatsu 2010), directly affecting ecological interactions and possibly evolutionary trajectories of plant traits. Finally, the suggestion that rapid evolutionary changes in phenotypic trait values, occurring in the same time spectrum as ecological processes, may directly feedback to change the ecological interactions and responses of the species (Schoener 2011) is represented by arrow 6 on Fig. 1. These feedbacks between evolution and ecology, both occurring at the same temporal scales, have been termed eco-evolutionary dynamics (Fussman, Loreau & Abrams 2007; Pelleiter, Grant & Hendry 2009).

There is growing evidence that human activities can be associated with rapid evolutionary changes (Hendry & Kinnison 1999; Palumby 2001; Stockwell, Hendry & Kinnison 2003; Schoener 2011). But so far, potential effects of habitat fragmentation have not received the attention they deserve. In plant species, high evolutionary rates (quantified by the units Haldanes and Darwins) have been reported for plants adapting to metal and herbicide tolerance, and to increased atmospheric ozone and CO₂ concentrations (Bone & Farres 2001). Bone & Farres (2001) have provided considerable evidence that, for some plant traits, measurable evolutionary change may occur within 20 generations or less. They also found evidence for higher accumulation of evolutionary change in physiological plant traits (such as heavy metal and herbicide resistance) than in morphological traits (such as leaf length and biomass).

In this paper, we first review the available evidence on how habitat fragmentation may drive the evolution of ecologically relevant plant traits, focusing on reproductive traits and seed dispersal traits. Second, because the implications of altered plant traits for population fitness are still poorly understood, we aim to clarify how demographic models can help to track the long-term population-level consequences of micro-evolution.

Habitat fragmentation and plant mating systems

The abundance and diversity of pollinators in remnant fragments is likely to decrease as fragmentation increases (e.g. Sih & Baltus 1987; Aizen & Feinsinger 1994; Kearns, Inouye & Waser 1998; Tewksbury et al. 2002; Krauss, Steffan-Dewenter & Tscharntke 2003; González-Varo, Arroyo & Aparicio 2009), which can lead to significant pollen limitation through reduced pollen deposition or lower pollen quality (Ashman et al. 2004; Knight et al. 2005; Aguilar et al. 2006; Yang, Ferrari & Shea 2011). In fragmented habitats, insect populations no longer find enough resources and/or nesting sites to complete their life cycle, leading to a gradual decrease in the number of insect species in remnant patches and in the population size of pollinators. Environmental conditions may also change to such an extent that they are no longer suitable to sustain populations of all insect species that were present in intact patches, ultimately leading to strongly altered pollinator communities in fragmented habitats. Given that insect populations are known to fluctuate substantially from year to year, even under the best circumstances (e.g. Kalisz, Vogler & Hanley 2004), this may further increase the extent of pollen limitation in fragmented populations. With ongoing habitat alteration, climate change and agricultural chemical usage, changes in pollinator assemblages are even expected to increase further in the near future (Ricketts et al. 2008; Winfree et al. 2009; Potts et al. 2010). Ultimately, this can lead to losses of outcrossing plant species that rely on pollinators for successful seed set (Biesmeijer et al. 2006) unless species can adapt to the altered pollinator environments.

Whereas the ecological impact of habitat fragmentation on plant reproduction has been well studied (e.g. Ashman et al. 2004; Ghazoul 2005; Aguilar et al. 2006), relatively little attention has been given to the potential evolutionary consequences of anthropogenic disturbances on plant mating systems (Eckert et al. 2010; Harder & Aizen 2010). Theory suggests that disturbance of the pollination environment and loss of specialist pollinators can generate diverse selective forces on plant mating systems that are mainly driven by the extent and causes of pollen limitation (Lloyd 1992; Morgan & Wilson 2005; Eckert et al. 2010; Harder & Aizen 2010). However, it is difficult to predict which evolutionary trajectory a population or species will take when its pollination environment becomes critically disturbed. In case of severe and chronic pollen limitation following habitat fragmentation, it is expected that floral traits are selected that either promote outcrossing or provide autonomous self-fertilization and thus reproductive assurance. When pollinator abundance and pollinator limitation vary in space and time (Goodwillie, Kalisz & Eckert 2005; Eckert et al. 2010), plants may evolve to a mixed mating system. Under such a scenario, establishment of a delayed selfing mechanism will be most favourable, as it increases female fitness with little seed or pollen discounting (Kalisz, Vogler & Hanley 2004). Additionally, floral adaptations that favour autonomous selfing are expected to act in the opposite direction of traits that are associated with the promotion of cross pollination, and therefore, changes in these two suits of traits may be closely linked.

Although it is very likely that significant evolutionary shifts in plant breeding systems are currently happening in a large number of plant species inhabiting human disturbed habitats, there are currently few reports on detectable responses of anthropogenic disturbances on plant trait evolution (Eckert et al. 2010). A relatively long period of time may be required for significant floral adaptations to become detectable after populations have become fragmented, particularly in long-lived species. Evidence of human disturbances and habitat
Habitat fragmentation and plant trait evolution

Fragmentation on mating strategies in plant populations was reviewed recently by Eckert et al. (2010) and Harder & Aizen (2010). Eckert et al. (2010) showed that in 17 species from seven different families, the mean outcrossing rate ($t_m$) was significantly (paired t-test, $P = 0.004$) lower in fragmented habitats than in undisturbed, contiguous habitats ($t_m = 0.753$ and $0.820$, respectively) (Fig. 2). Moreover, this study focused on trees and shrubs, with only one herb species included, suggesting that this assessment may be more conservative in assessing the effects of habitat fragmentation compared with studies that focus on short-lived species. The effects are expected to be most pronounced in herbs, particularly monocarpic herbs, due to a faster generation time and a more stringent need for reproductive assurance (Barrett, Harder & Worley 1996; Schoen et al. 1997). Using a different approach, Harder & Aizen (2010) compared several pairs of related species in a number of genera inhabiting disturbed, pollinator-poor environments with closely related congeners occurring in intact or optimal habitats. In response to anthropogenic disturbances, selfing and a concomitant reduction in flower size evolved three to four times more often than an increase in outcrossing. These results indicate that human-mediated disturbances can have profound effects on mating patterns in plant species and most likely result in changes in plant traits that favour selfing.

Increased levels of autonomous selfing may result from reductions in the level of herkogamy or protogyny (Cruden & Lyon 1989; Lloyd 1992; Morgan & Wilson 2005; Porcher & Lande 2005). Eckert & Herlihy (2004) and Herlihy & Eckert (2007), for example, showed a significant increase of the autonomous component of total selfing with decreasing herkogamy in Aquilegia canadensis. Similarly, comparison of outcrossing rates between populations occurring at the centre and the edge of their distribution range has shown that herkogamy was lower and selfing more prevalent in edge populations where natural pollinators were scarcer (Moeller 2006). In fragmented populations of the dune plant Centaurium erythraea, plants growing in pollinator-rich environments had markedly higher anther–stigma separation than plants growing in pollinator-poor environments (Fig. 3) (Brys & Jacquemyn 2011). At the same time, this reduction in the level of herkogamy was associated with higher levels of autonomous selfing. Similar reductions in the level of herkogamy have been reported in fragmented populations of the Chiltern gentian (Gentianella germanica), in which the mean level of herkogamy was significantly lower in small populations, probably associated with reductions in pollinator-mediated pollen deposition (Luijten et al. 1999). In heterostylous taxa, the transition from obligate outcrossing to selfing often involves the replacement of heterostylous variants, which are characterized by a heteromorphic self-incompatibility system, with self-compatible homostyles (e.g. Charlesworth & Charlesworth 1979; Barrett & Shore 1987).

![Fig. 2. Mean outcrossing rates ($t_m$) in seventeen plant species occurring both in fragmented and contiguous, undisturbed habitats (data from Eckert et al. 2010).](image)

![Fig. 3. Flowers of Centaurium erythraea originating from populations occurring in two contrasting pollinator environments. (a) Plants from pollinator-rich environments have larger and more herkogamous flowers than plants from (b) pollinator-poor environments plants, which are characterized by smaller flowers that lack herkogamy (from Brys & Jacquemyn 2011).](image)
As autonomous selfing evolves, a concomitant selection for reduced investment in pollinator attraction (such as reductions in flower size, corolla diameter, number of flowers, floral longevity, etc.) and rewards (such as reduced nectar and pollen production) is also likely to occur (Ornduff 1969; Eckert et al. 2010). Plants of C. erythraea growing in pollinator-poor environments indeed had smaller flowers and fewer flowers per plant than plants growing in pollinator-rich environments (Fig. 3). Similarly, pollen-ovule ratios were significantly larger in plants occurring in pollinator-rich than in pollinator-poor populations (Brys & Jacquemyn 2011). In this case, the lower pollen to ovule ratio in pollinator-poor environments was mainly caused by lower investment in pollen production rather than by smaller ovule numbers, confirming earlier findings that plants with a higher capacity of autonomous selfing allocate a smaller amount of resources to traits that contribute to the male function relative to the female function (Lloyd 1987).

In the most extreme case, plants may loose their capacity to reproduce sexually and only regenerate by vegetative (clonal) offspring. The balance between clonal reproduction and sexual reproduction varies between different species, but also within species, there can be extensive variation in clonal reproduction (Honnay & Jacquemyn 2008; Vallejo-Marín, Dorken & Barrett 2010), which can often be related to deteriorating environmental conditions (e.g. Jacquemyn et al. 2005; Vandepitte et al. 2009). As habitat fragmentation may negatively affect sexual function, this balance may shift in favour of clonal reproduction (Rossetto et al. 2004), ultimately resulting in a degeneration of life-history traits associated with sexual reproduction (Eckert 2002). For example, in the aquatic herb Decodon verticillatus, Eckert & Barrett (1993) demonstrated that populations had become infertile at the northern edge of the species’ range where populations only reproduce clonally.

Size at flowering and plant size
Habitat fragmentation may also affect the optimal timing to reproduce because local environmental conditions and pollinator environments are likely to change within fragmented habitat patches. Decreased light availability due to shrub encroachment, for example, led to larger threshold sizes for flowering in fragmented populations of the perennial orchid Orchis purpurea (Jacquemyn, Brys & Jongejans 2010). Moreover, costs of flowering were higher in shaded populations, which resulted in a threefold increase in the threshold size that was required to flower for two consecutive years. Several studies have documented heritable variation for the timing of flowering and the number of flowering events (Law, Bradshaw & Putwain 1977; Wesselingh et al. 1997; Johnson 2007), suggesting that both of these life-history traits may be prone to selection and evolve in different ways depending on the degree of fragmentation and associated changes in environmental conditions and pollinator environments. For example, lower survival in fragmented habitats due to altered environmental conditions (such as conditions resulting from increased edge effects) may lead to a decreased optimal size of flowers in fragmented habitats. Selection may therefore induce a shift from iteroparity in undisturbed habitats to semelparity in disturbed habitats. The reverse may be true as well. Some species may benefit from the new environmental conditions in fragmented habitats and therefore increase the size of optimal flowering.

However, to our knowledge, there are no studies that have compared size-dependent flowering and evolutionary changes in optimal flowering size between fragmented and undisturbed, contiguous habitats. Wesselingh et al. (1997) showed that threshold sizes for flowering were significantly different in the facultative biennial plant Cynoglossum officinale between populations occurring in open dune habitats and in closed poplar thickets. Similarly, Hesse, Rees & Müller-Schärer (2008) showed that threshold sizes for flowering in the clonal herb Veratrum album were significantly different between populations occurring in forests, hay meadows and pastures. These results clearly indicate a pervasive influence of local habitat conditions on flowering behaviour and threshold sizes of flowering and therefore suggest that habitat fragmentation can affect the evolution of life histories of plant species.

In addition to effects on flowering, habitat fragmentation may also select for larger plant sizes, as larger plants are more attractive to pollinators than small plants. Using data from 16 populations, Weber & Kolb (2011) found that selection for increased inflorescence size decreased with increasing population size and density, suggesting that larger plants are particularly favoured in small plant populations, or in low-density populations. However, because the degree of pollen limitation was independent of population size or density, the authors suggested that the observed selection gradients were mediated by local environmental conditions (light and base saturation). The opposite may also occur, when plants are susceptible to herbivores or pathogens. In this case, habitat fragmentation may select for smaller plant sizes if fragmentation is associated with increased abundances of herbivores or pathogens. For example, in the Mediterranean herb Erysimum mediohispanicum, Gómez (2003) found significant selection on flower number, reproductive stalk height, basal stalk diameter, petal length and inner diameter of the flowers when herbivores were absent. When ungulates were present, selection on floral traits completely disappeared and selection strength on flower number and vegetative traits decreased.

Nectar production
To increase their reproductive success, most animal-pollinated plants produce rewards to entice insect pollinators to visit their flowers (Mitchell 1993). Nectar is by far the most common floral reward and primarily consists of water, sugars and amino acids, although there is high variability in nectar composition between species (Baker & Baker 1975; Baker 1977; Petanidou 2005). Nectar plays a crucial role in the interactions between plants and their pollinators and hence in mating success and mating patterns. Important insights into the functioning of nectar come from experiments adding nectar-surrogates to nectarless orchid species. For example, adding sugars to
flowers of *Disa pulchra* increased the number of flowers probed by insect pollinators, the time spent on a single flower and the number of pollinia removed (Jersákova & Johnson 2006). In similar experiments, artificial supplementation of nectar to flowers resulted in significantly higher seed set in the rewardless *Dactylorhiza sambucina* (Jersákova et al. 2008).

High variability in nectar volume and composition is also observed within species (Klinkhamer & van der Lugt 2004; Herrera, Perez & Alonso 2006; Canto et al. 2011). This variability is partly inheritable and partly regulated by environmental conditions (Leiss, Vrielings & Klinkhamer 2004; Leiss & Klinkhamer 2005). Due to this phenotypic variation in nectar production and composition, its inheritability and the direct link between nectar production and plant reproductive success, it can be expected that nectar characteristics are subject to strong selective forces. Given the reduced pollinator abundance in small and isolated plant populations, individuals with high nectar production (or a specific chemical nectar composition) are expected to have a strong selective advantage because they are more attractive to the scarce insect pollinators than plants with limited nectar production. In large populations with high abundances of pollinators, this selective advantage will be absent. Work on *Echium vulgare* has indeed shown that individuals with high nectar production receive more pollinator visits, but only in sparse populations (Klinkhamer & van der Lugt 2004; Leiss & Klinkhamer 2005). This suggests that selection is possible and may result in different nectar characteristics in small vs. large plant populations. It is unknown whether the specific nectar composition (including both sugar and amino acid components) is also affecting the attractiveness of individual plants, and therefore, whether there are different selective pressures to be expected on nectar production and nectar composition.

The production of additional, or more attractive, nectar is not cost free, however. In addition to its energetic cost (Pyke 1991), the increased production of nectar and the subsequent increased attraction and changing behaviour of pollinators may incur considerable fitness costs through more self-pollination and associated inbreeding depression. This may be particularly severe in small and isolated populations where the risk of inbreeding depression is already considerable (Keller & Waller 2002). Jersákova & Johnson (2006) noticed more self-pollination when flowers of the nectarless orchid *Disa pulchra* were artificially supplemented with a sucrose solution. Johnson, Peter & Ågren (2004) predicted that a mutation towards nectar production in the non-rewarding orchid *Anacamptis morio* would result in an initial four-fold increase in pollinariaum removal, but at the same time, a 40% increase in geitonogamous self-pollination occurred. Leiss, Peet & Klinkhamer (2009), on the other hand, could not report significantly higher selfing rates in *E. vulgare* individuals with high nectar production.

To summarize, two opposing selective forces may be active on the volume of nectar and on the nectar composition of individuals occurring in small and isolated plant populations. The production of higher amounts of nectar, or more attractive nectar, may increase attractiveness to pollinators and increase the degree of sexual reproduction. Concomitantly, this may increase self-pollination, resulting in a loss of fitness through inbreeding depression. Exploring which factors tip the balance in these alternative evolutionary outcomes may lead to important insights into how habitat fragmentation shapes populations. Experimental modification of nectar composition, for example through adding fertilizer, is likely a very promising way to proceed.

### Seed dispersal

The dispersal of propagules between fragmented habitats is essential as it allows both the recolonization of empty habitat fragments and the survival of small populations through a rescue effect. Parallel to the observed loss of dispersal capacity in insect and bird species on oceanic islands (Carlquist 1965; Roff 1990), it can also be expected that selection for genotypes with decreased dispersal ability is likely in small and isolated plant populations. The idea is that high dispersal is associated with increased mortality in fragmented habitats because diasporas end up in a hostile landscape matrix and die. As there is a trade-off between dispersal capacity and other life-history traits (e.g. seed size and associated competitive power of emerging seedlings; Soons & Heil 2002; Jakobsson & Eriksson 2003; but see Skarpaas et al. (2011) for confounding environmental effects on this trade-off), individuals with low dispersal capacity will be favoured in isolated plant populations as they can invest more in other fitness-related traits. Common garden experiments have indeed demonstrated that seed dispersal traits such as the length of the pappus can have a genetic basis and may undergo rapid adaptations (Imbert 2001; Riba et al. 2005). Studies on oceanic islands confirm this result, where reduced seed dispersal capacity has been reported for *Cirsium arvense*, *Lactuca* (*Mycelis*) *muralis* and *Hypochaeris radicata* (Cody & Overton 1996; Fresnillo & Ehlers 2008). However, compared to reported rates of physiological adaptation (for example to heavy metals), the rates of evolutionary change in seed morphology leading to enhanced dispersal were found to be very low for the two latter species (Bone & Farres 2001).

If the reduction of seed dispersal ability in plant populations on oceanic islands is paralleled in terrestrial habitat fragments, the detrimental consequences of habitat fragmentation for population viability and recolonization rates can be expected to increase with time. In this case, evolutionary changes of plant traits feedback on population fitness components, for example through increasing inbreeding, which may ultimately result in population extinction (Gyllenberg, Parvinen & Dieckmann 2002). However, it is important to note that the response of a population within a habitat fragment may differ from that of established populations on oceanic islands because plant populations in terrestrial habitat fragments may be subject to rapid turnover and meta-population dynamics. Spatially explicit models have shown that if local extinction is so high that empty patches remain uncolonized for a long time, migration between habitat fragments will be evolutionarily favoured instead of hampered, resulting in evolutionary rescue (Heino
& Hanski 2001). Second, the degree of isolation of terrestrial habitat fragments is not that extreme as that of oceanic islands. Therefore, evolution towards higher dispersal capacity is possible because, mainly for well dispersing species, dispersal costs remain relatively low.

The scarce empirical evidence so far clearly suggests that there is selection against seed dispersal capacity in fragmented terrestrial habitats. Cheptou et al. (2008) showed that Crepis sancta, a species with heteromorphic seeds, produced more non-dispersing seeds in highly isolated urban populations than in well-connected rural populations. Applying a quantitative genetic model, the authors suggest that, under strong selection against seed dispersal, evolutionary changes are possible within 5–12 generations. Riba et al. (2009) found evidence that seeds of Mycelis muralis had lower wind dispersal capacity in low connectivity landscapes, both at a landscape scale and larger interregional scale. Interestingly, these authors found no such a relation for populations at the northern edge of their range in Sweden, likely resulting from the high dispersal capacity of the individuals that reached the range margin. This clearly shows the importance of population history for the potential of seed dispersal capacity evolution.

Implications for population fitness

From the previous sections, it is clear that habitat fragmentation may alter life-history traits that are important in governing the reproductive success of plant populations and dispersal of seeds. To what extent this is already happening at a large scale is not clear, however, because empirical evidence for habitat fragmentation-driven selection remains rather scarce. From the previous examples, it is also not always clear whether the trait changes are genetically based or whether they are a result of phenotypic plasticity. In many cases, measuring plant traits in common garden environments during several generations to purge maternal effects is required to exclude the possibility of phenotypic plasticity and to quantify heritability of the trait changes. The available data suggest that for some traits, there is a heritable genetic component to the observed phenotypic variation. For example, estimates of broad-sense heritability of herkogamy based on the regression between parents measured in the field and progeny measured in the greenhouse gave a heritability index $H^2 = 0.62$ in the dune plant C. erythraea (determined on progeny derived from selfing, R. Brys and H. Jacquemyn, unpublished data; see Fig. 3). Similar levels of heritable variation in the level of herkogamy have been documented in Mimulus guttatus (mean $H^2 = 0.58$; Carr & Fenster 1994), Gentianella campestris (mean $H^2 = 0.86$; Lemmartsen et al. 2000), Datura stramonium (mean $H^2 = 0.30$; Motten & Stone 2000) and Aquilegia canadensis (mean $H^2 = 0.42$; Herlihy & Eckert 2007). Regarding seed dispersal traits, Imbert (2001) showed that the narrow sense heritability of the percentage of dispersing central achenes vs. non-dispersing peripheral achenes in Crepis sancta was 0.25.

When genetically based changes in plant traits occur rapidly after habitat fragmentation has taken place, it is often unclear whether they are beneficial to a population as some of these changes may incur severe fitness costs and therefore may be maladaptive in the long term. In general, changes in plant traits may result (i) from evolutionary changes that appear to be adaptive in the short term, but in the long term may lead to evolutionary suicide; and (ii) from evolution of plant traits that increase survival in a fragmented landscape. One example of the latter is the increased investment in nectar production, which may result in a temporary increase in seed set, but in the long term may translate into higher mortality rates of established individuals due to inbreeding depression or costs of reproduction. In addition, the pressure of one selective agent may be influenced by that of another. For example, pollinator-mediated selection was found to be disrupted by conflicting effects of plant enemies acting during or subsequent to pollination (Gómez 2003).

The next important step would be to find out how changes in plant traits affect the long-term viability of plant species in fragmented habitats. To do so, comparative analyses of long-term demographic data between populations in fragmented and continuous habitats are required. The most accurate picture of the role of habitat fragmentation as a selective pressure ideally requires the consideration of the entire life cycle of the plant, including survival and fertility, as well as the ecological scenario in which all possible interactions occur (Metcalf & Pavard 2007). Demographic components of fitness and all possible interactions that affect demography can then be linked to specific aspects of habitat fragmentation, such as fragment size, isolation, connectivity or edge effects.

One approach for studying the population impact of plant responses to habitat fragmentation is to construct a population model that explicitly includes links between demographic vital rates, responding plant traits and habitat fragmentation. Such hierarchical population models (Jongejans, Huber & de Kroon 2010) can also include correlations between traits and can be used to analytically quantify how much plant responses to habitat fragmentation contribute – both directly and indirectly through correlations with other traits – to population dynamical parameters such as the net reproductive rate or the per capita population growth rate (van Tienderen 2000). These sensitivity analyses can also be used to calculate selection gradients for traits of individuals (van Tienderen 2000; Coulson et al. 2003). Using this approach, Ehrlein & Münzbergova (2009) showed that directional selection on the start of flowering in the perennial herb Lathyrus vernus occurred via both mutualistic and antagonistic interactions. However, these interactions acted in opposed directions and affected different components of fitness. Moreover, the effects of first flowering date on population growth rates varied between years, showing negative selection is some years and positive or no selection in others.

 Whereas the previous models use stage-based matrix models, we believe that evolutionary demography will also benefit from the development of integral projection models (IPMs) (Easterling, Ellner & Dixon 2000; Ellner & Rees 2006) that use continuous, rather than discrete state variables. This is important because many demographic vital rates are continuous functions (e.g. plant size), and demographic consequences
of changes in plant traits can therefore be best described with continuous functions (Jacquemyn, Brys & Jongejans 2010). Moreover, IPMs allow the evolution of important life-history strategies, such as the evolution of flowering strategies, to be studied as functions of size and age. Although the majority of studies have been applied to monocarpic plants (e.g. Rees & Rose 2002; Childs et al. 2003; Ellner & Rees 2006; Hesse, Rees & Müller-Schärer 2008; Kuss et al. 2008; Williams 2009), recent studies have extended the IPM approach to polycarpic plants (T.E.X. Miller, J.L. Williams, E. Jongejans, R. Brys and H. Jacquemyn, unpublished data). Because vital rate functions may vary between years, extending the IPM framework to stochastic environments allows stochastic variation to be incorporated into the calculation of population parameters (Childs et al. 2004; Rees et al. 2004, 2006; Ellner & Rees 2007; Metcalf et al. 2008). Rees & Ellner (2009) recently provided a very thorough outline of how to apply IPMs to stochastic environments using a mixed models framework.

A few animal studies provide an exciting evolutionary demography outlook of these hierarchical population models using IPMs as modelling framework (Coulson et al. 2010). For instance, Ozgul et al. (2010) used a long-term data set to show how changes in various life-history components contributed to larger body masses and increased population size in yellow-bellied marmots. They showed that earlier emergence from hibernation and earlier weaning of young led to a longer growing season and larger body masses before hibernation. To assess the role of phenotypic and genotypic variances in driving population dynamics of species, Coulson et al. (2010) developed models that generated insights into the joint dynamics of populations, quantitative characters and life history. Using the IPM framework, they developed a theoretical model that linked IPMs, the Price equation, generation length and heritability estimates. The key finding of their approach was that changing any of the character-demography functions generated a wide range of eco-evolutionary dynamics. To apply these new approaches to plants, the heritability of the involved traits in the field must be known. However, parent–offspring relationships are rarely known in plant demography studies, and, to our knowledge, there are no studies that have used these models for plants. We therefore argue that future research should incorporate the ecological and evolutionary factors that drive population dynamics of plant species to get better insights into the evolutionary aspects of fragmentation for plant species. Ideas exist to bridge the gap between genetic and demographic studies (Metcalf & Mitchell-Olds 2009), and we expect important theoretical and empirical progress in this field in the coming years.

Spatial dynamics are inherent to the study of the evolutionary effects of habitat fragmentation. We have already discussed the effects of fragmentation on seed dispersal and gene flow. Dispersal components can be added to hierarchical population models in a very similar way as demographic components (Jongejans, Huber & de Kroon 2010). The resulting spatial population models can be spatially explicit using simulations or spatially implicit using either a meta-matrix approach (Hunter & Caswell 2005) to study metapopulations or an invasion wave approach. The latter integro-difference equations approach was developed by Neubert & Caswell (2000) and can be used to analyse differences in the spatial spread of different populations (Caswell, Lensink & Neubert 2003; Jacquemyn, Brys & Neubert 2005; Jongejans et al. 2008). This invasion wave approach was recently combined with IPMs into a spatial integral projection model (SIPM) that includes both demography and dispersal with continuous state and trait variables (Jongejans et al. 2011). Stochastic versions of all these models are becoming available as well as tools to analyse transient dynamics in addition to asymptotic dynamics (Caswell, Neubert & Hunter 2011; Schreiber & Ryan 2011).

Another promising approach that does not involve plant traits, but analyses various aspects of demographic vital rate differences between populations involves a recent extension of stochastic Life Table Response Experiment (SLTRE) analyses (Davison et al. 2010). These analyses are based on simple matrix models and on Tuljapurkar’s (1990) small-noise approximation of stochastic population growth (SNA-LTRE; Davison et al. unpublished data; Jacquemyn et al. 2011). This approach allows the quantification of contributions from: (i) mean vital rates, (ii) differential variability of vital rates, (iii) correlations between vital rates and (iv) elasticities of vital rates. As such, these four components provide important information about (i) gross differences in performance between populations, (ii) responses of vital rates to environmental fluctuations, (iii) demographic trade-offs or synchrony of stage transitions and (iv) differences in local selection pressures.

Using this approach, Davison et al. (unpublished data) used fragmented populations of the perennial herb _Anthyllis vulneraria_ to show that scaled contributions of elasticity were significantly larger in shallow (<10 cm) soils than in deep (>10 cm) soils, suggesting stronger selection pressures in populations occurring in sites with shallow soils. Given that increased periods of thermal stress and drought are expected to produce directional selection, these results thus suggest that local selection pressures may be more important in shallow soils, where the growing environment is the harshest. Scaled contributions of variability also tended to be larger in deeper soils, whereas contributions of correlation were not related to soil depth. This can be explained by the fact that deeper soils maintain moisture longer into the dry season, whereas shallower soils dry out quickly. Deeper soils also spend more of the year in high-moisture states and vary more between years based on annual rainfall. In contrast, shallow soils spend more of the year in low-moisture states and therefore vary less between years. Finally, the finding that correlation contributions were not related to soil depth suggests that extreme weather conditions affected correlations in similar ways, independent of soil moisture content.

**Conclusions**

In fragmented habitats, three types of evolutionary responses are possible. Habitat fragmentation may (i) reduce population genetic diversity through genetic drift, (ii) drive adaptive changes in plant traits and increase individual plant fitness in a
fragmented landscape or (iii) incur changes that at first sight appear to be adaptive in the short term, but turn out to be maladaptive in the long term, resulting in decreasing fitness and in evolutionary suicide of the fragmented population. The results presented here highlighted several plant traits that may be subject to micro-evolutionary changes due to habitat fragmentation. However, direct evidence is still limited, and more research is needed to conclude that the observed changes in a particular trait reflect adaptations to the altered environmental conditions imposed by habitat fragmentation or environmentally induced plastic responses. Moreover, since demographic data of the entire life cycle of species are still largely lacking, there is very little evidence that the observed changes in plant traits have marked effects on the long-term viability of these species.

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