

LETTER

Dispersal failure contributes to plant losses in NW Europe

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Abstract

The ongoing decline of many plant species in Northwest Europe indicates that traditional conservation measures to improve the habitat quality, although useful, are not enough to halt diversity losses. Using recent databases, we show for the first time that differences between species in adaptations to various dispersal vectors, in combination with changes in the availability of these vectors, contribute significantly to explaining losses in plant diversity in Northwest Europe in the 20th century. Species with water- or fur-assisted dispersal are over-represented among declining species, while others (wind- or bird-assisted dispersal) are under-represented. Our analysis indicates that the ‘colonization deficit’ due to a degraded dispersal infrastructure is no less important in explaining plant diversity losses than the more commonly accepted effect of eutrophication and associated niche-based processes. Our findings call for measures that aim to restore the dispersal infrastructure across entire regions and that go beyond current conservation practices.

Keywords

Colonization deficit, dispersal infrastructure, dispersal vectors, diversity loss, eutrophication, functional traits, land-use changes.

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INTRODUCTION

Growing concern about the ongoing loss of biodiversity has resulted in increased efforts throughout the world to protect endangered species and to conserve and restore endangered ecosystems (Balmford *et al.* 2005). In view of the large input of financial and human resources into nature conservation and restoration, improving our insights into the mechanisms behind observed losses of biological diversity is therefore

one of the great scientific challenges for the 21st century. Changes in plant species composition of vegetations in man-made temperate landscapes are often explained in terms of habitat degradation, especially by eutrophication (Vitousek *et al.* 1997; Bobbink *et al.* 1998; Grime 2001; Tilman *et al.* 2002; Stevens *et al.* 2004; Suding *et al.* 2005). Restoration of habitat quality, however, often fails to deliver the expected plant diversity (Dobson *et al.* 1997; Bakker & Berendse 1999). It has therefore been questioned during the past

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decade to what extent community composition is also constrained by limited rates of seed dispersal on a regional scale (Tilman 1997; Poschlod & Bonn 1998; Poschlod *et al.* 1998; Römermann *et al.* 2008; Turnbull *et al.* 2000; Mouquet *et al.* 2004; Ozinga *et al.* 2005; Nathan 2006). Metapopulation theory asserts that regional survival of species requires that local populations are connected by sufficient rates of dispersal (Hanski 1998). The newly emerging concept of 'metacommunities' extends metapopulation theory towards the community level and tries to integrate the processes that drive the dynamics of species across local and regional scales (Leibold *et al.* 2004).

In contrast to mobile animal species, plants depend for the transport of their seeds among sites on external vectors, including water, wind, birds and large mammals, each with their own characteristics. At the landscape level, these dispersal vectors act like a complex 'dispersal infrastructure' (Poschlod & Bonn 1998; Ozinga *et al.* 2004). Although changes in the relative availability of dispersal vectors during the 20th century have been documented in many parts of the industrialized world (see Appendix S2 in Supporting information), their impact on plant diversity has never been examined in large-scale studies. We might expect that such impacts will be strongly vector-specific. For example, dispersal by water has been restricted by the regulation of the natural flood regimes of rivers and brooks for the purpose of flood control, while dispersal by large mammals has declined due to the change from livestock grazing on common grounds to grazing in fenced fields or livestock housing. In Northwest Europe, these changes in dispersal infrastructure mostly took place some 50–150 years ago (see Appendix S2).

The potential effect of changes in the availability of dispersal vectors on species losses is founded upon two premises. First, vascular plant species show interspecific differences in the kind of dispersal vectors that can effectively transport their seeds (known as 'dispersal syndromes' (Poschlod & Bonn 1998; Ozinga *et al.* 2004). Second, in any terrestrial habitat type, a variety of dispersal syndromes is represented in the habitat species pool, and a variety of dispersal vectors may be available in the landscape (Ozinga *et al.* 2004). A decline in the availability of specific dispersal vectors is then expected to result in a decline of those species that, given their traits, depend on these vectors. The effect of limited availability of dispersal vectors on plant diversity has never been tested on large spatial and temporal scales, due to a lack of suitable data. By using two large databases that only recently became available, we test the hypothesis that differences between species in population trends over the 20th century in Northwest Europe can be explained by interspecific differences in their dispersal traits.

The first database contains information on long-term changes in the frequency of occurrence of flowering plant species (Angiospermophyta), and is based on repeated

floristic inventories of over 200 000 grid cells in three countries (the Netherlands, Great Britain, and Germany) recorded over the 20th century. The second is a recently completed database containing quantitative information for more than 20 key plant characteristics for over 3000 vascular plant species in NW Europe. This combination allowed us to compare characteristics of declining and non-declining species. We selected the plant characteristics best able to discriminate between two competing explanations for plant diversity losses:

- (1) *Nitrogen requirement*. Loss of low-productivity habitats and eutrophication of remaining habitat patches (with associated niche-based processes) are currently regarded as one of the major drivers of species losses in large parts of the world (Vitousek *et al.* 1997; Bobbink *et al.* 1998; Grime 2001; Tilman *et al.* 2002; Stevens *et al.* 2004). For the possible effects of changes in water and light availability see Appendix S1 in Supporting information.
- (2) *Dispersal capacity*. The ability to track the changes in habitat configuration, through seed dispersal in space (long-distance dispersal by various dispersal vectors) and/or time (formation of a persistent soil seed bank) can be a major determinant of regional species dynamics (Tilman 1997; Turnbull *et al.* 2000; Leibold *et al.* 2004; Ozinga *et al.* 2005; Nathan 2006).

MATERIAL AND METHODS

Quantification of trends in frequency of occurrence during the 20th century

Trends in frequency of occurrence were assessed using published national surveys of the occurrence of vascular plant species in grid cells (quadrats). As trend data are sensitive to various sources of bias and to differences in spatial and temporal scale (Telfer *et al.* 2002; Hartley & Kunin 2003; Tamis 2005), we used a binary classification for species trend: declining vs. not declining. Stochastic effects of rarity were included in the analysis by assigning to each species a rarity index related to its frequency of occurrence at the beginning of the period over which the trend analysis was performed. Rarity in itself may increase the risk of local extinction due to random processes such as demographic and environmental stochasticity or genetic drift (Gilpin & Soulé 1986; Nee & May 1997; Hubbell 2001; Tilman 2004). The species lists from various data sources were linked using the SynBioSys species checklist (Schaminée *et al.* 2007; <http://www.synbiosys.alterra.nl/eu/>). Technical details of the survey methods of national lists of declining species differ between countries and therefore the three countries were analysed separately. This diversity of approaches provides a valuable check of the generality of our results across regions.

The Netherlands

Trends during the 20th century were based on the occurrences of plant species in the Netherlands in 1-km² grid cells during two periods: 1902–1949 and 1975–1998 (over 7 million records; Van der Meijden *et al.* 2000). The analysis was based on a selection of 7374 grid cells with multiple observations within the grid cell across both periods (nearly 25% of the land surface of the Netherlands) and corrected for temporal differences in sampling intensity (Van der Meijden *et al.* 2000; Tamis 2005). Species were labelled as declining if the number of grid cell occurrences had declined by at least 25% over the 20th century, representing local extinction at the 1-km² scale. The historical frequency of occurrence was defined as the log₃ transformed number of grid cells occupied in the 1902–1949 period, ranging from 1 (very rare) to 9 (very common) (Tamis 2005).

Great Britain

The list of declining species for Great Britain was based on the change index published in New Atlas of the British and Irish flora (Preston *et al.* 2002). The change index is based on the comparison of the results of two nationwide surveys of British plant distribution at a 10 × 10-km scale (1930–1969 and 1987–1999) and takes into account differences in recording intensity (Telfer *et al.* 2002). In contrast to the change index for the Netherlands, this index cannot be interpreted as a percentage of change in the number of occupied grid cells, but refers to the change in the frequency of occurrence compared to that of an ‘average species’. The change indices of all species sum to zero. In this study, species were regarded as declining if they had a change index of –0.30 or less. The historical frequency in the species pool was derived from the log₂ transformed number of 10 × 10-km quadrats for the 1930–1969 period. This transformation resulted in data that better approached a normal distribution and that are better comparable to the Dutch data (i.e. ranging from 1 for very rare species to 9 for very common species).

Germany

The list of declining species for Germany is based on the trend index (tendency to decline or increase) given by Ellenberg *et al.* (2001), ranging from 1 (almost disappeared) to 9 (strongly expanding). This trend index is based on a combination of floristic data over the 20th century and expert judgments by several experienced botanists, and refers to changes in species frequency in 110-km² quadrats and their dominance within these quadrats. Declining species were defined as those with a trend index ≤ 3. As floristic inventories in the first half of the 20th century in Germany focused on rare species only, it was not possible to find reliable information on species frequency in the historical species pool for all species. Therefore, we have

analysed the German data without this variable (unlike the two other datasets).

Classification of nitrogen requirement

To compare the effects of changes in the frequency of occurrence due to dispersal limitation with those due to habitat change (e.g. eutrophication), we used Ellenberg indicator values for nitrogen requirement (Ellenberg *et al.* 2001). These indicator values are species-specific scores, ranging from 1 to 9, for the optimal occurrence of species along environmental gradients. For Great Britain, we used adjusted indicator values (Hill *et al.* 1999). Evidence for the accuracy of Ellenberg indicator values has been provided by several studies reporting a close correlation between average indicator values and corresponding measurements of environmental variables (see Diekmann 2003 for a review). For the possible effects of changes in water and light availability, see Appendix S1.

Classification of dispersal traits

Data on dispersal ability by various vectors were extracted from the LEDA database with life-history traits of the Northwest European flora (Knevel *et al.* 2003, 2005; Kleyer *et al.* 2008) and adapted to a binary classification (Table 1 and 2). We considered the following dispersal vectors, all capable of providing highly effective long-distance dispersal (> 100 m): water, wind, the fur of large mammals, the digestive tract of large mammals and the digestive tract of frugivorous birds. Humans as a complex dispersal vector were not taken into account, as this would involve various trait syndromes, and comparative data for large sets of species are lacking. We aggregated the available data into a binary classification, assigning each species to one of two classes for each dispersal vector: ‘1’ if the species has attributes for long-distance dispersal by a given vector and ‘0’ if the species has no such attributes (Tables 2). Although the binary classification of the continuum is less precise for individual species, it allows generalizations at the level of large species pools. It is important to note that many species have a high dispersal potential (i.e. a ‘1’ in the database) for more than one long-distance dispersal vector (Ozinga *et al.* 2004). As regards dispersal through time, species were classified as being capable of accumulating a persistent seed bank if their seeds can remain viable in the soil for ≥ 1 year, as indicated by a seed longevity index ≥ 0.3 (Knevel *et al.* 2005).

Analysis

The relative importance of nitrogen requirements and dispersal traits for the probability of a negative trend in frequency of occurrence was quantified for each country by

Table 1 Variables used in the multiple logistic regressions

Plant characteristic	Classification
Frequency in historical species pool	Number of occupied grid cells in the first recording period (log-3 transformed for the Netherlands, log-2 transformed for Great Britain): 1 (very rare) – 9 (very common)
Dispersal potential – water	Potential for Long Distance Dispersal by water (0 = low, 1 = high)
Dispersal potential – wind	Potential for Long Distance Dispersal by wind (0 = low, 1 = high)
Dispersal potential – fur	Potential for long distance dispersal by mammalian fur (0 = low, 1 = high)
Dispersal potential – dung	Potential for long distance dispersal by mammalian dung (0 = low, 1 = high)
Dispersal potential – birds	Potential for long distance dispersal by bird droppings (0 = low, 1 = high)
No LDD	Species with no attributes for long distance dispersal by any of the five vectors considered (0 = no, 1 = yes)
Seed longevity	Persistence in the soil seed bank (0 = seeds persist in the soil < 1 year, 1 = seeds persist in the soil ≥ 1 year)
Nitrogen requirements	Ellenberg indicator value for nitrogen requirements (1 = low, 9 = high)

For further details on the classification of dispersal traits see Table 2.

LDD, long-distance dispersal.

Table 2 Classification criteria for the capacity for long-distance dispersal by individual dispersal vectors

Dispersal vector	Criterion
Dispersal potential – water	Propagules float on water surface for at least 7 days
Dispersal potential – wind	Falling velocity of propagules after a phase of acceleration (terminal velocity in m/s): < 0.5 (for species with a release height < 0.2 m); < 0.6 (release height 1 m); < 0.75 (release height 2 m)
Dispersal potential – dung	High survival of seeds after passing through the digestive tract (at least three germinating seeds and relative abundance in dung higher than 5% of relative abundance in the diet) and seeds frequently eaten
Dispersal potential – fur	Propagules with awns, spiny teeth, burrs, pappus with barbs, style with barbs, hooked hairs or excreting viscid substances
Dispersal potential – birds	High survival of seeds after passing through the digestive tract (at least three germinating seeds and relative abundance in dung higher than 5% of relative abundance in the diet) and morphological adaptations to attract birds (fleshy fruit)

means of multiple logistic regression, which is considered an effective method to analyse binary ecological data (McCullagh & Nelder 1989; Trexler & Travis 1993). The statistical analyses were performed using SPSS 16.0 (©SPSS Inc. 1989–2007). Variables were tested for inclusion in the model using the likelihood ratio test, which assesses the improvement of the fit between the predicted and observed values of the response variable caused by adding the predictor variable. Only variables for which the likelihood ratio χ^2 had a P -value < 0.05 were included in the model. The relative effect of individual variables was assessed by means of Wald χ^2 . Wald statistics and the corresponding probability are based on the squared ratio of the unstandardized logit coefficient to its standard error.

Excluded from the analyses were species restricted to aquatic or alpine habitats, species that are often planted (such as many trees), apomictic microspecies (which can be regarded as pseudoreplicates) and a few species groups presenting taxonomic problems (see Van der Meijden *et al.* 2000 and Preston *et al.* 2002 for details for the Netherlands and Great Britain respectively). Actual species numbers are listed in Table 3.

Table 3 Number of species included in the analysis for the three countries (C; total number of species 1274), relative to the total number of terrestrial, non-alpine species (A)

	The Netherlands	Great Britain	Germany
(A) Total number of terrestrial, non-alpine species	1351	1583	2226
(B) Subset of A with trend data	1268 (94)	1252 (79)	1851 (83)
(C) Subset of B with data on plant characteristics	1017 (80)	841 (67)	1085 (59)
(D) Subset of C labelled as declining	322 (32)	355 (42)	558 (51)

Values in parenthesis represent percentages.

As model parameters for individual variables are expressed as differences in logistic values, which are difficult to interpret in an ecologically meaningful way, the effects of dispersal traits have been illustrated graphically for the Netherlands, the country for which the most detailed information was available.

The robustness of the results was tested for the Dutch dataset (see Appendix S1), as this dataset has been recorded with the highest resolution and has the smallest proportion of missing values (Table 3). A potential problem in evaluating the importance of individual variables is that they might be interrelated (multicollinearity). We checked for this potentially confounding effect by calculating Pearson correlations between the explanatory variables, and by performing a combination of conditional and marginal tests for all explanatory variables. In addition we checked for confounding effects due to relationships between dispersal traits and other environmental variables by comparing the performance of variables in an 'environmental model' (including preferences for nitrogen, moisture and light), a 'dispersal model' (excluding the environmental variables) and a full model (in which individual variables were entered in the full model).

To check for possible confounding effects of phylogenetic non-independence, we performed a *post hoc* test of bivariate relationships between each of the independent variables and the species trend, using phylogenetically independent contrasts. Technical details on these additional tests are available in Appendix S1.

RESULTS

Overall, dispersal traits make a large and significant contribution to explaining interspecific patterns of species losses, of the same order of magnitude as the effect of eutrophication (Table 4, Appendix S1). Interspecific differences in dispersal traits are thus good predictors of the extinction risk for plant species. The results are consistent across all three countries (Table 4).

Interaction effects were insignificant and did not change the effect of the dispersal vectors on the risk of species decline. The results proved to be unbiased by possible confounding effects such as multicollinearity among variables, correlation of dispersal traits with other environmental conditions and phylogenetic non-independence of species as data points (see additional analyses in Appendix S1). Moreover, we found that the dispersal model performed better than the environmental model (Table S1).

The direction of the relationship between dispersal traits and extinction risk differs between dispersal vectors. Species with a high potential for dispersal in the fur of large mammals or by running water are significantly more likely to decline than those using other dispersal vectors (Fig. 1). On the other hand, species with a high potential for dispersal by wind or birds are less likely to decline. Remarkably, even those species with no adaptations for long-distance dispersal are doing better than those adapted to dispersal by water or animal fur. The results also demonstrate that species with the ability to accumulate a persistent soil seed bank ('dispersal through time') perform relatively well (Fig. 1).

Independent from the effect of dispersal vectors is the effect of eutrophication. Species that are adapted to nutrient-poor conditions are over-represented among the declining species (Table 4). Interspecific differences in the risk of a negative population trend can thus be predicted from the combination of nitrogen requirement of a species (indicating risks on local extinction due to eutrophication) and adaptations to various dispersal vectors. On the other hand, there is no consistent effect of historical abundance. We expected rare species to be more likely to decline (cf. Hubbell 2001). This is true for the Netherlands, but the opposite is true in the UK.

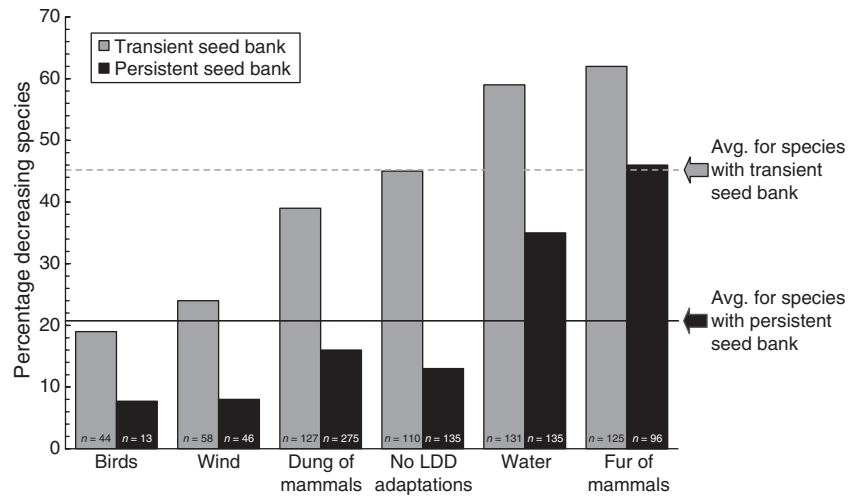
Table 4 Effects of plant characteristics on the probability of decline

Variable	The Netherlands				Great Britain				Germany			
	B	SE	Wald χ^2	Sign.	B	S.E.	Wald χ^2	Sign.	B	S.E.	Wald χ^2	Sign.
Frequency in historical species pool	-0.28	0.04	57.5	< 0.001	0.42	0.06	46.3	< 0.001	-	-	-	-
Nitrogen requirements	-0.36	0.04	75.6	< 0.001	-0.19	0.04	22.1	< 0.001	-0.33	0.03	108.1	< 0.001
Dispersal potential – fur	1.34	0.19	47.8	< 0.001	0.65	0.18	13.5	< 0.001	0.83	0.16	25.6	< 0.001
Dispersal potential – water	1.21	0.18	46.6	< 0.001				n.s.	0.65	0.15	18.8	< 0.001
Seed longevity	-1.01	0.17	36.2	< 0.001				n.s.				n.s.
Dispersal potential – birds	-1.33	0.42	10.0	0.002				n.s.	-0.91	0.31	8.8	0.003
Dispersal potential – wind	-0.99	0.32	9.7	0.002	-0.83	0.29	8.3	0.004	-0.46	0.23	4.0	0.047
Dispersal potential – dung				n.s.	-0.33	0.15	4.5	0.035				n.s.
No LDD				n.s.				n.s.				n.s.
Constant	2.36	0.30	64.0	< 0.001	-2.24	0.46	24.208	< 0.001	1.29	0.17	60.1	< 0.001

Results are given for multiple logistic regressions for three countries, with decline during the 20th century as the dependent variable and plant characteristics as the independent variables. Wald χ^2 gives an indication of the strength of the effect for individual variables. Positive values of B indicate that the decline is increased by the given variable, negative values indicate less than average decline. Model performance as indicated by Nagelkerke's R^2 : the Netherlands, 0.40; Germany, 0.20; Great Britain, 0.16. The highest performance in the Netherlands probably reflects the more detailed information on species trends available for that country.

Sign., significance; LDD, long-distance dispersal.

Figure 1 Percentage of plant species declining by more than 25% over the 20th century, for five long-distance dispersal (LDD) vectors. Species are divided into two groups for each dispersal vector, according to their ability to accumulate a persistent soil seed bank. Horizontal lines indicate the average percentages (geometric means) for species with a persistent soil seed bank (black) and those with a transient soil seed bank (grey) (data from the Netherlands, the country with the most detailed information on species decline).



Widespread nature conservation activities in the UK have generally succeeded in slowing the decline of very rare species, while scarce species (often not targeted by conservation activities) are doing worse. In the Netherlands, very rare species have generally performed worse than scarce species. There was no correlation between historical abundance and other explanatory variables (Appendix S1).

DISCUSSION

Our results imply that differences between species in adaptations to various dispersal vectors are an important but largely overlooked factor in explaining losses in plant diversity in Northwest Europe in the 20th century, with water- or fur-assisted dispersal being over-represented among declining species. This is what we had expected, as free roaming furred mammals and freely running water almost disappeared from the Northwest European landscape (see Appendix S2 for historical overview). Our analysis indicates that dispersal limitation due to a degraded dispersal infrastructure is no less important in explaining declines in regional plant diversity than the effects of eutrophication and associated niche-based processes. A possible clue for the relative independence of niche- and dispersal-based processes is provided by the fact that, in any terrestrial habitat type, a variety of dispersal syndromes is represented in the habitat species pool (Ozinga *et al.* 2004). The crucial process of actual seed dispersal depends on the availability of dispersal vectors, and thus impoverishment of the dispersal infrastructure limits the effectiveness of the regional species pool as a seed source for local colonization.

In the emerging field of metacommunity ecology (Leibold *et al.* 2004), the degree of dispersal between local communities is regarded a key parameter in the assembly and disassembly of local communities. Metacommunity studies traditionally focus on trait-neutral processes (cf. Hubbell

2001), but our results underscore the importance of taking into account differences between species in their dispersal traits. The present study thus indicates that the degree of connectivity of local communities through seed dispersal is not a general characteristic of local plant communities but instead should be differentiated for individual species and linked to the availability of the various dispersal vectors across the landscape.

Our result that species with the ability to accumulate a persistent soil seed bank perform relatively well (Fig. 1) indicates that possession of a seed bank may buffer species from local extinction. The delayed response of long-lived plant species (above or belowground) to habitat fragmentation and degradation is well known as 'extinction debt' and represents a future ecological cost of present day and past land-use changes (Tilman *et al.* 1994; Lindborg & Eriksson 2004; Helm *et al.* 2006; Ozinga *et al.* 2007). It can be expected that there are also delays, following degradation of the services provided by dispersal vectors, before species reach a new equilibrium corresponding to the dispersal services currently provided by the landscape. Restoration measures in most NW European landscapes are therefore likely to take many years to show the desired effects in terms of (re)establishment of less-mobile species. To keep up the metaphor of extinction debt, this time delay in (re)colonization after restoration measures can be termed 'colonization deficit'. Our results suggest that the colonization deficit differs between species and landscapes. On larger spatial and temporal scales, an impoverished dispersal infrastructure may hamper the ability of many species to track changing habitat configurations due to climate change.

For endangered species, which have become rare in the regional species pool and have low dispersal abilities, management at larger spatial and temporal scales at the level of the landscape will be necessary to prevent regional extinction.

Options here are rehabilitation of river and brook systems leading to more natural flooding dynamics in terms of magnitude, frequency, duration and timing (flood-pulse concept, cf. Tockner & Stanford 2002), which in turn may lead to enhanced seed dispersal (see Appendix S2), especially for species with floating seeds. Floating seeds are not restricted to wetland plants but also occur among plant species from dryer habitats (see Appendix S1). Although inundations of high-elevation areas (e.g. river dunes) might be sporadic and short, our results indicate that their impact on colonization probabilities and hence on local species composition is probably high.

Another option is the creation of robust ecological networks for large mammals such as the Pan-European Ecological Network (Council of Europe 2000, Opdam *et al.* 2003; Lindenmayer *et al.* 2008). However, for mammals with a large home range such as Red deer (efficient vectors for long-distance seed dispersal, see Appendix S2), Groot Bruinderink *et al.* (2003) showed that even with robust ecological networks the spatial cohesion of large parts of Central-Europe will remain too low. From a plant perspective, this implies that the creation of ecological networks, although very valuable, will on its own not be sufficient for the conservation and restoration of plant diversity and stresses the importance of complementary approaches.

Governments in the European Union spend roughly €35 billion a year on agri-environmental schemes that cover a quarter of farmland in the EU (Whitfield 2006). The challenge will be to develop new varieties of traditional farming systems that meet modern criteria with regard to biodiversity and socioeconomic sustainability, as today's rapidly vanishing low-intensity farming systems with herded and/or free-ranging livestock on common grounds (cf. Bignal & McCracken 1996) will increase the rate of seed dispersal in the landscape (see Appendix S2).

In the end, for the most endangered species, some form of direct management at the species level may be required, which may include conscientious but deliberate re-introduction schemes.

In conclusion, our research has shown that in fragmenting landscapes, dispersal is an underrated key process in explaining plant diversity losses, and there is an urgent need to face the consequences of this conclusion by designing a different, efficient and cost-effective form of nature conservation for the 21st century. Traditional habitat restoration measures that are directed at improving local habitat quality, although very useful, may be insufficient to halt losses in plant diversity. Our findings clearly show that survival of sessile plant species in fragmented landscapes requires 'moving corridors' such as free flowing waters, dispersing birds and free ranging or herded large mammals. Hence, the effects on the regional persistence of endangered vascular plant species

provided by ecological networks such as the EU's prestigious and costly 'Nature 2000' framework will critically depend on the parallel conservation or restoration of an appropriate infrastructure of dispersal vectors.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Check for possible confounding effects.

Appendix S2 Overview of changes in dispersal infrastructure in NW Europe.

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