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Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity

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Abstract Particularly in the temperate climate zone many forests have, at some moment in their history, been used as agriculture land. Forest cover is therefore often not as stable as it might look. How forest plant communities recovered after agriculture was abandoned allows us to explore some universal questions on how dispersal and environment limit plant species abundance and distribution. All studies looking at the effects of historical land use rely on adequate land use reconstruction. A variety of tools from maps, archival studies, and interviews to field evidence and soil analyses contribute to that. They allow us to distinguish ancient from recent forests and many studies found pronounced differences in forest plant species composition between them. A considerable percentage of our forest flora is associated with ancient forests. These ancient forest plant species (AFS) all have a low colonization capacity, suggesting that dispersal in space (distance related) and time (seed bank related) limit their distribution and abundance. However recent forests generally are suitable for the recruitment of AFS. There is clear evidence that dispersal limitation is more important than recruitment limitation in the distribution of AFS. Dispersal in time, through persistent seed banks, does not play a significant role. Ancient forests are not necessary more species-rich than recent forest, but if diversity is limited to typical forest plant species then ancient forests do have the highest number of plant species, making them highly important for nature conservation. The use

of molecular markers, integrated approaches and modelling are all part of the way forward in this field of historical ecology.

Keywords Historical ecology · Dispersal limitation · Recruitment limitation · Conservation · Forest cover · Research needs · Future research

Introduction

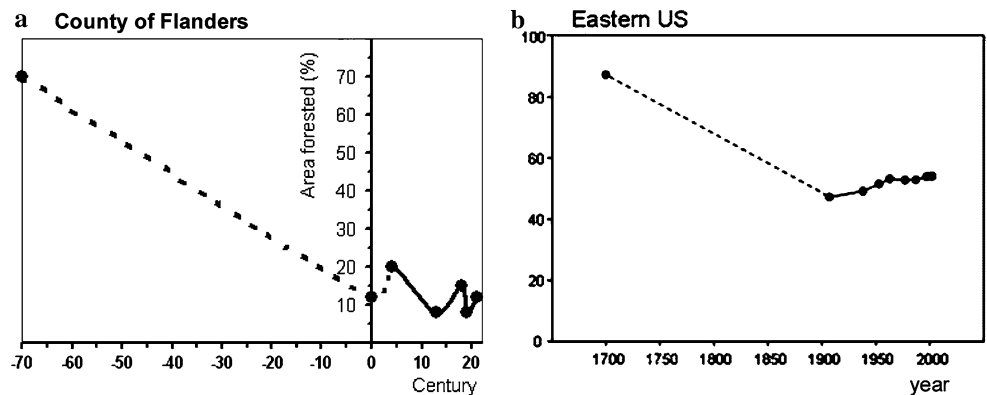
Global change, referring both to climatic and land-use change, has attracted enormous interest in both science and policy and its impact worries politicians, ecologists and conservationists. An increasing number of scientific papers is devoted to the consequences of climatic change. However, at the same time we tend to forget that these changes interfere with huge land-use changes. Between 1990 and 2000, the Food and Agriculture Organization (FAO) of the United Nations (2001) estimated the yearly worldwide deforestation at 14.6 million ha, 97.2% of which occurred in the tropical zone. In non-tropical areas, losses were largely compensated by afforestation both spontaneously (2.6 million ha year⁻¹) and through planting (0.7 million ha year⁻¹). Afforestation mainly occurred on agricultural land. Given the extent of afforestation, research on the recovery of forest plant communities is an important topic both for managers and ecologists (Flinn and Vellend 2005). The intended and natural restoration of forest communities may also yield insights into fundamental questions on how plant species disperse and recruit in these new forests. But as forest species colonization is generally slow, it will take many decades or centuries before the results of the recent afforestations will be visible.

However, afforestation is not new. Today many landscapes worldwide continue to bear the imprint of historical land-use changes. Particularly across north-western Europe and northeastern North America phases of forest clearance were followed by agricultural

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Fig. 1 Changes over time in forest cover in northwestern Belgium (former county of Flanders, calculated from Tack et al. 1993) **a** and eastern US, **b** (all states east of the Mississippi River, from Flinn and Vellend 2005). Forest cover estimates are approximate between 7000 BC and 400 AD in Flanders and before 1700 in US



abandonment and forest regeneration (Fig. 1). While in northeastern North America the first large-scale deforestation largely took place during the 18th and particularly the 19th century (e.g., Foster 1992; Hall et al. 2002; Flinn and Vellend 2005, but see Burgess and Sharpe 1981), in much of northwestern Europe deforestation goes back much further in time (e.g., Rackham 1980; Tack et al. 1993; Verheyen et al. 1999). In some regions, for example the county of Flanders in Belgium, several phases of abandonment and reforestation occurred (Fig. 1), resulting in a complex pattern of forest patches of different age. Furthermore, in some regions forests that have developed on farmland since the 19th century may represent as much as 80% of the current forest cover (Foster 1992; Foster et al. 1998; Grashof-Bokdam and Geertsema 1998). In Flanders only about 23,000 ha (16%) of the present-day forests already existed in 1770 (De Keersmaecker et al. 2001). As expected, these recent forests do differ in vegetation and soils from forests that were never cleared (so called primary forests, sensu Peterken 1974, 1981) or from forests that already existed before a certain threshold date (so-called ancient forests, sensu Hermy et al. 1999). Such observations lead ecologists to ask whether recent forests will ever recover from the past deforestation and the impact from former agricultural land use (Dupouey et al. 2002; Flinn and Vellend 2005), and if so, how long will it take? And if not, do we need to intervene, for instance by actively introducing forest plant species?

Here we want to review some of the results of empirical studies done since the 1950s in both northeastern North America and northwestern Europe. Furthermore we will embark on the basic ecological questions raised by the latter on dispersal and recruitment limitation. We will thereby focus on herbaceous understory plants of deciduous forests (cf. Flinn and Vellend 2005), as in many cases the woody layer in these forests has been strongly manipulated and trees have often planted by men, limiting the conclusions that can be drawn with respect to the ongoing demographic processes for woody species. We finish with some suggestions on new directions for research.

Land use reconstruction

All studies looking at the effects of historical land-use change rely on adequate reconstructions of history. Historical land-use maps, aerial photographs in combination with written sources and archaeological research may document the change in forest cover over time. They will show large differences between northwestern Europe and northeastern North America, for example (Fig. 1). In the latter large-scale deforestation mainly started early in the 19th century and forest cover progressively decreased to a minimum in about the end of the 19th or early 20th century, after which it increased to the current forest cover of somewhere between 20 and 50% (Smith et al. 2004; Flinn and Vellend 2005) or even up to 80% (Foster 1992; Hall et al. 2002). In Europe deforestation often goes back much further in time. In the northwestern part of Belgium (i.e., the former county of Flanders) for example, a considerable forest area was already lost from the Neolithic onwards (Tack et al. 1993) and reached a first minimum during the Roman era (about 12% of the land had forest cover at that time). Afterwards it significantly increased during the dark ages, probably reaching about 20% around 400 AD. Then a new deforestation phase took place, reaching a new low point around 1,300 when all peat reserves in that region were exhausted. As a result, the value of fuel wood increased tremendously and agricultural land was afforested again. A new maximum was reached around the end of the 18th century. Then coal gradually took over as an energy source and forest cover declined again. However, gradually more wood was needed in coal mining and forest area increased and this was later combined with renewed multifunctional interest in forests to reach its actual cover of about 12% in this region. Although this shows the overall long-term trend in forest cover, for detailed more spatially explicit information about forest-cover changes, data are mostly only reliable from the 18th century onwards (but see Verheyen et al. 1999).

The criterion for distinguishing primary from secondary forests is forest continuity. Primary forest has

never been reclaimed, but the status is often difficult to prove. So instead ancient and recent forest were used as terms (Peterken 1981). Ancient forest is then defined as forest that has existed continuously since at least a specified date (threshold date), selected on the availability of historical land-use information and differing between studies and countries (see Fig. 2, Hermy et al. 1999). So using historical sources one can distinguish remnants of ancient forest, mostly managed, from recent forests, also managed but restored on former farmland. It also enables one to estimate the age of recent forest patches (Peterken 1981; Smith et al. 1993; Hermy et al. 1999). The use of threshold dates to distinguish ancient from recent forest stands is particularly essential in northwestern Europe with its complex land-use history (cf. Fig. 1). It may mean that at least some part of the ancient forest is in fact secondary in origin (Fig. 2). So to be sure about the actual history of a parcel of forest land-use maps should be complemented with interviews with landowners, observations of field evidence such as stone and earth walls, tree fall pits and mounds, open-grown trees (Rackham 1980; Peterken 1981; Marks and Gardescu 2001), and with historical information from

other approaches such as palynology and archeology (e.g., Dupouey et al. 2002; Vanwalleggem et al. 2004). Chemical soil analysis, such as the measurement of the total phosphate content, may be a helpful tool indicating former agricultural land use, even if it dates back from Roman times or earlier (see, e.g., Provan 1971; Gebhardt 1982; Wulf 1994; Wilson et al. 1997; Honnay et al. 1999; Verheyen et al. 1999). However, even then uncertainties about the exact nature and scale of land-use changes remain (Whitney 1994; Verheyen et al. 1999; Hall et al. 2002). The increased and obvious use of geographical information systems (GIS) in historical land-use reconstruction, creating accurate and detailed maps, may therefore create an illusion of certainty.

Differences in flora, plant traits and colonization capacity

After abandonment, former agricultural land is gradually colonized by herbaceous plant species favouring open habitats. A rapid succession of ruderal to highly competitive plant species (sensu Grime 1979) is observed and within 5–20 years pioneer tree and shrub species (e.g. *Pinus* spp., *Betula* spp., and *Salix* spp.) may start to dominate and shade out open-habitat species. In both the northwestern European and northeastern North American temperate zone within a time span of about 100 years the pioneer tree species are gradually replaced by later successional tree genera such as beech (*Fagus*), oak (*Quercus*), lime (*Tilia*) or maple (*Acer*) (e.g. Ellenberg 1978; Packham and Harding 1982). However, long after the reconstitution of the tree layer in recent forest, considerable differences with ancient forests in the composition and abundance of particularly herbaceous species persist (e.g. Rackham 1980; Hermy and Stieperaere 1981; Peterken and Game 1984; Whitney and Foster 1988; Matlack 1994; Petersen 1994; Wulf 1997; Bellemare et al. 2002, for a review see Hermy et al. 1999; Verheyen et al. 2003a). From a review of the European literature Hermy et al. (1999) found that about 30% of all forest plant species are confined to ancient forests [so-called ancient forest plant species (AFS)]. AFS seem to exhibit a common ecological profile (Table 1): they tend to be more shade-tolerant than other forest plant species, avoid dry and wet sites and tend to be more stress-tolerant

Decreasing age of site as forest		
Ancient		Recent
Primary	Secondary	
Threshold date	Country	Study
1600	GB	Peterken (1974)
1700	GB	Rackham (1980)
1746-1786	NW Germany	Zaccharias (1994)
1770-1800	Belg., Denm.	(B) Hermy & Stieperaere (1981), Hermy (1985); (D) Petersen (1994)
1789	Denmark	Lawesson et al. (1998)
1804-1805	N. Germany	Hårdtje (1994)
1812-1820	S. Sweden	Brunet (1994)
1850	Netherlands	Grashof-Bokdam (1997)

Fig. 2 The relationships between primary, secondary, and ancient and recent forests in Europe (a) (cf. Peterken 1981). Ancient forests is defined as forest that has existed continuously since at least a specified date (threshold date), selected on the availability of historical land-use information and differing between studies and countries (b) (cf. Hermy et al. 1999)

Table 1 Ancient forest plant species share a number of common characteristics (summarized from Hermy et al. 1999; Verheyen et al. 2003a)

Hermy et al. (1999): AFS	Verheyen et al. (2003a) added: AFS
Preferentially occur on rich, moist but not wet soils	Have relatively large seeds
Prefer weakly acid to neutral soils	Do not form no persistent seed banks
Have intermediate N availability	Require specific germination requirements/conditions
Are preponderance of geophytes and hemicryptophytes	Have delayed age of first reproduction
Mainly are summergreen spp.	Predominantly show vegetative reproduction (clonal growth)
24% are considered: myrmecochores	Have limited fecundity
Mainly show a stress-tolerant plant strategy	

than other forest plant species that belong more to the competitive plant strategy type. But, it also became clear that considerable regional variation in AFS existed, indicating that in some regions a species may be typical of ancient forests, while in others it may be capable of colonizing recent forests. This suggests that AFS are not a black-white or all-or-nothing phenomenon; they may all be able to colonize to some extent. Therefore another, more species-specific approach is needed. Based on an extensive quantitative study of all available high quality data sources from both north-eastern North America (eight sources) and north-western Europe (12 sources) Verheyen et al. (2003a) suggested calculating per species a so-called colonizing capacity index (CCI):

$$CCI_i = \left[\frac{(1.5RE^* + RE)(1.5AN^* + AN)}{AN^* + AN + RE^* + RE} \right] \times 100/1.5.$$

RE* means the number of studies in which species *i* is statistically significantly more frequent in recent forest; RE refers to the number of studies in which species *i* is equally or more frequent in recent forest; AN* represents the number of studies in which species *i* is statistically significantly more frequent in ancient forest and AN is then the number of studies in which species *i* is more frequent in ancient forest.

The index ranges from +100 (species strongly associated with recent forest) to -100 (species strongly associated with ancient forest) and thus expresses the colonization capacity of an individual species: the lower the value, the lower the colonization capacity. Table 2 gives an overview of the forest plant species with the lowest colonization capacity. Apart from relatively rare

taxa, such as *Carex pendula*, *Ranunculus lanuginosus*, *Melica uniflora*, *Corydalis cava* in NW Europe, it also includes relatively common species such as *Lamium galeobdolon*, *Carex sylvatica*, *Circaea lutetiana* in NW Europe. Although not formally analyzed, some closely related species (e.g. *Allium ursinum* vs. *A. tricoccum*, *Asarum europaeum* vs. *A. canadense*, *Paris quadrifolia* vs. *Trillium* spp., *Polygonatum multiflorum* vs. *Polygonatum* spp.) exhibit similar responses on both continents. Yet, this work also found some remarkable, yet unrevealed continental contrasts within the same species, for example, *Oxalis acetosella* (CCI Europe -75, 87 in N. America) and *Circaea lutetiana* (CCI Europe -67 vs. N. America 0). More importantly, plant trait correlation structure was similar in the European and North American datasets. Species having relatively large seeds, low fecundity, unassisted (short-distance) dispersal, specific germination requirements, delayed age of first reproduction, clonal growth and no persistent seed bank generally proved to be slow colonizers (see Table 1 and also Whigham 2004). Many of these life-history traits may make AFS more sensitive to habitat loss and fragmentation (Flinn and Vellend 2005) and therefore also prone to extinction (cf. Peterken 1977).

In the examples given above ancient forest has been defined as forest existing since at least the 19th century (see Fig. 2). But what if the deforestation occurred much earlier, and thus the threshold date goes back much further, e.g. to Roman times? Perhaps unexpectedly, in the northeast of France Dupouey et al. (2002) showed that even 2,000 years after reforestation forests still exhibit clear floristic differences compared to forests that were never cleared. Similar, but less convincing, results

Table 2 Forest plant species most strongly associated with ancient deciduous forests of northwestern Europe and northeastern North America

European herb species (174 species; <i>n</i> = 12)	CCI	American herb species (44 species; <i>n</i> = 8)	CCI
<i>Carex pallescens</i>	-100	<i>Cardamine diphylla</i>	-100
<i>Carex pendula</i>	-100	<i>Chimaphila maculata</i>	-100
<i>Hypericum pulchrum</i>	-100	<i>Clintonia borealis</i>	-100
<i>Luzula sylvatica</i>	-100	<i>Coptis trifolia</i>	-100
<i>Lysimachia nemorum</i>	-100	<i>Caulophyllum thalictroides</i>	-87
<i>Lysimachia vulgaris</i>	-100	<i>Claytonia caroliniana</i>	-87
<i>Scilla non-scripta</i>	-100	<i>Osmorhiza claytoni</i>	-87
<i>Succisa pratensis</i>	-100	<i>Trillium erectum</i>	-87
<i>Veronica montana</i>	-100	<i>Trillium undulatum</i>	-87
<i>Galium odoratum</i>	-95	<i>Viola macloskeyi</i>	-87
<i>Corydalis cava</i>	-83	<i>Asarum canadense</i>	-80
<i>Lathyrus sylvestris</i>	-83	<i>Uvularia perfoliata</i>	-80
<i>Ranunculus lanuginosus</i>	-83	<i>Actaea rubra</i>	-67
<i>Lamium galeobdolon</i>	-79	<i>Allium tricoccum</i>	-67
<i>Anemone nemorosa</i>	-77	<i>Hepatica acutiloba</i>	-67
<i>Oxalis acetosella</i>	-75	<i>Medeola virginiana</i>	-67
<i>Paris quadrifolia</i>	-75	<i>Viola rotundifolia</i>	-67
<i>Carex sylvatica</i>	-74	<i>Geranium maculatum</i>	-33
<i>Melica uniflora</i>	-71	<i>Aster acuminatus</i>	-20
<i>Viola reichenbachiana</i>	-71	<i>Cypripedium acaule</i>	-20
<i>Circaea lutetiana</i>	-67	<i>Erythronium americanum</i>	-20
<i>Euphorbia dulcis</i>	-67	<i>Galium circaeans</i>	-20
<i>Primula elatior</i>	-67	<i>Podophyllum peltatum</i>	-20
<i>Luzula pilosa</i>	-59	<i>Polygonatum biflorum</i>	-20

Values show the colonizing capacity indices (CCI), which range from -100 (strongly associated with ancient forest) to +100 (strongly associated with recent forests) (recalculated from Verheyen et al. 2003a) *n* number of studies

were found by Vanwalleghem et al. (2004) in central Belgium.

Why do forest plants fail to colonize new sites? Recruitment versus dispersal limitation

The strong association of many forest plant species with ancient forest suggests that dispersal in space (distance related) and time (seed bank related) may be limiting the distribution and abundance of many forest plant species. But it might also be that the habitat of recent forest is unsuitable for the recruitment of these species, as the latter has been considerably modified by the former agricultural land use. Particularly in Europe, a long

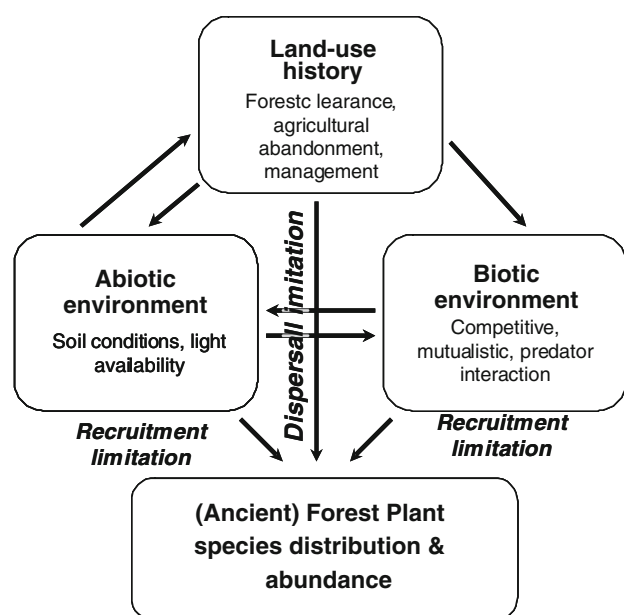


Fig. 3 Diagram showing the direct and indirect effects of land-use history on forest plant species distribution and abundance (adapted from Flinn and Vellend 2005)

history of management also adds to these effects (Fig. 3). Basically all forests, whether ancient or recent, have been managed as coppice, coppice-with-standards or high forest.

Does land-use affect environmental conditions?

Agriculture potentially affects vegetation both directly, by locally eliminating plants and their diaspores, and indirectly, by altering environmental conditions. Numerous researchers have indeed found that soils under recent forest have higher pH, nutrient concentrations and lower organic matter than soils under ancient forests (e.g. Koerner et al. 1997; Bossuyt et al. 1999a; Honnay et al. 1999; Verheyen et al. 1999; Flinn et al. 2005). However the magnitude and persistence of these effects shows variation between regions (see Verheyen et al. 1999; Koerner et al. 1997 vs. Bellemare et al. 2002; Compton and Boone 2000; Flinn et al. 2005) and between elements (compare mobile basic cations vs. persistent phosphate; e.g. Honnay et al. 1999). If differences persist to some extent in recent forests, and for total phosphate differences may persist for even 2,000 years (cf. Dupouey et al. 2002), this may suggest that recruitment is limiting the presence of AFS.

Recruitment limitation

Tests of this hypothesis may come from two sources (Flinn and Vellend 2005): research investigating the performance of forest plant species and in particular AFS in recent forests—as many of the AFS do show some colonization—and studies monitoring experimental introductions of forest plant species in recent sites. Contrary to expectations, performance in recent forests has often been similar or even been better (Table 3, cf. Endels et al. 2004). Similar results were found in central Massachusetts by Donohue et al. (2000) for the

Table 3 Performance of two forest plant species in an alluvial recent and ancient forest (Langerode, central Belgium) (adapted from Endels et al. 2003)

	Ancient forest			Recent forest		
	<i>n</i>	mean ± SE	*	<i>n</i>	mean ± SE	*
<i>Primula elatior</i>						
No. of flowers per plant	179	15.79 ± 1.18	a	86	43.9 ± 7.03	b
No. of fruits per plant	110	9.75 ± 0.87	a	39	16.9 ± 4.24	b
Total no. of seeds per plant	110	338.19 ± 38.25	a	39	516.2 ± 155.76	b
Germination %	110	33.75 ± 3.54	a	40	35.6 ± 5.89	a
<i>Geum urbanum</i>						
No. of flowers per plant	93	5.18 ± 0.31	a	140	7.5 ± 0.37	b
No. of fruits per plant	93	4.01 ± 0.27	a	140	5.5 ± 0.30	b
Total no. of seeds per plant	93	394.18 ± 32.30	a	137	626.4 ± 39.17	b
Germination %	91	69.88 ± 2.75	a	135	71.1 ± 2.50	a

Primula elatior is usually considered an ancient forest plant species and *Geum urbanum* is not. The significance of differences using the Mann–Whitney *U* test is indicated by different letters. Recent forest: planted after 1945; ancient forest: forest since at least 1775

* Values are averages, and differences between two forest types that are significantly different are indicated with different letters

evergreen, woody clonal understory species, *Gaultheria procumbens*. In contrast, Vellend (2005) found that for *Trillium grandiflorum* plants of the same age were smaller and less likely to flower in recent forests than in ancient forests in central New York. Yet, only very few studies are available for a very limited number of species. So more work is needed here.

In experiments where forest plant species have been introduced, seed sowing and adult transplants in recent forests usually proved successful (e.g. Petersen and Philipp 2001; Heinken 2004; Verheyen and Hermy 2004; Graae et al. 2004). These all seem to suggest that recruitment may not be the prime problem (cf. Ehrlén and Eriksson 2000). However no long-term studies on the performance of the introduced plants in recent forests are available. As many forest plant species have long life spans (e.g. Inghe and Tamm 1985; Cain and Damman 1997)—Ehrlén and Lethilä (2002) inferred an average life span of 64 year for forest field layer species as opposed to 22 year for species from open habitats—really long-term studies are needed. At the same time, it seems to suggest that dispersal limitation may be the main problem.

Dispersal limitation in space and in time

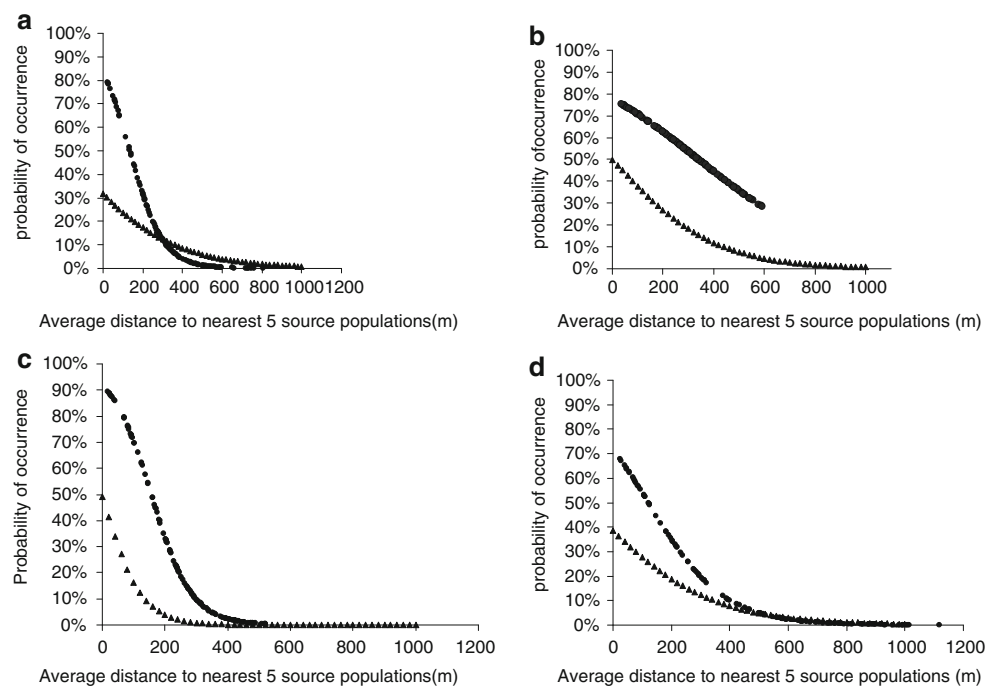
Dispersal in plant species covers two aspects: dispersal in space, referring to dissemination of diaspores away from sexually reproductive parent plants and often categorized as dispersal modes based on the morphology of dispersal units, and dispersal in time, referring to the ability of plant species to build seed banks in the soils. These again may take two forms: transient versus

persistent seed banks. The former persist in the soil for less than one year and the latter persist in the soil for at least one year (Bakker 1989; Thompson et al. 1997).

Dispersal in space, or the transport of diaspores away from a parent, is an essential prerequisite for recruitment and as such is an important step in the colonization process (see also Fig. 7). It is to be expected that dispersal limitation will increase with the increasing isolation of recent from ancient forest. In the available literature two useful extremes in isolation may be encountered: (1) recent forests stands immediately bordering ancient forest stands on the same soils and with similar light conditions and (2) recent forests isolated from ancient forests by a hostile—mostly agricultural—landscape matrix. In the former, the available studies came up with colonization rates between ± 20 and $100 \text{ m century}^{-1}$ depending on the plant species (northeastern North America: Matlack 1994; southern Sweden: Brunet and von Oheimb 1998; central Belgium: Bossuyt et al. 1999b; Honnay et al. 1999). These rates are all based on the furthest individual and in all studies it is assumed that colonization started at the edge of the ancient forest. Colonization rates are thus generally low and difficult to reconcile with the high rates of migration found after the last glacial period (cf. Cain et al. 1998).

Colonization success in isolated recent forest patches, defined as the ratio of occupied target fragments (in the example given, between 30 and 42 years old) over the sum of the number of occupied target fragments and the number of suitable but not occupied target fragments, proved to be very low for 85% of the forest plant species and strongly decreased with increasing distances. However, colonization success was clearly linked to the connectivity of the landscape (Fig. 4; Honnay et al.

Fig. 4 Probability of occurrence of forest plant species in a forest patch as a function of the average distance to the five nearest source populations of that species in two landscapes differing in connectivity and forest cover. Triangles, for the more-fragmented landscape and filled circles for the high-connectivity landscape. **a** *Arum maculatum*, **b** *Geum urbanum*, **c** *Adoxa moschatellina*, **d** *Primula elatior* (from Honnay et al. 2002a)



2002a). In high-connectivity landscapes (in the example, 42% forest cover) colonization success was clearly higher than in low-connectivity landscapes (with 7% forest cover).

Although colonization rates of most forest plant species were on average less than a few metres per year, one must be careful about generalizations. Indeed, chance events may disperse plant diaspores over long distances. It all relates to the importance of the tail of the seed shadow (cf. Cain et al. 1998; Higgins and Richardson 1999; Cain et al. 2000). Indeed, Cain and colleagues could explain the high Holocene colonization rates of the North American forest herb *Asarum canadense* based on the tail of the seed dispersal curve of the species.

Given the more or less unique response of individual forest plant species, one might expect a relation between species dispersal mode and colonization success. Endo- and epizoochores are generally clearly more successful in colonizing recent forests than the other groups (cf. Honnay et al. 2002a; Dzwonko and Loster 1992; Matlack 1994; Grashof-Bokdam and Geertsema 1998; Brunet and von Oheimb 1998; Bellemare et al. 2002; Takahaskhi and Kamitani 2004). Dispersal distances of seeds transported by ants in Japanese deciduous forest have been reported to range from 0.28 to 0.64 m (Ohara and Higashi 1987; Higashi et al. 1989; Ohkawara and Higashi 1994; Ohkawara et al. 1996). However, others (e.g. Mabry et al. 2000; Singleton et al. 2001; Ito et al. 2004; Wulf 2004) found no association between dispersal mode and colonization ability. Although an intuitively attractive and logical approach, attempts to relate dispersal mode to colonization ability have not always been successful, mainly because dispersal classes are based on seed morphology and may poorly represent realized dispersal modes and distances (Vellend et al. 2003). Some myrmeco- and barochores do occur frequently in secondary stands (e.g. *Trillium erectum*, *Carex* spp. in W. Massachusetts, Bellemare et al. 2002, *Viola riviniana*, *Glechoma hederacea* in W. Europe) and conversely some anemochores (e.g. *Adiantum pedatum* in W. Massachusetts, Bellemare et al. 2002, *Pteridium aquilinum*, *Dryopteris carthusiana* in W. Europe) are strongly confined to ancient forests. This suggests that additional empirical data on dispersal of forest plant species are needed, and the potential of perhaps unusual dispersal events, such as vertebrate (including men) dispersal of baro- and myrmecochores should not be overlooked (cf. Bellemare et al. 2002).

Deforestation and transformation to agricultural land use completely destroys the forest plant communities. Yet if diaspores of forest plant species form persistent seed banks, they could at least survive a temporary agricultural land use if it lasts less than a few decades. So dispersal in time could overcome a temporal agricultural land-use phase. However, many forest plant species and most of the AFS do not form a persistent seed bank (cf. Brown and Oosterhuis 1981; Bierzychudek 1982; Bossuyt and Hermy 2001; Bossuyt

et al. 2002; Verheyen et al. 2003a, Table 1). By definition their transient seed banks do not allow the recovery of ancient forest plant communities even if agricultural land use is only for a few years. So, seed banks are mostly of no significance in the restoration of forest plant communities, at least for the AFS (Bossuyt et al. 2002; Honnay et al. 2002b). In contrast species of edges and clear cuts often do have persistent seed banks (e.g. Ash and Barkham 1976; Brown and Oosterhuis 1981; Bossuyt and Hermy 2001; Bossuyt et al. 2002). The number of seed bank papers specifically related to the impact of past land use of forests is however scarce, and hence we still have little insight on how past land-use changes remain visible in the seed banks of forests.

Are ancient forests more diverse than recent forests?

As AFS are dispersal limited one could expect that recent forest stands are less species-rich than ancient forests. Peterken (1974) showed that ancient forest species are quality indicators and their diversity is a means to estimate the nature conservation value of forests. Yet as there is a lot of regional variation in AFS it is difficult to compare across regions and comparisons therefore depend on how species pools or on how the sampling units (plots vs. forest patches) are defined. Our group (e.g. Tack et al. 1993; Jacquemyn et al. 2001; Butaye et al. 2001) used a list of 203 plant species that are restricted to forests, including species typical of forest interiors, forest edges and woody species that are usually not planted. Others used the entire flora of forest patches (e.g. Peterken and Game 1984); still others used plots (e.g. Hermy 1985; Motzkin et al. 1996; Bellemare et al. 2002; Flinn and Marks 2004). If total plant species richness is used, ancient forests plots are not necessarily richer in plant species than recent forests (cf. Hermy 1985). If some quality aspect is introduced (e.g. AFS, or typical forest plant species), then ancient forests patches/plots usually are more species rich than recent forests (Fig. 5), at least if the environmental conditions are comparable (cf. Graae 2000). This makes ancient forests important hot spots for forest quality indicating plant species and an important issue in conservation. We essentially need to conserve forests for forest species and not for open habitat species. However, forests may be important for open-habitat species as well, particularly if associated with ancient open habitats such as rides (Peterken and Francis 1999). Ancient forests have been assigned as past-natural forests (Peterken 1977), although often having a simple, artificial structure due to management, but having a composition reflecting those of natural forests. So the conservation value of ancient forests, even with their artificial structure, is highly important, as their recreation within a few hundreds of years is unfeasible. Conversion to conifer or other exotic species stands must be avoided as it is usually a way of no return (cf. Peterken 1981).

Are ancient forest plant species affected by traditional management practices?

Many of the ancient forests in Europe have been converted from coppice and coppice-with-standards to some form of high forest. The fundamental feature of the coppice system is the restocking method: each coppice stand grows mainly from shoots that spring from the cut stumps of the previous stand; rotation usually occurs between 5 and 30 years, depending on the regeneration rate of species and the demand for wood products. Coppices mixed with trees (so called standard trees) grown on a multiple of the underwood rotation (usually about 100 years) are indicated as coppice-with-standards. Coppice-with-standards therefore traditionally yielded three main products, namely sticks and brushwood from the underwood, timber from standard trees scattered amongst the underwood, and pasture from the herbaceous field layer and the grassy rides and clearings (Peterken 1981). Ancient forests if combined with

ancient coppice stools and trees—as is particularly often the case in northwestern Europe (Rackham 1980; Peterken 1981; Tack et al. 1993)—are an important cultural heritage and reflect the values society put on these ecosystems in the past. As many ancient forests have been managed for centuries under these traditional management schemes, it may have influenced their composition and therefore also the distribution and abundance of many of the AFS. The regular cutting of the coppice—typically with a rotation cycle of 5–30 years—causes a temporary increased light intensity from about 5% of full daylight to virtually 100% (cf. Buckley 1994). Over the years, this—together with the cutting itself—has favoured those species that are tolerant to this treatment. This may have enhanced the abundance of a number of particularly spring flowering plant species in northwestern Europe such as *Primula elatior*, *Viola riviniana*, *Cardamine pratensis* and *Anemone nemorosa* (cf. Rackham 1975; Ash and Barkham 1976; Peterken 1981) (Fig. 6). It is clear that these effects are included in most

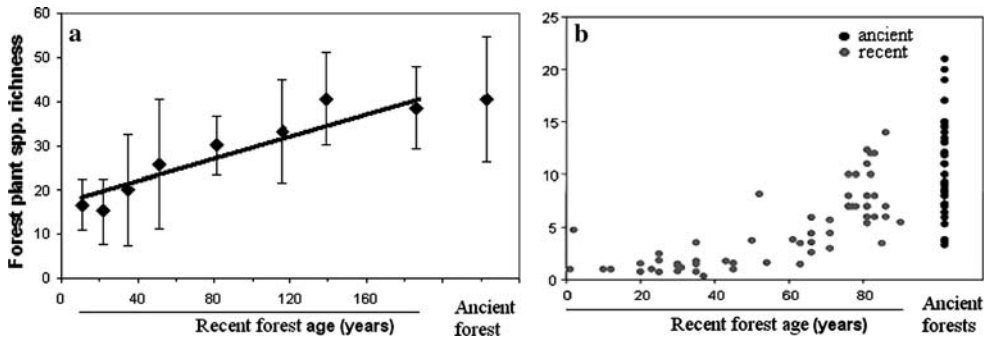
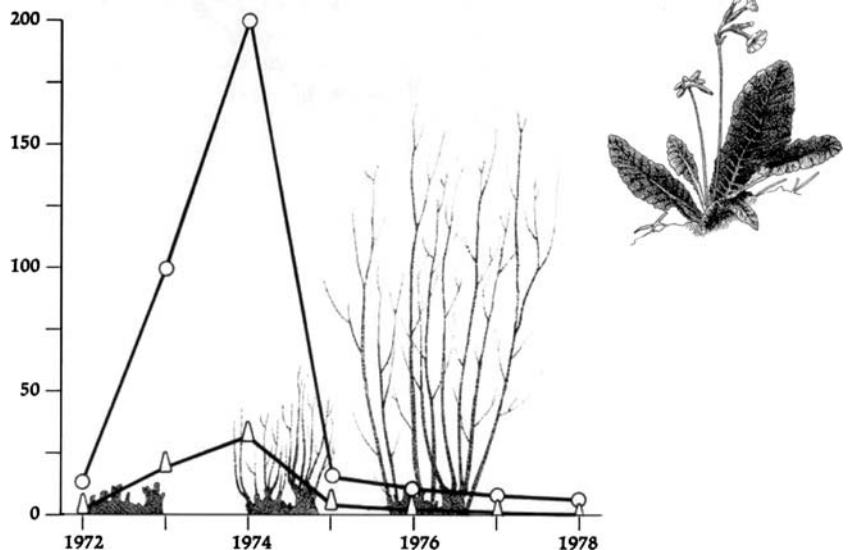


Fig. 5 Forest plant species richness increases with forest age and ancient forests do have on average more typical forest plant species. **a** Forest patch data from central Belgium; average values per age class, error bars and fitted regression line (adapted from:

Jacquemyn et al. 2001); **b** forest plot (herb species richness per 180 m²) data from central New York (figure from: Flinn and Vellend 2005)

Fig. 6 Response between 1972 and 1978 of *Primula elatior*, a typical spring-flowering perennial plant species of ancient forests on rich soils, on coppicing in the winter of 1971–1972 and regrowth on coppice stools is shown as well. Circles indicate the number of flowers and triangles the number of inflorescences (adapted from Rackham 1975)



comparisons of the flora of ancient and recent forests, particularly in Europe as there is here a long tradition of coppice or coppice-with-standards management. Until now, field experience suggests that management effects are mainly reflected in the abundance of some AFS; carpets of spring vernalis are indeed typical of many ancient coppiced forests and far less typical for high forest management systems. Whether management also affected presence-absence patterns of AFS remains unclear and it is not clear what the exact long-term effects will be of the conversion of traditional systems to high forest management.

Recent developments and the way forward

Since the first papers on ancient forest plant species in the 1950s (for a review see Hermy et al. 1999), much progress has been made in elucidating the effects of past land use on today's patterns of (ancient) forest plant species distribution and diversity. The dispersal of diaspores in recent forests appears to be the most critical step limiting the whole colonization process from seed to adult. Recruitment does play a role, but overall it is of secondary influence, and in fact also the second big step in the whole colonization process (Fig. 7). Results to date also point to some important directions for further research (see also Flinn and Vellend 2005): (1) elaborating the impact studies of past land use on forest composition and diversity of

regions other than North America and northwestern Europe such as Japan (see Ito et al. 2004) and NE China, (2) elaborating the approach to other taxa than plants (e.g. Desender et al. 1999), (3) the need for integrated approaches for explaining the distribution and abundance of forest plant species (cf. Verheyen et al. 2003b) and the comparison of results from multiple landscapes with different land-use histories (cf. Vellend 2003; Vellend et al. 2006), (4) the use of molecular markers to document the impacts of land-use history on genetic variation or the origin of colonists (cf. Jacquemyn et al. 2004; Vellend 2004; Honnay et al. 2005), (5) the role of multitrophic interactions (e.g. mutualism, predation) in determining the establishment of forest plant species, (6) modeling the impact of land-use changes on forest plant species distribution and diversity (cf. Matlack and Monde 2004; Verheyen et al. 2004), (7) quantifying possible extinction debts for ancient forests as a consequence of fragmentation (cf. Vellend et al. 2006). These are not only ecologically sound questions, but they are also important for the conservation of forest plant species and their communities.

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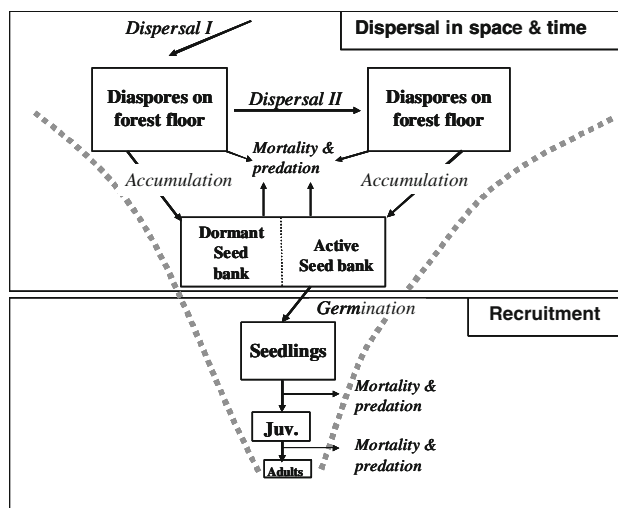


Fig. 7 A conceptual diagram showing the bottle-neck model of the colonization process with a dispersal and a recruitment step. The primary dispersal from the parent plant (dispersal I) may be followed by a secondary dispersal phase (dispersal II). After dispersal, diaspores are incorporated in a seed bank, which may be dormant or active. From that diaspores may germinate and grow up. At each life stage losses may occur through mortality and predation, ultimately yielding a low number of adults (box size relative to number of recruits). The decreasing number of individuals is emphasized by the bottle-neck pattern of *dots*

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