



# How important is long-distance seed dispersal for the regional survival of plant species?

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## ABSTRACT

Long-distance seed dispersal is generally assumed to be important for the regional survival of plant species. In this study, we quantified the importance of long-distance seed dispersal for regional survival of plant species using wind dispersal as an example. We did this using a new approach, by first relating plant species' dispersal traits to seed dispersal kernels and then relating the kernels to regional survival of the species. We used a recently developed and tested mechanistic seed dispersal model to calculate dispersal kernels from dispersal traits. We used data on 190 plant species and calculated their regional survival in two ways, using species distribution data from 36,800 1 km<sup>2</sup>-grid cells and 10,754 small plots covering the Netherlands during the largest part of the 20th century. We carried out correlation and stepwise multiple regression analyses to quantify the importance of long-distance dispersal, expressed as the 99-percentile dispersal distance of the dispersal kernels, relative to the importance of median-distance dispersal and other plant traits that are likely to contribute to the explanation of regional survival: plant longevity (annual, biennial, perennial), seed longevity, and plant nutrient requirement. Results show that long-distance dispersal plays a role in determining regional survival, and is more important than median-distance dispersal and plant longevity. However, long-distance dispersal by wind explains only 1–3% of the variation in regional survival between species and is equally important as seed longevity and much less important than nutrient requirement. In changing landscapes such as in the Netherlands, where large-scale eutrophication and habitat destruction took place in the 20th century, plant traits indicating ability to grow under the changed, increasingly nutrient-rich conditions turn out to be much more important for regional survival than seed dispersal.

## Keywords

Anemochory, long-distance dispersal, seed dispersal, species distribution, species survival, wind dispersal.

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## INTRODUCTION

Many plant species have morphological traits to enhance dispersal of their seeds by specific vectors. These traits are considered to be adaptations to dispersal over specific ranges of distances or to specific microsites, or both, which benefits species survival through (1) escape from kin-competition, predators, and pathogens and (2) colonization of unoccupied habitat patches (Howe & Smallwood, 1982; Nathan & Muller-Landau, 2000; Willson & Traveset, 2000). Species with traits that enhance long-distance seed dispersal (e.g. a pappus that enhances seed dispersal by wind) usually disperse the majority of their seeds over – somewhat – longer distances than other species, but disperse a small number of their seeds over very long distances (Soons *et al.*,

2004b). The few seeds that are dispersed over long distances make up the rare long-distance dispersal (LDD) events that are considered an important component of the survival strategy of such species.

Theoretical studies have demonstrated that LDD enhances species range expansion and migration (e.g. Higgins *et al.*, 1996; Kot *et al.*, 1996; Clark, 1998; Higgins & Richardson, 1999). Theoretical studies also demonstrated that LDD enhances regional survival of species in dynamic landscapes, especially landscapes with high turnover of habitat patches or habitat fragmentation (e.g. Malanson & Armstrong, 1996; Valverde & Silvertown, 1997; Hanski, 1998, 1999). The positive effect on regional survival is based on the assumptions that LDD (1) increases the frequency and speed of colonization of unoccupied habitat patches and

(2) increases gene flow between occupied habitat patches so that the probability of extinction in these patches is reduced. Studies on geographical range and on plant migration have provided evidence that LDD occurs and enhances plant range expansion and migration (e.g. Macdonald, 1993; Pitelka *et al.*, 1997; Cain *et al.*, 1998; Petit *et al.*, 2002). Empirical studies have related basic plant traits such as seed mass to species distributions and changes in distributions (Thompson, 1994; Thompson *et al.*, 1999; Kahmen & Poschlod, 2004; Ozinga *et al.*, 2005). However, no empirical studies have been able to link morphological plant traits that indicate LDD by a specific dispersal vector to (1) the actual ability for LDD and (2) the regional survival of plant species. This is partly because ecologists are only starting to establish quantitative relationships between plant traits and dispersal distances including LDD (for wind dispersal most progress has been made, see Nathan *et al.*, 2002; Soons *et al.*, 2004a; Nathan *et al.*, 2005). It is also partly because the analyses needed to test for such links require detailed data on plant traits and plant distributions of a large number of species, which until now were not readily available.

This study aims to quantify the importance of LDD for regional species survival. We do this by using a new approach: We first relate plant species' dispersal traits to seed dispersal kernels and then relate these kernels to regional survival of the species. This approach could not be used before, because no tools were available to relate plant traits to realistic seed dispersal kernels including LDD. For this purpose, we employ a recently developed and tested mechanistic seed dispersal model (Nathan *et al.*, 2002; Soons *et al.*, 2004a, 2004b). Also, detailed data on plant traits and distributions of many species were until now not readily available. We use data from large databases that are currently being made available to ecologists in digital form. This allows us to include data on many plant species and their distributions and makes our results robust. Other advantages of our approach are: first, we can directly quantify the link between LDD and regional survival, without having to use various single estimators of ability for LDD (such as seed terminal velocity and release height) in our analysis. Second, we can distinguish between the importance of rare LDD events in the tail of the dispersal kernel and the importance of overall, or median, dispersal distances. To quantify the relative importance of LDD for regional species survival, we also include other plant traits that are likely to contribute to the explanation of regional survival in our analysis: plant longevity, seed longevity and plant nutrient requirement (Thompson, 1994; Tilman, 1994; Thompson *et al.*, 1999; Ozinga *et al.*, 2005).

## METHODS

We selected seed dispersal by wind as dispersal mechanism for our study. We chose wind dispersal as example for other dispersal mechanisms, because quantitative relationships that have been established between plant traits and dispersal distances, including LDD, are currently more realistic for wind dispersal than for other dispersal mechanisms (cf. Nathan *et al.*, 2002; Soons *et al.*, 2004a). Also, wind dispersal is a very common dispersal

mechanism, making it a general and global example. We selected 190 wind-dispersed plant species of open to relatively open vegetation types in Northwest Europe (see Appendix S1 and S2). Selection criteria were: (1) occurrence in the selected vegetation types, (2) presence of morphological adaptations to reduce falling velocity (pappus, balloon-like structure or wing-like structure > 0.1 times achene length) or to eject seeds from capsules during wind movement, and (3) data on seed terminal velocity and release height available. We studied regional survival of these species in the Netherlands, a suitable study area for our analysis because species distributions have been well-documented for a long period (almost the entire 20th century).

To quantify the importance of LDD and the other plant traits (median dispersal distance, plant longevity, seed longevity and plant nutrient requirement) for regional survival, we carried out correlation analyses between the plant traits and regional survival. To quantify the relative importance of the plant traits in explaining regional survival, we carried out stepwise multiple regression analyses with all traits as independent variables and regional survival as dependent variable. We quantified ability for LDD as the 99-percentile dispersal distance of the seed dispersal kernel of a species. Similarly, we quantified median dispersal distance as the median distance of the dispersal kernel. Dispersal kernels were obtained from simulations with a mechanistic model (see Simulation of dispersal kernels). We included median dispersal in our analysis to separate the importance of rare LDD events from the importance of 'bulk' dispersal, which is usually over relatively short distances. We quantified plant longevity using life history strategy categories (annual = 1, biennial = 2, perennial = 3), seed longevity in the seed bank (Thompson *et al.*, 1997) using the seed longevity index of Bekker *et al.* (1998), and nutrient requirement using Ellenberg indicator values for nitrogen (Ellenberg *et al.*, 1992). These data were derived from the IRIS plant trait database ([www.synbiosys.alterra.nl/IRIS](http://www.synbiosys.alterra.nl/IRIS)). We quantified regional survival using species distribution data at two different scales: nationwide 1 km<sup>2</sup>-grid data and small-scale plot data.

### 1-km<sup>2</sup> grid data

First, we used frequencies of occurrence of species in 1 km<sup>2</sup> grid cells covering all terrestrial area of the Netherlands. We used frequency classes from Tamis & van't Zelfde (2003), wherein several forms of recording bias were eliminated. We used frequency classes for the time periods 1902–1949 ('previous frequency of occurrence') and 1988–1999 ('current frequency of occurrence') and quantified species survival as the change in frequency of occurrence between the two periods. The frequency classes are on a <sup>3</sup>log scale, so we transformed them back to linear scale before subtraction and then transformed the absolute differences to <sup>3</sup>log scale again, afterwards adding the sign of the difference. These data give a good overview of the survival of plant species in the Netherlands. A limitation is, however, that changes in occurrence of species may result simply from changes in the total area of their habitat in the Netherlands (i.e. from changes in the number of grid cells in which their habitat occurs).

### Small-scale plot data

Second, we used frequencies of occurrence of species in small-scale (1–10 m<sup>2</sup>) plots of specific habitat types in the Netherlands. For this, we obtained data from the Dutch Vegetation Database, comprising > 35,000 descriptions of species composition in small plots (relevés) throughout the Netherlands from 1930–1999 (Hennekens & Schaminée, 2001). For our analysis, we selected 11 vegetation types (see Appendix S1) using the following selection criteria: (1) representative of (semi-)natural, open to relatively open vegetation types in the Netherlands, (2) sufficient data available (> 100 plots for both time periods), and (3) area of plots approximately equal for both time periods. We again quantified regional survival as the change in frequency of occurrence between two time periods: 1930–1975 ('previous frequency of occurrence') and 1975–1999 ('current frequency of occurrence'). This measure of survival is not a measure of nationwide survival, but of survival in a specific habitat where changes in the occurrence of species caused purely by changes in the total nationwide area of their habitat do not play a role. Effects of the spatial pattern of their habitat and processes such as (re-)colonization of habitat patches and gene flow between habitat patches do however play a role in these data.

### Simulation of dispersal kernels

For the calculation of dispersal kernels, we assumed that seeds of the selected species are dispersed only by wind and that there is no secondary dispersal. We calculated dispersal kernels from plant traits using a mechanistic seed dispersal model: the Synthetic Turbulence Generation (STG) Markov chain model (Soons *et al.*, 2004a). This model is a slightly modified version, adapted for wind dispersal in relatively open ecosystems, of a model previously developed by Nathan *et al.* (2002). The model simulates dispersal trajectories of individual seeds as determined by gravity, air resistance and wind flow, including wind turbulence. The main difference between this model and other mechanistic dispersal models (e.g. Andersen, 1991; Tackenberg, 2003) is its simulation of realistic wind turbulence, hence realistic LDD (Nathan *et al.*, 2002; Soons *et al.*, 2004a, 2004b). The simulated wind turbulence is stochastic, so that seeds experience unique dispersal trajectories. For each species, we simulated 10,000 dispersal trajectories to create a dispersal kernel.

The model uses two plant traits as input parameters: seed terminal velocity and release height. We obtained the species'

mean terminal velocity and mean release height from the IRIS plant trait database ([www.synbiosys.alterra.nl/IRIS](http://www.synbiosys.alterra.nl/IRIS); IRIS terminal velocity data are partly from Tackenberg, 2001). A third plant trait, period of seed release, determines the model wind velocity input. We estimated the 2-month period during which each species' seed release peaks from Bouman *et al.* (2000). For each 2-month period of the year, we used the natural distribution of horizontal wind velocities in the Netherlands as wind velocity input (wind velocity distributions from Wieringa & Rijkoort, 1983; averages for the Netherlands excluding the coast). The model also uses height and leaf area index (LAI) of the vegetation as input parameters. Vegetation height is the height of the dense part of the vegetation (i.e. excluding flowering stalks). Because all selected species occur in the same open and relatively open vegetation types, and for practical reasons, we set the vegetation height to 2/3 of seed release height and calculated the wind flow inside and above the vegetation using the median vegetation height (0.35 m, data from IRIS) and a standard LAI (3.5). This assumption is realistic for the majority of species because the vegetation types where they occur have similar heights, but it overestimates dispersal distances for tall species that may occur in monospecific tall stands (e.g. *Typha*). For model details and model reliability, we refer to Nathan *et al.* (2002) and Soons *et al.* (2004a, 2004b).

### Statistical analyses

We carried out statistical analyses in SPSS 10 (SPSS Inc. 1989–1999). We used Spearman's correlation coefficient for the correlation analyses, because most data were not normally distributed. In the stepwise multiple regression analyses we excluded species for which any independent variable was missing. Regression models were tested for normality of unstandardized residuals, and if necessary the dependent variables were transformed. To get more insight in the relationships between the independent variables and regional survival we also carried out correlation and regression analyses for the frequencies of occurrence in both time periods. In the analyses for regional survival and current frequency of occurrence we added previous frequency of occurrence as independent variable.

## RESULTS

Some independent variables in our analyses were correlated (Table 1). As expected model output, simulated LDD and

**Table 1** Correlations between long-distance dispersal (LDD), median-distance dispersal, plant longevity, seed longevity and nutrient requirement. For each variable  $N = 190$ , except for nutrient requirement ( $N = 170$ ) and seed longevity ( $N = 124$ ), \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$

Spearman's $\rho$	Median dispersal	Nutrient requirement	Plant longevity	Seed longevity
LDD	0.995***	0.24**	0.27***	NS
Median dispersal		0.26**	0.28***	NS
Nutrient requirement			-0.19*	0.27**
Plant longevity				-0.48***

**Table 2** Results of the analysis of the 1-km<sup>2</sup> grid data. Correlation analyses show which variables are related to frequency of occurrence and regional survival of species. Spearman's  $\rho$  is the correlation coefficient. Stepwise multiple regression analyses show which independent variables best explain frequency of occurrence and regional survival of species. The (+) indicates a positive relationship (–) a negative relationship.  $R^2$  values indicate percentage of variation explained.  $R^2$  values are given for individual variables and full models. Dispersal distances were log-transformed for the analysis. Frequencies of occurrence and regional survival were arctan (arc tangent)-transformed for the regression analyses. <sup>+</sup> $P < 0.10$ , <sup>\*</sup> $P < 0.05$ , <sup>\*\*</sup> $P < 0.01$ , <sup>\*\*\*</sup> $P < 0.001$

	Correlating variables		Explaining variables in stepwise multiple regression	
		Spearman's $\rho$		$R^2$
Frequency in period 1 (1902–1949)	(+) Nutrient requirement <sup>+</sup>	0.13	—	
Frequency in period 2 (1988–1999)	(+) Frequency in period 1 <sup>***</sup>	0.80	(+) Frequency in period 1 <sup>***</sup>	0.66
	(+) Nutrient requirement <sup>***</sup>	0.40	(+) Nutrient requirement <sup>***</sup>	0.08
	(+) Seed longevity <sup>+</sup>	0.15	(+) Seed longevity <sup>***</sup>	0.04
	(+) LDD <sup>+</sup>	0.14	(+) LDD <sup>*</sup>	<u>0.01</u>
	(+) Median distance <sup>+</sup>	0.13		0.79
Regional survival: change in frequency from period 1 to period 2	(+) Nutrient requirement <sup>***</sup>	0.49	(+) Nutrient requirement <sup>***</sup>	0.24
	(+) Seed longevity <sup>***</sup>	0.39	(+) Seed longevity <sup>***</sup>	0.08
	(+) LDD <sup>**</sup>	0.23	(+) LDD <sup>*</sup>	<u>0.03</u>
	(+) Median distance <sup>**</sup>	0.23		0.35
	(–) Plant longevity <sup>*</sup>	–0.18		

median-distance dispersal were almost fully correlated using Spearman's correlation coefficient. Dispersal distance was also correlated with nutrient requirement and plant longevity. The plant species with an optimal occurrence under nutrient-rich conditions and perennial species disperse their seeds over longer distances than the plant species with an optimal occurrence under nutrient-poor conditions and annuals. There was, however, also a weaker but significant negative correlation between nutrient requirement and plant longevity. Seed longevity was positively correlated to nutrient requirement, indicating that the species with an optimal occurrence under nutrient-rich conditions have longer-lived seed banks. Seed longevity was negatively correlated to plant longevity.

### Results for the 1-km<sup>2</sup> grid data

Results of the analyses are presented in Table 2. Frequency of occurrence of the selected plant species in the period 1902–1949 was correlated to plant nutrient requirement, but could not be explained by any of the independent variables used in our analysis. Frequency of occurrence in the period 1988–1999 was correlated with nutrient requirement, seed longevity, LDD and median-distance dispersal. However, by far the highest correlation was with frequency of occurrence in the previous time period. The regression analysis showed that previous frequency of occurrence, nutrient requirement, seed longevity and LDD contribute to explaining the variation in current frequency of occurrence. Together they explained 79% of the variation, of which only 13% was explained by the plant traits. Regional survival was correlated to all plant traits included in the analysis. The regression analysis showed that three independent variables contribute significantly to explaining the variation in survival: nutrient requirement, seed longevity and LDD.

### Results for the small-scale plot data

Results of the analyses for all vegetation types together are presented in Table 3. Again, frequency of occurrence of the selected plant species in the first time period (1930–1975) could not be explained by any of the independent variables in our analysis. Frequency of occurrence in the period 1975–1999 was highly correlated with frequency of occurrence in the previous period and also with nutrient requirement, LDD, and median-distance dispersal. The regression analysis showed that current frequency of occurrence is best explained by previous frequency of occurrence and for a small part also by nutrient requirement. Regional survival was correlated to all independent variables except to plant longevity. The regression analysis showed that survival could be explained by previous frequency of occurrence, nutrient requirement and LDD. However, the total explaining power of these three variables was relatively low (15%).

Results of the analyses for the vegetation types separately are presented in Table 4. Because in all vegetation types specific sets of species occur, relationships of regional survival and frequency of occurrence with plant traits differed between vegetation types. Frequency of occurrence in the first time period was explained by nutrient requirement, LDD, and seed and plant longevity. Current frequency of occurrence was explained best by previous frequency of occurrence, followed by nutrient requirement, and LDD. The  $R^2$  values of the full regression models for frequency of occurrence in 1930–1975 ranged from 0.06 to 0.33 and were much lower than for frequency of occurrence in 1975–1999 (0.36–0.76). Note, however, that the models for 1975–1999 included an extra explanatory variable. Regional survival was explained best by previous frequency of occurrence, nutrient requirement, seed longevity and dispersal (both LDD and

**Table 3** Results of the analysis of the small-scale plot data when all vegetation types are analysed together. Correlation analyses show which variables are related to frequency of occurrence and regional survival of species. Spearman's  $\rho$  is the correlation coefficient. Stepwise multiple regression analyses show which independent variables best explain frequency of occurrence and regional survival of species. The (+) indicates a positive relationship, (–) a negative relationship.  $R^2$  values indicate percentage of variation explained.  $R^2$  values are given for individual variables and full models. Dispersal distances were log-transformed for the analysis. Frequencies of occurrence and regional survival were arctan (arc tangent)-transformed for the regression analyses.  $^{\dagger}P < 0.10$ ,  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$

	Correlating variables		Explaining variables in multiple regression	
		Spearman's $\rho$		$R^2$
Frequency in period 1 (1930–1975)	(–) Seed longevity**	– 0.13	—	
	(+) Plant longevity <sup>†</sup>	0.07		
Frequency in period 2 (1975–1999)	(+) Frequency in period 1***	0.63	(+) Frequency in period 1***	0.55
	(+) Nutrient requirement***	0.17	(+) Nutrient requirement***	<u>0.03</u>
	(+) Median distance*	0.08		0.58
	(+) LDD*	0.07		
Regional survival: change in frequency from period 1 to period 2	(–) Frequency in period 1***	– 0.35	(–) Frequency in period 1***	0.08
	(+) Nutrient requirement***	0.25	(+) Nutrient requirement***	0.06
	(+) LDD***	0.12	(+) LDD *	<u>0.01</u>
	(+) Median distance**	0.12		0.15
	(+) Seed longevity*	0.08		

**Table 4** Results of the stepwise multiple regression analyses of the small-scale plot data when all vegetation types are analysed separately. Results show which independent variables best explain frequency of occurrence and regional survival of species. Per independent variable the number of vegetation types (out of 11) for which the variable is significant ( $P < 0.05$ ) is indicated. Dispersal distances were log-transformed and frequencies of occurrence and regional survival were arctan (arc tangent)-transformed for the analyses.  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$

	Explaining variables in multiple regression	
		Number of vegetation types
Frequency in period 1 (1930–1975)	Nutrient requirement <sup>*-***</sup>	7
	Seed longevity**	2
	LDD <sup>*-***</sup>	2
	Plant longevity <sup>*-***</sup>	2
Frequency in period 2 (1975–1999)	Frequency in period 1***	10
	Nutrient requirement <sup>*-***</sup>	5
	LDD <sup>*-***</sup>	2
Regional survival: change in frequency from period 1 to period 2	Frequency in period 1 <sup>*-***</sup>	7
	Nutrient requirement <sup>*-***</sup>	4
	Seed longevity*	3
	Median distance <sup>*-***</sup>	2
	LDD**	1

median-distance dispersal). Interestingly, the relationship with previous frequency of occurrence was always negative, as in the analysis for all vegetation types together. This indicates that many previously common species decreased in abundance, whereas a group of previously rare species in the selected vegetation types (but not so rare elsewhere in the Netherlands) increased in abundance. This corresponds to the finding that previous frequency of occurrence was most often negatively related to nutrient requirement, whereas current frequency of occurrence was always positively related to nutrient requirement. This indicates that in several vegetation types a shift occurred from species with an optimum at nutrient-poor conditions to species with an optimum at more nutrient-rich conditions. The  $R^2$  values of the full regression models for survival ranged from 0.15 to 0.89.

## DISCUSSION AND CONCLUSIONS

We quantified the importance of LDD for the regional survival of wind-dispersed plant species in the Netherlands. We used a new approach, by first linking plant traits to ability for LDD and then linking ability for LDD to regional survival. The main advantage of this approach is that realistic, consistent, quantitative measures of species' ability for LDD are related to their regional survival. It should be kept in mind, however, that the quantification of LDD is based on several key assumptions (including dispersal by wind exclusively and equal vegetation height and LAI for all vegetation types) and simulated LDD is an indication, not the exact value, of actual LDD. We used data on 190 plant species and species distribution data for > 36,000 1 km<sup>2</sup>-grid cells and > 10,000 small

plots, covering the largest part of the 20th century. These large numbers, the nationwide coverage of our data, and the good agreement between results from different analyses make our results robust. Our results give implications for species conservation (see Trakhtenbrot *et al.*, 2005).

The LDD of plant seeds plays a role in determining regional survival of the plant species. LDD is more important than median-distance dispersal. The large differences in ability for LDD between species explain differences in regional survival better than the much smaller differences in median-distance dispersal. LDD is also more important in explaining regional survival than plant longevity. However, the explaining power of LDD is not very great: the ability for LDD explains only approximately 1–3% of the variation in survival. This is comparable to seed longevity, but much less than nutrient requirement, which explains the variation in survival best (by 6–24%). Patterns for the explanation of current frequency of occurrence by plant traits are similar to those for regional species survival. Current frequency of occurrence is, however, by far best explained by previous frequency of occurrence (by 55–66%). Previous frequency of occurrence cannot be explained by any of the plant traits when all vegetation types are analysed together, but within vegetation types some plant traits do explain frequency of occurrence. The vegetation-specific results are likely caused by interactions between environmental conditions and plant traits (Ozinga *et al.*, 2004).

Several explanations may contribute to our finding that LDD is of relatively little importance for regional species survival in comparison to nutrient requirement. First, the positive correlation between nutrient requirement and ability for LDD, as well as seed longevity, may have obscured the relationships between survival and LDD and seed longevity in the stepwise multiple regression analyses. However, in the correlation analyses the relationship between survival and nutrient requirement was also much stronger than the relationships between survival and LDD and seed longevity. Second, the assumption that LDD enhances regional survival by increasing the frequency and speed of colonization of unoccupied habitat patches may be wrong. Not necessarily because dispersal distances are too low (in some species 99-percentile dispersal distances were very long; see Appendix S2), but because during the 20th century, many (semi-)natural vegetation types in the Netherlands were destroyed or severely fragmented (Vos & Zonneveld, 1993; Soons, 2003) and very few new, suitable but unoccupied habitat patches came into existence. Lack of unoccupied habitat patches reduces the positive effect of LDD on regional survival through increased colonization. Third, the assumption that LDD enhances regional survival by increasing gene flow between occupied habitat patches, so that the probability of extinction in these patches decreases, may be wrong. If habitat destruction and fragmentation resulted in isolation of all remaining populations (e.g. Soons, 2003), LDD does not reduce patch extinction because it does not increase gene flow anymore. This is not very likely though, because several of the selected vegetation types are still relatively common and some species have very long dispersal distances (see Appendix S2). It is more likely that isolated popu-

lations have not suffered from lack of gene flow and a positive effect of gene flow on regional survival is not (yet) discernible. Fourth, the assumption that the selected plant species achieve LDD primarily through primary wind dispersal may have been wrong. Seeds of many plant species have adaptations for dispersal by more than one potential LDD vector (Ozinga *et al.*, 2004) or may be dispersed over long distances by non-standard processes, including secondary dispersal (Higgins *et al.*, 2003). If the selected plant species achieve LDD through a range of different mechanisms, the importance of LDD by wind may be obscured, even though it may be important for regional survival (cf. Hodkinson & Thompson, 1997). Fifth, and most likely, is the explanation that habitat requirements are simply much more important for regional survival in the Netherlands than dispersal ability. During the 20th century all vegetation types in the Netherlands experienced changes in abiotic conditions, most notably nitrogen enrichment as a result of intensification of agriculture (Vos & Zonneveld, 1993; Bobbink *et al.*, 1998; Aerts & Bobbink, 1999). In many vegetation types this resulted in shifts from species with an optimum at nutrient-poor conditions to species with an optimum at more nutrient-rich conditions (Bobbink, 1991; Bobbink *et al.*, 1998; Aerts & Bobbink, 1999), as we also found. Results indicating that species with high competitive ability under nutrient-rich conditions are currently increasing most in the Netherlands and other countries with high nutrient emissions have also been found by Thompson (1994), Schaminée *et al.* (2002) and Tamis *et al.* (2004).

Finally, the relatively low total amount of variation in regional survival that is explained (15–35%, up to 89% for the vegetation types separately) indicates that other plant traits, random processes, or both are also very important. Pollen dispersal distance, success of self-fertilization, and ability to grow under increasingly common environmental conditions other than high nitrogen availability (e.g. tolerance to low groundwater levels) may contribute to the explanation of survival. Detailed quantitative data on these plant traits were not available for our analysis, but are being collected and will be available for future analyses, which may find a higher amount of variation in survival explained by plant traits. Alternatively, such future analyses may find that random processes (cf. Hubbell, 2001) have a relatively great importance for regional species survival.

We conclude that plant species' ability for LDD by wind is important for their survival in the Netherlands. Ability for LDD by wind dispersal is approximately of the same importance as seed longevity in the seed bank. However, under the increasingly nutrient-rich environmental conditions in the Netherlands, the ability of species to grow and survive under nutrient-rich conditions is far more important for their regional survival than their ability for LDD.

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## SUPPLEMENTARY MATERIAL

The following material is available at <http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI148/DDI148sm.htm>

**Appendix S1.** Overview of the vegetation types included in the analysis.

**Appendix S2.** List of plant species selected for the analysis.

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