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Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species

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Contents

Summary

Habitat fragmentation is one of the major threats to species diversity. In this review, we discuss how the genetic and demographic structure of fragmented populations of herbaceous forest plant species is affected by increased genetic drift and inbreeding, reduced mate availability, altered interactions with pollinators, and changed environmental conditions through edge effects. Reported changes in population genetic and demographic structure of fragmented plant populations have, however, not resulted in large-scale extinction of forest plants. The main reason for this is very likely the long-term persistence of small and isolated forest plant populations due to prolonged clonal growth and long generation times. Consequently, the persistence of small forest plant populations in a changing landscape may have resulted in an extinction debt, that is, in a distribution of forest plant species reflecting the historical landscape configuration rather than the present one. In some cases, fragmentation appears to affect ecosystem integrity rather than short-term population viability due to the opposition of different fragmentation-induced ecological effects. We finally discuss extinction and colonization dynamics of forest plant species at the regional scale and suggest that the use of the metapopulation concept, both because of its heuristic power and conservation applications, may be fruitful.

I. Introduction

During the second half of the 20th century, the rate of species extinction reached an almost unprecedented level in earth's history and some authors (e.g. Thomas *et al.*, 2004) have suggested that the world is experiencing its sixth major extinction event. Four major human-induced processes are responsible for the present biodiversity crisis: (1) over-exploitation of species by hunting and fishing; (2) environmental deterioration, leading to decreased habitat quality (e.g. through eutrophication or salinization); (3) introduction of exotic species; and (4) fragmentation of habitats. The relative contribution of each of these processes to biodiversity loss is not clear, but it has been suggested that habitat fragmentation may be one of the most important threats to species diversity (Wilcox & Murphy, 1985; but see Kellman, 1996).

The habitat fragmentation process encompasses essentially three components (Andrén, 1994): (1) pure loss of habitat; (2) reduction of patch size; and (3) increasing spatial isolation of the remnant habitats. Pure loss of habitat directly leads to species extinction. The role of decreasing patch area and increasing isolation on species diversity, however, is much more complicated and elucidating it has become a major topic in ecological research (reviewed in Thrall *et al.*, 2000). Small habitat fragments can only contain small populations, whereas isolated habitat patches do not receive or send migrants to other fragments. Species become extremely vulnerable to extinction below a certain population size, even when the habitat quality of the fragment where they reside is optimal (Shaffer, 1981; Lande, 1988). Extinction probabilities are expected to increase further when these small populations are isolated from each other, preventing them being 'rescued' from extinction by colonizing individuals from other fragments (Brown & Kodrick-Brown, 1977) and hampering recolonization of empty fragments after extinction (Hanski, 1999). Thus, populations are expected to become extinct when a certain threshold value of patch size and isolation is reached.

A second important consequence of decreasing fragment area is not directly related to the population size of the occurring species, but to the relative increase of the edge length of the habitat fragment, which allows potentially negative edge effects to penetrate into the fragment and affect the viability of the occurring species. Edge effects can be defined as the flux of matter, energy and species directed from the landscape matrix into the habitat fragment, and their extent increases significantly in highly fragmented landscapes (Ryszkowski, 1992).

It is important to note that in reality all landscapes and habitats are naturally heterogeneous and in a certain sense fragmented. Windthrow in a forest or the flooding of a wetland, for example, can create naturally fragmented habitats. Natural landscape heterogeneity, however, generally differs from human-induced fragmentation in terms of the smaller temporal and spatial scale and the higher degree of connectivity between the remaining fragments (Haila, 1999). Therefore, it can be expected that many species are more or less adapted to a certain degree of natural habitat fragmentation.

Reviews of the effects of habitat fragmentation on more than one aspect of plant species biology are rare in literature (but see Eriksson & Ehrlen, 2001). Most reviews deal with specific issues such as population genetics (e.g. Ellstrand & Elam, 1993; Young *et al.*, 1996), metapopulation dynamics (e.g. Husband & Barrett, 1996; Freckleton & Watkinson, 2002) or pollination biology (e.g. Kwak *et al.*, 1998; Aizen *et al.*, 2002; Wilcock & Neiland, 2002). Moreover, to our knowledge, a forest-habitat-centred approach is completely lacking so far.

Here we review the reported effects of forest fragmentation on the performance of forest plant species and on the resulting changes in plant community composition and species richness. We start from the theoretically expected biological consequences of habitat fragmentation and confront empirical data with these predictions. We focus on herbaceous plant species from temperate regions and pay special attention to specific life-history features such as seed dispersal mechanisms, seed longevity, generation time and clonality, which may affect the response of forest plant species to fragmentation. We also focus on the large-scale spatial and temporal dynamics of fragmented forest plant populations. Finally, we deal with the important but almost neglected role of forest patch turnover on plant population persistence.

II. Forest plant diversity in a historical perspective

A major difference between forest and other vegetation types, such as grassland and heathland, is that forests are the climax vegetation in many parts of the world. This implies that when a nonforest land-use type is abandoned, spontaneous regeneration of the forest will occur. The most important consequence of this regeneration cycle is that the fragmented forest landscapes of Europe and the eastern part of the USA exist as a mixture of fragments of different ages and sizes (Fig. 1). This contrasts with other anthropogenically fragmented systems such as heathland and calcareous grassland where fragmentation has mainly resulted from the abandonment of specific management regimes (e.g. Piessens *et al.*, 2005).

Early successional forest patches differ strongly from mature forests in terms of vegetation structure, vegetation composition and soil characteristics. Early on, British ecologists recognised the major importance of forest history in both the ecology and nature conservation value of forests (Rackham, 1980; Peterken, 1981). In this context, not only the length of time since establishment (i.e. the age of the trees) but also the notion of forest continuity is important (Rackham, 1980). Sites that have been continuously wooded since a certain reference date in the past are referred to as ancient forests. This continuity is not broken by forest management such as coppicing or clear-cutting but only by an alternative land use such as cultivation (Peterken, 1996). The reference date in the past varies between regions and countries (e.g. 1600 in Britain; 1775 in Belgium) (Hermy *et al.*, 1999), and reflects the availability of the first
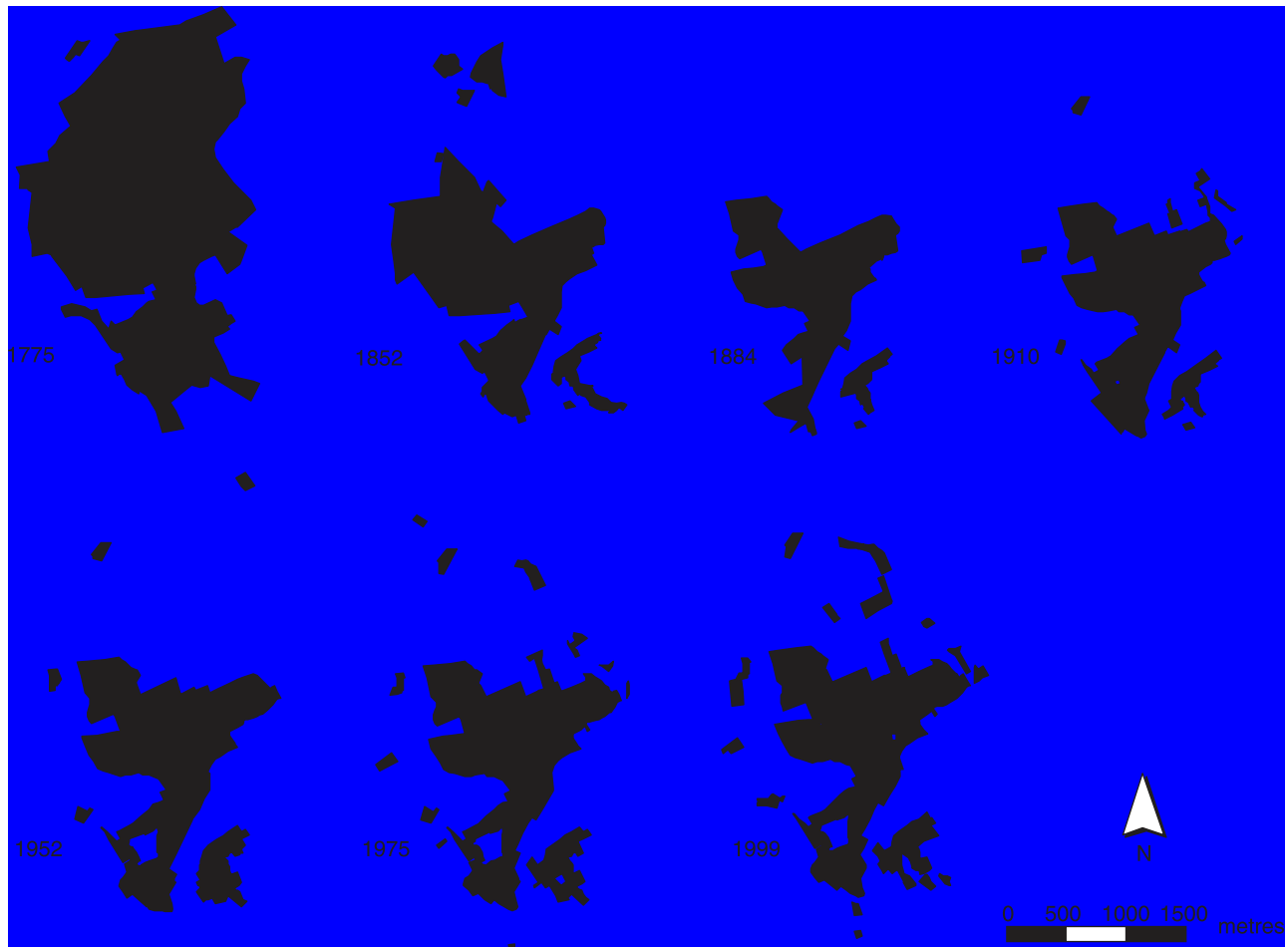
Fig. 1 The forest fragmentation process in a typical landscape in western Belgium between 1775 and 1999 (Raspaillebos, 50 km to the west of Brussels). The figure illustrates the three components of the fragmentation process: habitat destruction, decreasing fragment area and increasing fragment isolation. Also, the phenomenon of patch turnover is illustrated by the continuous emergence and disappearance of forest fragments. The total area of the forest complex decreased from 512 ha in 1775 to 128 ha in 1884 and then increased to 175 ha in 1999. The total area of the small fragments surrounding the central large fragment increased from 2 ha in 1775 to 35 ha in 1999.

detailed land-use maps. Recently established forests remain different from ancient forest in terms of herbaceous plant species composition even hundreds of years after re-establishment (Peterken & Game, 1984). Studying the effects of forest fragmentation on plant community composition should obviously account for these intrinsic differences in community composition between forest fragments of different age. In Section VI, we deal in detail with the effects of patch turnover on regional species persistence and with the factors affecting plant community composition differences between recent and ancient forests.

III. An ecological profile of forest plant species

Most of the typical forest plant traits can be seen as an evolutionary adaptation to the relatively stable forest ecosystem where disturbance is generally infrequent and very localized. Investments in high seed production, persistent seed banks

and long-distance seed dispersal structures may be considered as a waste of energy in this case. Bierzychudek (1982) and Whigham (2004) have extensively reviewed the ecology of temperate woodland herbs in relation to their life history traits. Although a formal comparison between traits of forest plants and plants from other habitat remains to be done (but see Salisbury, 1942), a clear profile emerges from both reviews, and confirms partial data from other sources (Hermy *et al.*, 1999; Verheyen *et al.*, 2003). Most forest plant species are long-lived perennials that are able to reproduce clonally. Empirical studies and demographic projections provide evidence of extremely long life spans for perennial forest plants (Inghe & Tamm, 1985; Cain & Damman, 1997; Ehrlén & Lehtilä, 2002). Using matrix population models, Ehrlén and Lehtilä (2002) inferred an average life span of 64 yr for forest species as opposed to 22 yr for species from open habitats. Clonal reproduction, on the other hand, can be considered as an alternative life cycle loop that allows population persistence

when the normal reproductive cycle cannot be completed (i.e. seed production, germination and recruitment) (Eriksson, 1996). Klimes *et al.* (1997) estimated that 85% of all European herbaceous forest plants show some form of clonal propagation (fig. 7 in Klimes *et al.*, 1997). Most forest plant species also lack specific adaptations for long-distance seed dispersal and their seed production is generally low (Bierzychudek, 1982; Hermy *et al.*, 1999). Seed dispersal distances typically do not exceed a few metres (Whigham, 2004). Long-distance seed dispersal events over hundreds of metres are rare, although not impossible (Cain *et al.*, 1998; Vellend *et al.*, 2003). Forest plant species generally produce large seeds that are not persistent in the soil (Bossuyt & Hermy, 2001), a pattern consistent with the widely recognized trade-off between seed longevity and seed size (Hodkinson *et al.*, 1998). Regarding the breeding system, three equally represented categories emerge: self-compatible, self-incompatible and partially self-compatible (Whigham, 2004). Almost all (90%) of the angiosperms are pollinated by animals, mainly insects (Wilcock & Neiland, 2002), and there is no reason to expect that this is different for forest plant species.

IV. Habitat fragmentation and population viability

In this section, we review the rather well-developed theory regarding the effects of habitat fragmentation on population viability, and we evaluate whether the available empirical evidence for forest plant species fits these theoretical predictions.

1. Population genetic consequences of small population size and isolation

Increased spatial isolation and decreased population size may lead to the erosion of genetic variation and increased genetic differentiation among populations through genetic drift, increased inbreeding and reduced gene flow between populations (Schaal & Leverich, 1996; Young *et al.*, 1996). Genetic drift is the random change in allele frequencies because alleles transmitted from the parental population to the offspring are a random sample of all available alleles. Genetic variation in small populations is likely to be reduced and allele frequencies become highly unpredictable due to genetic drift. Because the effect of genetic drift on genetic diversity largely depends on the number of generations during which the population remains small (Young *et al.*, 1996), it can be expected that the loss of variability through drift is relatively small in forest plant species with long generation times, prolonged clonal growth, low seed production and limited seedling recruitment. Unfortunately, there are few population genetic studies dealing with herbaceous forest plant species that allow testing this prediction. Reduced allelic diversity was found in small populations of *Viola pubescens* and *Primula elatior*, both of which show repeated seedling recruitment (Van Rossum *et al.*, 2002; Culley & Grubb, 2003). Jacquemyn *et al.* (2004), however,

could not confirm this trend for *P. elatior*. Neither the strongly clonal and rarely recruiting perennial *Maianthemum bifolium*, nor the perennial *Microseris lanceolata*, showed a relation between population size and population genetic diversity (O. Honnay, University of Leuven, unpublished results; Prober *et al.*, 1997, respectively). Young *et al.* (1996) suggested that species with long generation times and low seedling recruitment lose genetic diversity mainly through founder effects and population bottlenecks, in other words sudden reductions in population size. This is also what Tomimatsu & Ohara (2003) invoked to explain the low genetic diversity observed in small and isolated populations of the perennial *Trillium camschatcense* in Japan. Reduced genetic diversity may decrease the potential of a species to adapt to (slow) environmental change. In the relatively short term, reduced genetic diversity in a population may contribute to increased inbreeding and to lowered levels of heterozygosity. In small populations, the probability of bi-parental inbreeding or inbreeding through increased self-fertilization increases. Increased homozygosity is expected to directly affect fitness through inbreeding depression (Ellstrand & Elam, 1993). Studies that related forest fragmentation with decreased heterozygosity and reduced fitness are rare, however. Neither Tomimatsu & Ohara (2003) nor Van Rossum *et al.* (2002) found an effect of population size on heterozygosity for the forest plants *T. camschatcense* and *P. elatior*, respectively. On the other hand, Culley and Grubb (2003) found a heterozygosity deficit in small (< 300 individuals) populations of *V. pubescens*. This deficit was attributed to increased inbreeding, mainly by increased self-pollination in small and isolated populations due to a decline in the abundance of solitary bees, the main pollinator of the species, in small and isolated forests. This example shows the interrelatedness of fragmentation-related genetic effects and effects of changes in the pollinator community. The latter will be dealt with in Section IV.3.

Finally, increased fragmentation will increase genetic differentiation between populations (Young *et al.*, 1996). In the absence of gene flow (through seeds and/or pollen) between fragmented populations, and given a stable population structure, random genetic drift will increase genetic differentiation among populations (Schaal & Leverich, 1996). Because most herbaceous forest plants are insect pollinated and because most pollinating insects do not travel large distances (Wilcock & Neiland, 2002), especially when they have to cross a hostile landscape matrix, the proportion of pollen flow in the total gene flow between isolated populations is probably rather low. Consequently, long-distance gene flow between fragments occurs mainly by accidental seed transport through endo- or exo-zoochory (e.g. Vellend, 2003). A very low level of gene flow (*c.* 1 recruiting seed per generation) is sufficient to reduce genetic differentiation due to genetic drift (Wright, 1931). High levels of genetic differentiation (30–40%) were found for Anemona *nemorosa*, *Viola riviniana* and *V. pubescens* (Stehlik & Holderegger, 2000; Auge *et al.*, 2001; Culley & Grubb,

Table 1 Two counteracting processes determine the degree of genetic erosion and population differentiation of forest plant populations in fragmented landscapes

		Sensitivity to small population size	
		LOW Long generation time (limited seedling recruitment)	HIGH Short generation time (repeated seedling recruitment)
Sensitivity to isolation	HIGH Low seed dispersal capacity	Low differentiation (*Maianthemum bifolium*, *Trillium camschatcense*)	High differentiation (*Anemone nemorosa*, *Viola* *riviniana*, *Viola pubescens*)
	LOW High seed dispersal capacity	?	Low differentiation (*Primula elatior*)

2003, respectively). Although in some cases the studied species exhibited long lifetimes (genets of more than 200 yr old were discovered in *A. nemorosa*), all these species are characterized by extensive seed set and repeated seedling recruitment, which are enabling processes of genetic drift. Genetic differentiation was found to be much lower (*c.* 10%) for the strongly clonal *M. bifolium*, characterized by very low seedling recruitment and extreme seed dispersal limitation, and in small populations of *T. camschatcense* (Tomimatsu & Ohara, 2003). The perennial and abundantly recruiting *P. elatior*, exhibiting very good seed dispersal between fragmented forests, showed low population differentiation (*c.* 5%) (Van Rossum *et al.*, 2002; Jacquemyn *et al.*, 2004).

The available studies show how dispersal between fragments on the one hand and long generation times and prolonged clonal growth on the other hand may interact in determining population genetic differentiation (Table 1). The highest reported percentages of population differentiation (30–40%) for forest plants corroborate the average percentages for long-lived perennials and species of late successional habitats reported by Nybom and Bartish (2000). These percentages are still well below the reported range of population differentiation for annuals and short-lived perennials (40–70%).

As a general conclusion, we can say that for at least some species, even small populations may not have lost alleles, and that they may still contain high levels of genetic variability. It appears that knowledge of the degree of seedling recruitment, the extent of clonal reproduction and the seed dispersal capacity may give a first indication of the susceptibility of the populations to genetic erosion and genetic differentiation (Table 1). It is clear that this trend may be complicated by the degree of self-compatibility of the species and, although we excluded genetic studies covering a geographical gradient (e.g. Griffin & Barrett, 2004), also by the degree of spatial isolation of the populations.

2. Decreased mate availability in self-incompatible forest plant species

Self-incompatibility is the failure of a fertile hermaphroditic seed plant to produce zygotes after self-pollination (De Nettancourt,

1977). Almost one third of all forest plant species show a self-incompatible breeding system and almost all of them show prolonged clonal growth. The latter can strongly affect the number of genotypes in a population (for an extensive treatment, see Honnay & Bossuyt, 2005). Certainly under unfavourable environmental conditions such as low light availability through canopy closure, forest plant species may alter their growth form and exhibit prolonged clonal growth (e.g. Kudoh *et al.*, 1999; Lezberg *et al.*, 2001). The direct consequence of prolonged clonal reproduction and suppression of sexual reproduction is that locally less-adapted clones become outcompeted by expanding ramets of more adapted genotypes (Hartnett & Bazzaz, 1985; Eriksson, 1989). When the environmental pressure is diminished, for example by the opening of the canopy through forest management, sexual reproduction will be hampered or even completely impossible (i.e. sexual extinction, as in Eckert, 2000) due to very low genotypic diversity and lack of compatible pollen. Such a loss of genotypes has been described for the North American prairie plant *Asclepias meadii* (Schaal & Leverich, 1996). A similar process has resulted in monoclonal patches of *Maianthemum canadensis* in North American forests (Worthen & Stiles, 1988) and lowered genotypic diversity of the understorey species *Uvularia perfoliata* (Kudoh *et al.*, 1999). Thus, although prolonged clonal growth may offer an escape route from genetic drift, the consequences in the long term may be complete sexual extinction of the population. Although the described process is initially more related to forest management than to fragmentation, it can be expected that genotype loss will occur faster in isolated populations because of the lack of addition of new genotypes through seed inflow (Schaal & Leverich, 1996).

A second mechanism leading to sexual extinction in prolonged clonally propagating species is summarized by the *Somatic mutation theory of clonality* (Klekowski, 1988, 1997), which states that sexual reproductive success is inversely proportional to longevity. The older and larger a clone becomes, and the longer the periods between sexual reproduction between clones, the more likely that mutations will be accumulated that decrease the probability of successful sexual reproduction

in the population (Lamont & Wiens, 2003). Mutations inducing infertility will contribute to an acceleration of the above described process towards monoclonal patches because the number of available fertile genotypes for pollination further decreases. The precise role of mutations in sexual sterility, however, remains an open question (Eckert, 1999), but long-lived forest plants can be expected to be very susceptible. All of this suggests that forest management and the spatial isolation of populations may interact with and affect the genetic structure of forest plant populations. More work on the relation between forest management, clonal growth, isolation and genotypic diversity is necessary.

3. Changed interactions with pollinators in small and isolated populations

Most forest plant species show clonal propagation to some extent (see Section IV.2), but almost all of them also reproduce sexually. Sexual reproduction in forest plant species is important because it helps maintain genetic diversity within populations and because only seeds (or fruits containing seeds) are capable of long-distance dispersal, which may be essential in continuously changing landscapes (see Section VI.2). Like most other plant species, forest plant species also rely on animals (especially insects) for effective pollination and sexual reproduction. Fragmentation may negatively affect pollinator abundance and diversity in habitat fragments (Kearns *et al.*, 1998). Fragments can become too small to sustain pollinator communities or too isolated to attract a large diversity of pollinators (Steffan-Dewenter & Tscharntke, 1999), both of which affect pollinator efficiency and therefore the reproductive success of plant species. In addition to these direct effects of fragmentation through changes in pollinator guilds, indirect effects associated with altered pollinator behaviour and flight patterns within patches have been shown to affect reproductive success of forest plant species in fragmented forests (Didham *et al.*, 1996). Patterns of pollinator behaviour depend on the number and density of individuals in a population (Kunin, 1993, 1997). The relative importance of direct and indirect effects of fragmentation on pollination efficiency and hence on reproductive success can be expected to vary greatly among species, depending on the degree of dependence on pollinators for successful reproduction (generalist vs specialist species) (Bond, 1994; Waser *et al.*, 1996) and on the breeding system (Aizen *et al.*, 2002).

Although studies investigating the effects of forest fragmentation on pollinator community structure are very rare, the few available studies point to a clear decreased pollinator diversity and abundance in small forest fragments (Murcia, 1996). Aizen and Feinsinger (1994a) showed that both the abundance and species richness of native euglossine bees significantly declined in Argentinean small (< 1 ha) forest fragments compared to large (2–6 ha) fragments and continuous forest. Forest fragments were situated in an intensively used matrix of agricultural land, unsuitable for pollinating insects.

Further investigation of reproductive success of 16 plant species in these forest fragments showed that 81% of the plant species exhibited a significant decline in pollination and 73% exhibited a significant decline in seed set in the small fragments compared with the continuous forest (Aizen & Feinsinger, 1994b). The median decrease in the level of seed set between different species between small fragments and continuous forests was 20%.

In addition to changes in pollinator community structure, the small population size associated with the small patch sizes makes populations rather inconspicuous for pollinators, leading to lower visitation rates and hence decreased reproductive success. Sih and Baltus (1987), for example, found strongly reduced reproductive success in small populations of *Nepeta cataria* at the edges of woodlands. Similar results were obtained by Jacquemyn *et al.* (2002) and Aguilar and Galetto (2004), who showed decreased reproductive success in small populations of the forest herbs *Primula elatior* and *Cestrum parqui*, respectively. In both cases, a decreased number of visits in small populations partly explained the lower reproductive success. In the case of *P. elatior*, reduced mate availability strengthened the effects of small population size. This distylous species has two style morphs: a long (pin) and a short-styled (thrum) morph (Jacquemyn *et al.*, 2002). Successful reproduction is only possible between the two different morph types. In very large populations, it can be statistically expected that the morph occurrence is 50%. In very small populations, however, chance effects will bias morph type occurrence and hamper or even prevent successful reproduction (Fig. 2a,b; see also Endels *et al.*, 2002). Similar effects of limited mate availability on plant reproduction were demonstrated for the boreal forest plant *Linnaea borealis* (Wilcock & Jennings, 1999).

The strongly reduced reproductive success in small populations of the self-incompatible *P. elatior* may indicate that specialist species or species characterized by a self-incompatible breeding system should be more susceptible to fragmentation than generalist plant species or species with a compatible breeding system. However, this does not seem to be the case. Based on a review of 25 studies and 46 plant species, Aizen *et al.* (2002) found no significant relationship between the breeding system (self-compatible or self-incompatible) of a species and its response to fragmentation. This does not mean that the effects of lowered mate availability on population persistence are not important. These effects may be compensated by other habitat fragmentation-induced changes on population fitness through edge effects, pollinator limitation or genetic erosion, for example (see also Ashworth *et al.*, 2004). This is another piece of evidence showing that generalizations on the effects of habitat fragmentation are very difficult to make and that the ultimate effects on population fitness may be difficult to disentangle.

Even though these results demonstrate direct effects of forest fragmentation on reproductive success, it is not clear whether these reductions translate into reduced recruitment
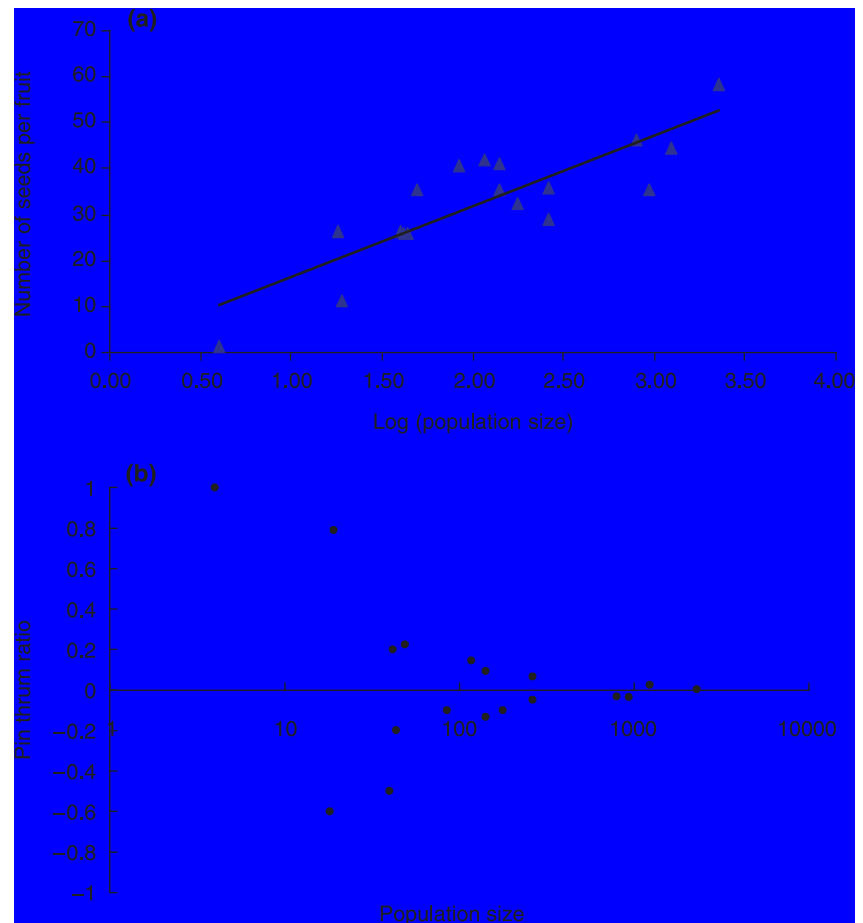
Fig. 2 Reduced reproductive success in small populations of *Primula elatior* (a) may be at least partially explained by reduced mate availability due to a bias between short- and long-styled individuals in small populations (b) (from Jacquemyn *et al.*, 2002).

rates and low population growth rates. There is some evidence that a reduced seed set may lead to decreased recruitment rates and hence to smaller growth rates. For individuals of *Trillium ovatum* occurring along clear-cut edges, recruitment was nearly nonexistent, and expected population declines ranged from 54% to 83%. The reduced recruitment rates at the forest edge were partly a result of a decreased seed production due to lower pollinator activity (fruiting in forest edge populations was more pollen-limited than in others) and increased seed predation (Jules, 1998; Jules & Rathcke, 1999). More research on the relationship between reproductive output and recruitment rates is needed to understand fully the impact of reduced pollination success on plant population persistence.

4. Edge effects

Forest fragmentation also implies a relative increase in edge habitat. For an identical shape, a small forest fragment has a higher edge : core ratio than a large forest fragment. Hence, edge effects become much more important in highly fragmented landscapes. It has been suggested that the effects of habitat fragmentation through edge effects may be more important than area and isolation effects per se (Turner *et al.*, 1996;

Harrison & Bruna, 1999). Edge effects may affect forest plant dynamics such as regeneration and interspecies competition and, as described above, also plant–animal interactions (predation, seed dispersal and pollination) (Murcia, 1995). The changed microclimate at the forest edge, characterized by increased light penetration, increased air and soil temperature, decreased air humidity and an increased level of agro-nutrients in the soil, directly affects population dynamics of the occurring plant species.

In temperate forests, most authors report a transient zone between the landscape matrix and the unaffected core area of the forest of between 20 and 50 m, depending on the aspect of the edge (in the northern hemisphere, edge effects are much more pronounced along south- than along north-facing edges) (e.g. Palik & Murphy, 1990; Matlack, 1993; Williams-Linera *et al.*, 1998; Honnay *et al.*, 2002b; and many others).

Studies focusing on changes in the population dynamics of forest plant species near edges, and thus giving direct insight in the ecological mechanism behind community composition changes, are much less common. Jules (1998) found a dramatic decrease in the recruitment in *T. ovatum* closer than 100 m to clearcut edges. In addition to changes in pollinator behaviour (see Section III.3), the ecological mechanisms behind this

demographic change were a direct consequence of a changed microclimate in the forest edge zone. Similar results were obtained for *T. camschatcense* where recruitment of juvenile stages through seed germination was even so strongly limited near forest edges due to microclimate changes (Tomimatsu & Ohara, 2004). These negative edge effects on plant reproduction cannot be generalized, however. In Australian mallee woodland strips, edges were characterized by decreased predation rate and increasing undamaged fruit production of the understorey species *Eremophila glabra* (Cunningham, 2000). Although edge effects in general appear to affect population viability negatively by hampering successful recruitment, complex interactions between abiotic and biotic edge processes hamper generalization.

Finally, edge effects may also enhance the invasion of the forest by species not normally occurring, or naturally occurring only at low densities in forest edges. Microclimate changes which are typical for edges often give extra competitive advantages to these invasive species over the naturally occurring forest plant species. Yates *et al.* (2004) found significantly higher abundances of the exotics *Rosa multiflora* and *Lonicera japonica* in forest edges. The effects on the naturally occurring forest plants species were not clear, however. Brothers & Spingarn (1992) and Honnay *et al.* (2002b) found that limited light availability in the forest core prevented most exotics and weedy species from penetrating more than a few metres into the forest edge. Generally, forests seem quite well buffered against invasion of nonforest plants due to the rapidly decreasing light availability when entering the forest fragment. Moreover, most forest fragments still possess a relatively large undisturbed core area. The remaining unaffected core area can be calculated given the shape of the forest fragment, the area, and the average penetration distances of the edge effects (Laurance & Yensen, 1991).

V. Evidence of community composition changes due to habitat fragmentation?

The ultimate consequence of reduced population viability is local extinction, leading to the disappearance of the species from the fragment, and consequently to decreased species richness and altered community composition. Hence, the study of long-term fragmented forest fragments may yield patterns that could not be revealed by relatively short-term, population-centred studies. Do small forest fragments contain fewer forest plant species than large forests? The answer to this question is undoubtedly yes (e.g. Game & Peterken, 1984; Peterken & Game, 1984; Dzwonko & Loster, 1989). The ecological mechanism behind this phenomenon, however, mainly seems to be lower habitat diversity in small forests, not increased extinction risk for small populations. Large forest fragments are characterized by a higher soil and geomorphologic diversity and a higher diversity of tree species, offering more microhabitats for plant species. To our knowledge, studies focusing on species richness in forest fragments have never attributed

impoverished plant diversity in small fragments to patch area per se, in other words to increased extinction risks of small populations (Helliwell, 1976; Weaver & Kellman, 1981; Game & Peterken, 1984; Peterken & Game, 1984; Simberloff & Gotelli, 1984; Dzwonko & Loster, 1989; Honnay *et al.*, 1999a,b). A more powerful approach, focusing on patch occupancy of individual species recently yielded other conclusions. Dupré and Ehrlén (2002) showed that the occurrence of 10 out of 57 forest plant species in forest fragments was related purely to area effects. Jacquemyn *et al.* (2003) demonstrated area effects for 30 out of 59 forest plant species, and Kolb and Diekmann (2004) for 36 out of 79 species in base-rich forests and for 9 out of 43 species in base-poor forests. Although these studies all agree that the impact of habitat quality and habitat diversity on species occurrence is paramount, they provide at least indirect evidence of higher extinction rates for some species in small habitat fragments.

In Section IV, we showed that fragmentation-induced processes indeed affect the reproductive success of many forest plant species. The studies at the species richness and patch occupancy level, however, seem to suggest that these processes have not resulted in large-scale, fragmentation-driven extinction of herbaceous forest plant species. Yet most observed extinction events appear to be deterministic and the result of changing environmental conditions through changed forest management (Honnay *et al.*, 1999a), disturbance (Aizen & Feinsinger, 1994b) or eutrophication (Lameire *et al.*, 2000). Why have the observed changes in genetic structure, plant–animal interactions and microclimate in forest fragments not yielded a clear decline in species richness? The main reason is very likely that a lot of forest plant species are long-lived perennials that form remnant populations by prolonged clonal growth, exhibiting a lowered susceptibility to habitat fragmentation. The result of this persistence is that current patch occupancy patterns for many long-living and clonally propagating species may be not in equilibrium with the present degree of habitat fragmentation (Eriksson & Ehrlén, 2001). This means that the time period since forest fragmentation (in most studies *c.* 100 yr, sometimes up to 250 yr) may be not sufficient to monitor extinction, and that we are dealing with a so-called extinction debt (Tilman *et al.*, 1994; Hanski & Ovaiskanen, 2002) in our fragmented forests. In this case, patch occupancy reflects the historical distribution of habitat fragments rather than the actual distribution. Very recently, Lindborg and Eriksson (2004) found evidence of an extinction debt in Swedish seminatural grasslands. Relating historical connectivity with the current species richness of forest fragments awaits study.

Effects of habitat fragmentation, which can indeed be noticed at the individual population level, and which are certainly affecting ecosystem integrity, are sometimes also difficult to disentangle and may have opposing and even compensating effects on reproductive success. Increased edge effects, for example, may lead to increased predation of seeds but also to increased pollination. Likewise, genetic drift due to reduced population

size may be counteracted by increased clonal growth due to inappropriate or absent forest management and to canopy closure in small forest remnants.

Although most authors studying species occupancy patterns have integrated isolation measures in their analysis, it is impossible to derive whether isolated populations are more prone to extinction than their less isolated counterparts. In other words, it is impossible to find evidence of a rescue effect due to a constant inflow of new individuals. The problem is that the effects of isolation have always been studied in fragmented forest landscapes, which are a mixture of fragments of varying ages. Age and isolation have no independent effects on species occurrence (Deckers *et al.*, 2005). When the effects of isolation on species occurrence are demonstrated, this reflects the inability of a species to colonize a recently established forest patch from an ancient source patch, rather than providing evidence for an additional negative effect of isolation on the extinction probability.

VI. Adding a regional dimension: forest plant species and metapopulation dynamics

1. A metapopulation concept for (forest) plant species?

Ouborg and Eriksson (2004) recently stated that the metapopulation concept is probably the most productive theoretical framework in stimulating studies on regional population dynamics and has contributed to our understanding of large-scale population dynamics, spatial distribution of species, dynamics of species interactions and, last but not least, the effects of habitat fragmentation on biodiversity. A metapopulation can be defined as a collection of local populations, discrete (or relatively discrete) in space, interacting with each other by dispersal of individuals or by gene flow (Hanski & Gaggiotti, 2004). The key idea of the metapopulation is that a species can become locally extinct but can persist at the landscape level by recolonization of empty but suitable habitat patches.

The question of whether plants in fragmented habitats are behaving as a metapopulation has been the subject of a vivid debate (e.g. Husband & Barrett, 1996; Freckleton & Watkinson, 2002; Ouborg & Eriksson, 2004). The answer to this question has far-reaching consequences. When plant species are indeed behaving as a metapopulation, plant ecology and plant biology may not only benefit from the enormous heuristic power of metapopulation theory but also from its practical conservation applications. Several arguments have been given as to why the metapopulation concept may be or may be not applicable to plant species. The key question for the future will be whether metapopulation theory will appear flexible enough to incorporate these arguments, or whether parallel spatial theories should be developed. Ouborg and Eriksson (2004) have given an overview and evaluation of the critics of the metapopulation concept for plants. These critics are fourfold. Two are related to the definition of suitable habitat

patches for plants (Ehrlén & Eriksson, 2000) and to the simplifying dichotomy of the landscape (suitable/not suitable) in a metapopulation model which is unrealistic for plant species (Jules & Shahani, 2003; Murphy & Lovett-Doust, 2004). The two most important features of the criticism are directly related to the lack of any metapopulation dynamics, as follows.
1 Many plant species are extremely long-lived or may produce long-term persistent seeds. This makes it virtually impossible to monitor extinctions as the species form so-called remnant populations (Eriksson, 1996).
2 Plants have a limited dispersal; hence colonization capacity and patch connectivity are at least extremely low in plant (meta)populations (Bullock *et al.*, 2002).

As has already extensively been illustrated, forest plant species may escape unfavourable environmental conditions by increased clonal growth, and they may exhibit very long life spans. Empirical data (e.g. Harmer *et al.*, 2001) and indirect evidence from patch occupancy studies (Dupré & Ehrlén, 2002; Jacquemyn *et al.*, 2003), however, provide evidence that many forest plants indeed have a measurable probability of extinction, even if these probabilities are very small. Similarly, the colonization capacity of forest plant species is extremely low, although there is much evidence available that colonization of recently established forest fragments occurs, albeit at a very slow rate (see Section VI.3). The issue in these cases is to extend the timescale of the metapopulation from years to decades or even centuries, as was recently successfully done for forest plant metapopulations by Verheyen *et al.* (2004).

2. Landscape dynamics and patch turnover

Even if the timescale of the model is extended, one can argue that metapopulation theory as described by the original model (Levins, 1969; Hanski, 1994; Hanski, 1999) is not useful for forest plants. Indeed, extension of the timescale also implies that the timescale of landscape dynamics may become smaller than the scale at which the local population extinctions and colonization occur. Almost all forest landscapes are dynamic due to the disappearance of some forest fragments and to the spontaneous emergence of others (e.g. Jacquemyn *et al.*, 2003). Especially for plant species having no evolutionary adaptations enabling them to cope with large scale disturbance, like most forest plant species, this may have dramatic effects on their persistence in the landscape. Landscape dynamics imply that local species extinctions may be more related to patch destruction than to area effects. Moreover, newly emerging patches may not be directly suitable for colonization by herbaceous forest plants. Thus, the colonization process in the metapopulation is characterized by a significant time lag (Honnay *et al.*, 2002a; Vellend, 2004; Section VI.3) To model the regional dynamics of forest plant species realistically, the destruction and regeneration of habitat patches or the successional pathway in newly established patches should be incorporated into metapopulation models. Metapopulation persistence in a

dynamic landscape can be expected to depend on the complex interplay among: (1) the spatial configuration (area and isolation) of the disappearing and emerging patches; (2) the rate of patch destruction; (3) the rate of patch emergence; and (4) the rate at which patches become suitable for recolonization after patch emergence. These landscape characteristics will interact with a whole range of plant species traits related to dispersal capacity, recruitment rate, age of first reproduction, seed bank persistence, and seed production (Husband & Barrett, 1996; Verheyen *et al.*, 2003), all influencing colonization and extinction dynamics. Recently developed models have only demonstrated the importance of small subsets of these factors (e.g. Amarasekare & Possingham, 2001; Johst *et al.*, 2002; Keymer *et al.*, 2002; Ellner & Fussman, 2003; Hastings, 2003). Johst *et al.* (2002) used a model that accounts for both internal patch population growth and species dispersal capacity. Metapopulations with small population growth rates and short-range dispersal were shown to be unable to persist in very dynamic landscapes. Parameterization of these theoretical models with real plant data remains problematic, however. Verheyen *et al.* (2004) were the first to parameterize a very simple patch occupancy metapopulation model accounting for patch turnover with real data from forest plant species in a fragmented landscape. They showed that a forest turnover rate of as little as 2% yr^{-1} guarantees the extinction of metapopulations of typical forest plants species like *Mercurialis perennis* and *A. nemorosa* within 500 yr. Although the applied model was an oversimplification in terms of the spatial and temporal dynamics of the patches, Verheyen *et al.* (2004) at least showed that the metapopulation concept can be successfully applied for (forest) plant species by extending the temporal dimension of the metapopulation and by introducing a measure for patch turnover.

3. Resilience of forest plant communities

Several studies have demonstrated the consequences of landscape dynamics for forest plant species, and in particular for the ecological restoration of recently established forests in terms of its herbaceous species composition. Because most herbaceous forest plant species are slow colonizers, it can be expected that population establishment will lag behind the restoration of the forest itself. The restoration success will depend on the ability of the diaspores to reach the empty habitat on the one side and on the ability of the diaspores to recruit in the recent forest on the other side (Honnay *et al.*, 2002a). The probability of the occurrence of a forest plant species in a recently established forest does in fact depend on the distance to the ancient source patch (Grashof-Bokdam & Geertsema, 1998; Bossuyt *et al.*, 1999; Jacquemyn *et al.*, 2001; Butaye *et al.*, 2002) and on the amount of ancient forest patches left in the landscape (Vellend, 2003). Honnay *et al.* (2002c) found that *c.* 85% of all occurring forest plant species in the central part of Belgium were dispersal-limited. Dispersal-limited species were simply

unable to colonize newly established forest or showed a strongly decreasing colonization probability with increasing distance from the source patch. It was also shown that colonization was more successful in high-connectivity landscapes (*c.* 50% forest cover) than in low-connectivity landscapes (*c.* 5% forest cover) (Honnay *et al.*, 2002c; Fig. 3). Environmental characteristics of recently established forest patches may also hamper recruitment of the diaspores due to the presence of competitive species (Hermy, 1994). This is especially the case when forests are restored on former arable land having high levels of phosphate in the topsoil. Seed-introduction studies (Ehrlén & Eriksson, 2000) and plant-trait-based approaches (Verheyen *et al.*, 2003) suggest, however, that dispersal limitation is the most important constraint during the colonization process. In general, a time lag of at least 100 yr is realistic between the establishment of the new forest fragment and the colonization of most herbaceous species. Forests more than 2 km away from ancient source forests will probably never completely recover in terms of herbaceous plant species composition (Honnay *et al.*, 2002a). Vellend (2004) has recently used metapopulation theory to model successfully the restoration of recently established forest incorporating the time lag between forest clearance and recolonization of new forests. This time lag was shown to have dramatic effects on patch occupancy of the species, especially when it was large.

4. A concluding paleoecological perspective

During the Quaternary period which began about 2.5 Myr ago, global climate has fluctuated enough to produce more than 20 glacial and interglacial cycles (Broecker & van Donk, 1970). The present interglacial, known as the Holocene, began only 10 000 yr ago. Pollen stratigraphic studies have shown that the current vegetation patterns and communities did not start to appear until a few thousand years ago and that apart from human disturbance, changes in community composition have even occurred the last 1000 yr (e.g. Lindbladh *et al.*, 2000). Hence, modern plant communities can be considered as transitory assemblages of co-occurring species (Hunter *et al.*, 1988). It is clear that, more than in more dynamic ecosystems, the slow colonization- and fragmentation-driven extinction rates of many forest plant species may interact with slowly changing climatic conditions, especially in the current global change context. Therefore, it has been suggested that conservation efforts should incorporate establishing regional forest corridors that allow species to change their geographical distributions (Hunter *et al.*, 1988).

VII. Conclusions

Forest fragmentation affects the demographic and genetic structure of forest plant populations through changed interactions with pollinators, edge effects, decreased migration between fragments, genetic drift and possibly inbreeding depression.
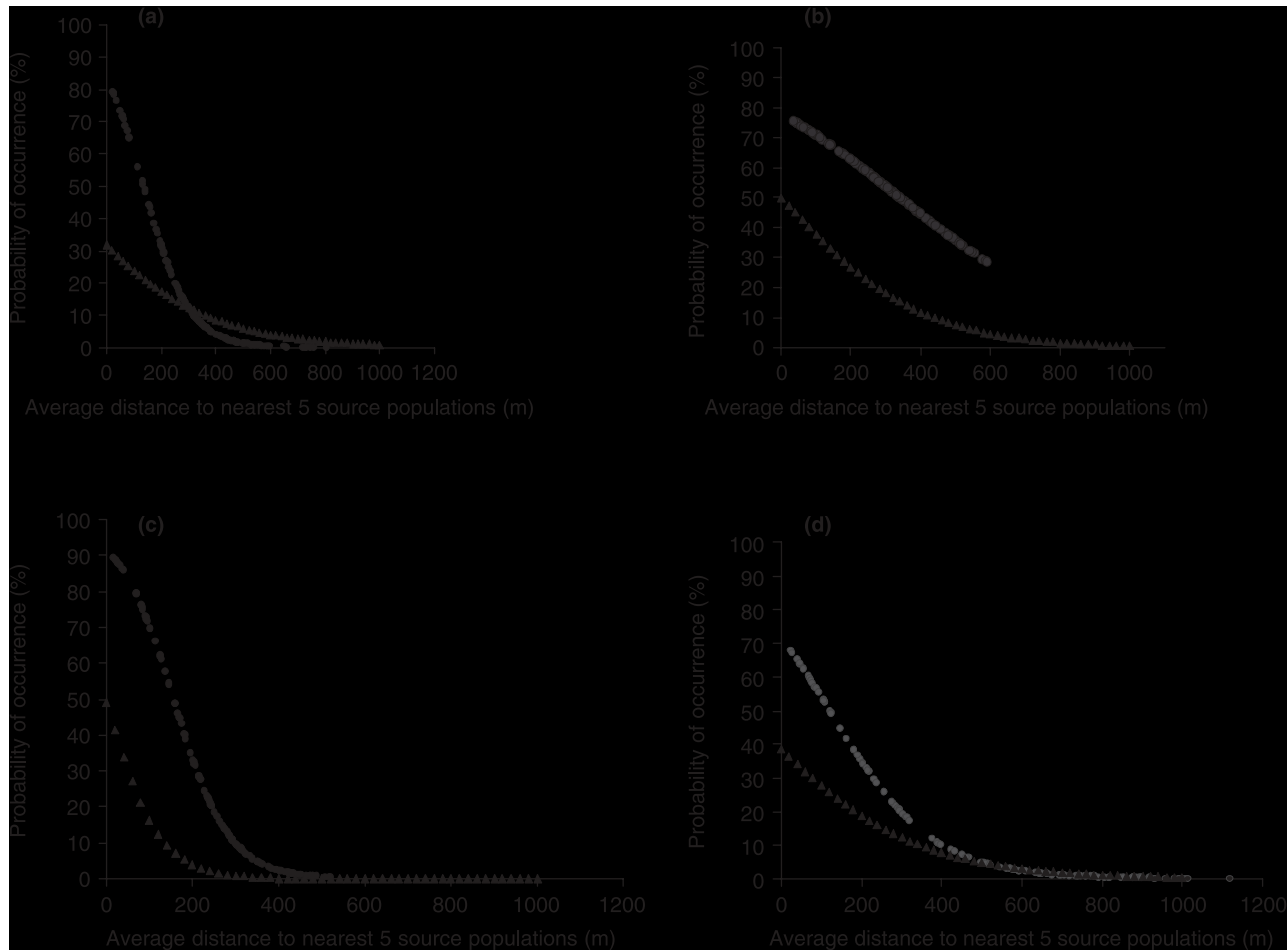
Fig. 3 Estimated probability of occurrence of a plant species in a more recently established fragment as a function of the average distance to the five nearest source populations of that species. For a more fragmented landscape (*c.* 5% forest cover, triangles) and for a high-connectivity landscape (*c.* 50% forest cover, filled circles). (a) *Arum maculatum*; (b) *Geum urbanum*; (c) *Adoxa moschatellina*; (d) *Primula elatior*. (From Honnay *et al*., 2002a.)

Although there is currently no evidence for large-scale extinctions of forest plant species, there is strong evidence that these habitat fragmentation-induced changes do indeed affect the patch occupancy of some species and hence must have led to local extinctions. The typical ecological profile of most forest plant species, especially their ability to form persistent populations through extended and prolonged clonal growth, may be responsible for their slow response to fragmentation. This implies that the currently observed patch occupancy of forest plant species is very likely not in equilibrium with the present landscape configuration, but rather reflects the historical landscape. Moreover, fragmentation effects may sometimes have confounding or even opposite effects on the reproductive success of a species, yielding no net negative result. In this case, it appears that forest fragmentation mainly affects ecosystem integrity, without resulting in reduced short-term population viability or species extinction.

Further population demographic and population genetic studies on forest plant species are needed. It is surprising how few forest plant species have been extensively studied in a fragmentation context. Because of their slow response to fragmentation, long time monitoring of demographic changes and the use of stochastic matrix population projection models over a range of population sizes and different degrees of isolation may be helpful to determine trends in long-term persistence of forest plant species in fragmented forests. In addition, we have argued that a metapopulation approach may be fruitful by expanding the timescale and including patch turnover measures. Parameterization of the models with field data and the introduction of a wide range of plant traits (like dispersal capacity, soil seed persistence, seed production and recruitment rate) may be more fruitful in this context than only simulating varying patch characteristics such as area and isolation.

Acknowledgements

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