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Dispersal potential in plant communities depends on environmental conditions

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Summary

1 Local plant communities can only function within a metacommunity context if they are connected by appropriate dispersal vectors, accommodating the transport of propagules between sites. The capacity for long-distance dispersal may be a key factor in the survival of local populations, especially in fragmented landscapes, and hence may have a large impact on local species composition. Dispersal vectors with a large efficiency for long-distance dispersal included in this study are: water, wind, large mammals and birds.

2 We tested the hypothesis that variation in dispersal traits across plant communities is related to the position of the communities along major environmental gradients. This hypothesis was tested for (i) separate long-distance dispersal vectors and (ii) multiple dispersal vectors (the number of potential long-distance dispersal vectors per species).

3 To quantify linkages between dispersal traits and environmental gradients, we coupled a data base containing dispersal attributes with another data base, containing 40 000 local vegetation descriptions aggregated into 123 plant communities. For each dispersal vector, the proportions of species that have access to this vector per community (weighted trait scores) were projected along three major environmental gradients: soil moisture, nutrient availability and light availability.

4 The potential importance of individual dispersal vectors showed clear differences along the three environmental gradients, with the greatest differences along the light availability gradient. The differences in dispersal traits probably reflect environmental constraints on the availability or efficiency of individual dispersal vectors.

5 The ability to be dispersed by multiple dispersal vectors is a common phenomenon in most plant communities (an average of 2.15 vectors per species). The mean number of potential long-distance dispersal vectors per species increases with light availability. This probably implies that plant communities differ in their response to both habitat fragmentation and habitat restoration.

6 Despite differences in trait spectra among communities, all dispersal syndromes are represented in nearly all communities. An important consequence of this complementarity in dispersal traits is that species within the same community may experience different connectivity.

7 The results emphasize the need for dispersal models based upon multiple dispersal vectors that explicitly include parameters for habitat characteristics.

Key-words: ecoinformatics, functional traits, polychory, trait-environment linkages, trait complementarity

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Introduction

Given a certain set of environmental conditions, the community composition at a site is influenced by both the rates of local extinction and the rates of colonization from the species pool (e.g. Freckleton & Watkinson 2002). It follows from basic metapopulation theory (Levins 1969; Hanski 1998) that species within a metacommunity (sets of communities connected by dispersal of component species; Mouquet & Loreau 2002) occupy only a fraction of the suitable habitat patches because species continually become locally extinct and these sites may not be reoccupied if colonization capacity is limited, at least at larger spatial scales. Within local communities, there is thus a continuous turnover of species, as has been demonstrated by detailed field observations in grasslands by Van der Maarel & Sykes (1993). Seed sowing experiments have underpinned the notion that dispersal limitation is almost universal in plant communities (Turnbull *et al.* 2000; Foster & Tilman 2003; Xiong *et al.* 2003). Interspecific differences in dispersal traits are therefore expected to affect local species composition.

Short-distance dispersal (i.e. within local populations) will generally be sufficient for the local survival of populations in habitats with a high level of spatial and temporal continuity. But in spatially heterogeneous landscapes (such as in many industrialized parts of the world) the survival probability of local populations increases for species that have higher rates of long-distance dispersal. Studies by Ellstrand & Elam (1993), Ouborg (1993) and Harrison *et al.* (2000) indicate that species in patches that are more isolated have a higher probability of becoming locally extinct, and such patches have a lower probability of becoming colonized or recolonized. The emphasis in our study was therefore on long-distance dispersal, which we define as dispersal between sites separated by more than 100 m, following Cain *et al.* (2000).

At the species level, there are large interspecific differences in seed attributes that determine the potential of the various dispersal modes to serve as long-distance dispersal vectors (e.g. Cain *et al.* 2000; Pakeman *et al.* 2002; Tackenberg *et al.* 2003). Moreover, species differ not only in the efficiency of dispersal by different dispersal vectors, but also in the number of dispersal vectors by which they are potentially dispersed between sites (specialists vs. generalists for long-distance dispersal or with no adaptations for long-distance dispersal at all), but reliable quantifications of this variation are lacking.

Interspecific differences in dispersal traits can be integrated at the community level by quantifying the proportions of potential dispersal vectors. There have been few studies on differences in dispersal traits between habitats (Gentry 1983; Willson *et al.* 1989; Willson *et al.* 1990; Hughes *et al.* 1994) and these studies show methodological limitations as both dispersal traits and habitat characteristics are poorly defined. The recent compilation of large data bases on community composition and on dispersal attributes for species offers new opportunities to quantify the relationship between environmental conditions and dispersal traits. Linking species composition and data on dispersal attributes may improve our understanding of the interactions between local (< 100 m) and regional (>> 100 m) processes.

The assembly of local communities from a given species pool is generally studied by means of two complementary approaches, relating to different scales. At the local scale, the so-called ‘niche assembly view’ focuses on interactions between individuals of different species and interspecific niche differences. According to this view, the species composition of a community is a deterministic consequence of physiological processes and biological interactions (e.g. MacArthur & Connell 1966; Tilman 1985; Keddy 1992). On the other hand, the so-called ‘dispersal assembly view’ focuses on larger scales, both in space and time, and assigns a more prominent role to stochastic events such as catastrophic changes in environmental conditions, local extinction and long-distance dispersal (e.g. MacArthur & Wilson 1967; Zobel 1997; Turnbull *et al.* 2000).

If environmental conditions constrain the availability or efficiency of individual dispersal vectors (cf. Grubb 1987), differences may be expected between communities with regard to dispersal attributes. If the relative importance of dispersal vectors is indeed influenced by environmental conditions, this implies that there is an uneven dispersal potential across landscapes dependent on the distribution of habitats. This will in turn affect the community assembly processes that determine local species composition and biodiversity. Linkages between dispersal traits and environmental gradients imply that communities will differ in their response to habitat fragmentation and habitat restoration.

We tested the hypothesis that variation in dispersal traits across plant communities is related to the position of communities along major environmental gradients. This hypothesis was tested for (i) the distribution of individual dispersal vectors in plant communities and (ii) the degree to which species within communities are served by multiple dispersal vectors.

Materials and methods

Our approach is based on combining large data bases containing species-level dispersal traits and environmental optima with those for community-level species co-occurrence. An overview of the data base linkages is given in Fig. 1.

DISPERSAL ATTRIBUTE DATA BASE

The efficiency of various dispersal vectors for a given species can be classified based either on differences in actually realized dispersal distance or on differences in attributes that (potentially) give access to dispersal modes with a high efficiency for long-distance dispersal (Muller-Landau *et al.* 2003). Long-distance dispersal (> 100 m,

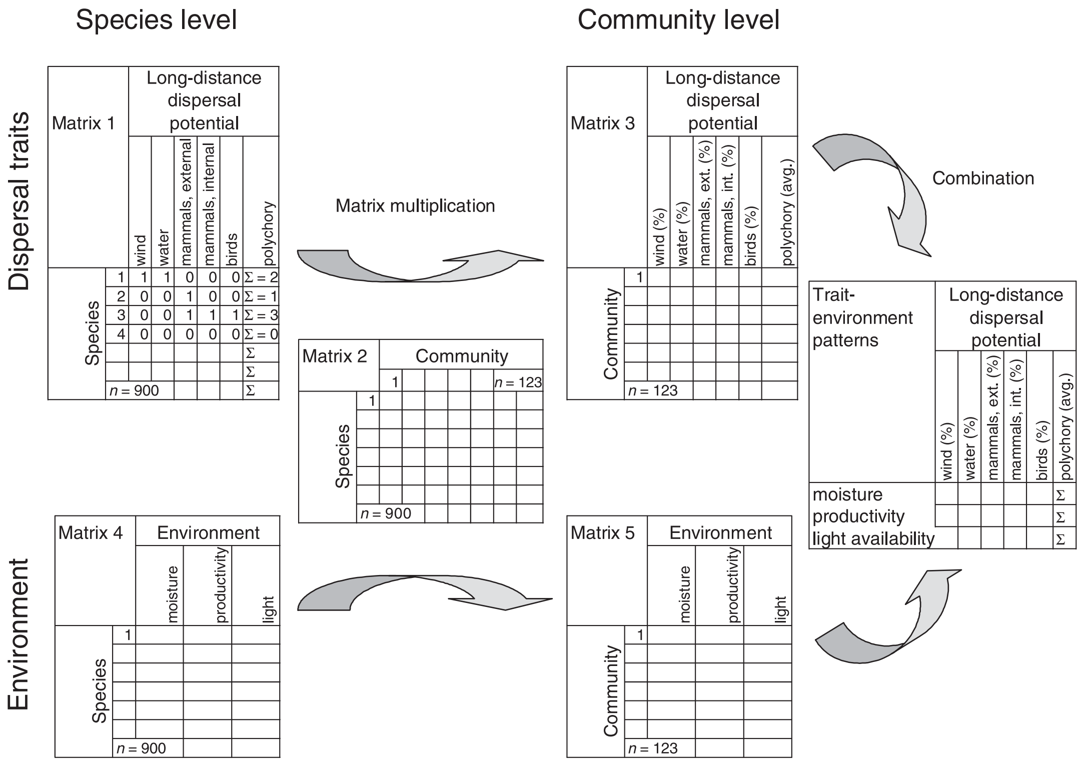

Fig. 1 Overview of the data base linkages needed for the establishment of the trait-by-environment pattern. Matrices 1 and 4 contain data at the species level for dispersal potential (matrix 1) and the optimum occurrence along environmental gradients as expressed by Ellenberg indicator values (matrix 4). Both matrices were multiplied by the species-by-community matrix (matrix 2) to calculate weighted means at the community level (matrices 3 and 5). The data from matrices 1 and 4 have been weighted by the percentage presence of the species within the communities (in the cells of matrix 2, based on 40 000 local plot descriptions). Combining matrix 3 (percentage of species within communities with a high potential for dispersal by each dispersal vector) and matrix 5 (position of communities along the three major environmental gradients) results in a set of relationships between environmental gradients (x-axis) and dispersal traits (y-axis). This combination of large ecological data bases on different organizational levels to reveal new information can be regarded as an example of 'ecoinformatics'.

cf. Cain *et al.* 2000) depends on the tail of the 'dispersal kernel' and is extremely difficult to quantify (Bullock & Clarke 2000; Cain *et al.* 2000; Nathan & Muller-Landau 2000). The probability of ending up in the tail of the dispersal kernel is not only dependent on species traits, but also on landscape characteristics, such as vegetation structure, presence of barriers and availability of dispersal vectors. Even perfect information on the dispersal distance of all seeds in a population would only provide a case-specific documentation of differences in realized dispersal distance (Nathan *et al.* 2003; Tackenberg *et al.* 2003). Realistic, mechanistic models, are only available for dispersal by wind (e.g. Nathan *et al.* 2002; Tackenberg *et al.* 2003; Soons *et al.* 2004), but are lacking for other dispersal vectors. It is therefore not realistic to quantify the probability of seeds dispersing over distances of > 100 m for many species under various conditions for all dispersal vectors.

On the other hand, differences in attributes that determine the degree of access to various dispersal modes can be quantified more easily (Weiher *et al.* 1999; Pakeman *et al.* 2002; Boedeltje *et al.* 2003; Cornelissen *et al.* 2003; Tackenberg *et al.* 2003). Therefore we have adopted a trait-based approach, and have compiled a data base for the Dutch flora called 'IRIS', with plant and propagule traits that are relevant to dispersal. We consider the following dispersal vectors to have a high efficiency for long-distance dispersal (for references see www. synbiosys.alterra.nl/IRIS): water (hydrochory), wind (anemochory), attachment to the fur of large mammals (epizoochory by mammals), survival in the digestive tract of large mammals (endozoochory by mammals) and frugivorous birds (endozoochory by birds). The degree to which species have access to these dispersal vectors is inferred from morphological and physical traits that have been shown to be related to the efficiency of dispersal by the various vectors (Weiher *et al.* 1999; Pakeman *et al.* 2002; Boedeltje *et al.* 2003; Cornelissen *et al.* 2003; Tackenberg *et al.* 2003; see www.synbiosys.alterra.nl/IRIS for a detailed explanation for each dispersal vector). This provides us with a relative classification of the potential of species for dispersal by various vectors that is independent of landscape characteristics, climatological conditions and the number of seeds produced. In order to include as many species as possible and to facilitate comparisons between different dispersal vectors, we aggregated the available data into a binary classification, assigning each species to one of two classes for each dispersal agent: '1' if the species has attributes that give access to a given vector and

'0' if the species has no such attributes (see www.synbiosys.alterra.nl/IRIS for criteria). This resulted in a species-by-trait matrix (matrix 1 in Fig. 1). Although the binary classification of the continuum is relatively imprecise for individual species, it allows generalizations to be made at the community level across habitats.

It is important to note that many species have a high dispersal potential (i.e. a '1' in the data base) for more than one long-distance dispersal vector. These species can be regarded as generalists in terms of long-distance dispersal. On the other hand, several species have low potential for all five long-distance dispersal vectors (although many of them have special adaptations for short-distance dispersal, such as mechanisms to release seeds ballistically or nutrient-rich appendages to attract ants). To summarize this information, we included a field with the number of long-distance dispersal vectors per species (a summation of the scores for the five dispersal vectors; see matrix 1 in Fig. 1). For dispersal in general, potential dispersal by multiple agents has been termed 'polychory' (e.g. Ridley 1930; Van der Pijl 1982), but since we restricted our analysis to dispersal vectors with a high efficiency for long-distance dispersal, we called this aggregated trait 'long-distance polychory'. Although long-distance polychory is probably closely related to total long-distance dispersal potential, it is not exactly the same and merely reflects the number of possible types of vectors for long-distance dispersal.

A total of 900 vascular plant species (*c*. 75% of the total terrestrial flora of the Netherlands) were included in the analysis. Trees, spore-plants and orchids were excluded.

VEGETATION DATA BASE

We quantified the proportions of species that have access to specific dispersal vectors at the community level using the Dutch Vegetation Database (Hennekens & Schaminée 2001), which comprises over 400 000 descriptions of species composition at specific plots (< 100 m^2) throughout the Netherlands. The Dutch vegetation classification (Schaminée *et al*. 1995–99), uses cluster analysis to analyse a subset of 40 000 plots, and assign them to 228 plant communities. We made a further selection to exclude plant communities occurring in saline and aquatic environments, to give a simpler data base representing terrestrial plant diversity in the Netherlands. This compressed the information into a species-by-community matrix (matrix 2 in Fig. 1) with 123 plant communities and 900 plant species, in which each cell contained the percentages of plots for a given community in which the species was present (% presence).

DISPERSAL ATTRIBUTES WITHIN COMMUNITIES

Combining the species-by-trait data base (matrix 1) with the species-by-community matrix (matrix 2) allowed us to quantify patterns of dispersal traits at the community level (community-by-trait matrix; matrix 3). The proportions of species that have access to specific dispersal vectors (trait scores) were weighted according to the percentage of plots in which the species were present (abundance in the 'habitat species pool').

POSITION OF COMMUNITIES ALONG ENVIRONMENTAL GRADIENTS

We characterized the environmental conditions of communities using Ellenberg indicator values (species-by-environment matrix; matrix 4). These indicator values give the ecological optima of species for a range of abiotic parameters and were obtained from Ellenberg *et al*. (1992). Evidence for the accuracy of the indicator values has been provided by several studies reporting close correlations between average indicator values and corresponding measurements of environmental variables (e.g. Thompson *et al*. 1993; Schaffers & Sykora 2000; Diekmann 2003). Multiplying the species-by-environment matrix (matrix 4) by the species-by-community matrix (matrix 2) resulted in a community-by-environment matrix (matrix 5) in which the position of each community is quantified relative to the three major environmental gradients. The Ellenberg indicator values were weighted with the percentage of plots in which the species were present.

We used two complementary ordination methods (DCA and CCA) to reveal relationships between the species-by-community matrix (matrix 2) and the community-by-environment matrix (matrix 5). Variation in species composition of terrestrial plant communities in the Netherlands was mainly related to three major environmental gradients (W.A. Ozinga, unpublished data), reflecting differences in the availability of water and oxygen, of nutrients and of light and open space. We restricted our analysis to these three environmental variables between which community-level correlations were low ($r < 0.25$; W.A. Ozinga, unpublished data).

TRAIT-ENVIRONMENT LINKAGES

Finally, relationships between the distribution of the five dispersal traits over the three major environmental gradients were quantified at both the species level and the community level. At the species level this was achieved by the combination of matrices 1 and 4.

At the community level the trait-environment patterns were quantified by the linkages between the community-dispersal trait data base (matrix 3) and the community-environment data base (matrix 5; Fig. 1). We also calculated the mean number of long-distance dispersal vectors per species within each community ('long-distance polychory index'). In comparison with the species level analysis, the community level analyses are less sensitive to misclassifications in the original Ellenberg indicator values (e.g. Diekmann 2003) and account for interspecific differences in regional abundance (species-trait combinations of very rare species are given less weight than those of common species).

Statistical analyses were conducted on the trait-environment data using SPSS 10.0 (© SPSS Inc. 1989–99). Relationships between the trait scores and the three main environmental gradients (availability of water, nutrients and light) were tested for significance for each dispersal vector separately. For the analyses at the species level we used stepwise logistic regression and for the analyses at the community level we used stepwise multiple regression.

Results

An overview of the regression models for each dispersal vector is given in Table 1 for the species level (not weighted by regional abundance) and in Table 2 for the community level. The directions of the relationships between dispersal traits and environmental conditions at the species level were consistent with the results at the community level. At the community level, however, the patterns were much more pronounced (Table 1 vs. Table 2), as indicated by higher beta-values and higher proportions of explained variance (R^2-values). At the community level the R^2-values were, in general, more than 10 times as high as those at the species level. Different dispersal vectors were only weakly correlated among species ($r < 0.30$ for all combinations; data not shown).

The strongest trait-environment linkages ($R^2_{\text{change}} > 0.25$) at the community level are illustrated in Fig. 2. In the panels of this figure, each point represents a plant community. The *x*-axes give the position of the communities relative to the environmental gradient as indicated by Ellenberg indicator values (mean for communities weighted by the percentage of plots in which each of the species was present), while the *y*-axes give the trait scores for each community (also weighted by the percentage presence).

The differences in the potential importance of individual dispersal vectors were greatest along the light availability gradient, and all of the dispersal vectors, except water, showed significant positive relationships with light availability (Table 2). Both epizoochorous and endozoochorous dispersal by mammals became more important with increasing light availability (Fig. 2c,d). The proportion of species with a high potential for dispersal by frugivorous birds (Fig. 2e) and the proportion of species with no adaptations for long-distance dispersal at all (Fig. 2f) showed the opposite pattern, decreasing significantly with increasing light availability.

Table 1 Significant trait–environment relationships at the species level. Binary logistic regression models were performed with the dispersal traits as the dependent variable and the Ellenberg indicator values for moisture, nutrient availability and light availability as independent variables. Models are based on the total species pool ($n = 900$). The percentage of variance explained is approximated with Nagelkerke's R^2 (comparable with the R^2 values in the linear regressions in Table 2)

Dispersal vector	Independent variable	Beta (standardized)	Nagelkerke R^2	Sig. (*G*-test)
Water	Moisture	0.49	0.300	< 0.001
Wind	Nutrient availability	−0.15	0.036	< 0.001
Mammals, externally	Light availability	0.17	0.013	0.002
Mammals, internally	Light availability	0.15	0.014	0.001
Birds, internally	Light availability	−0.36	0.050	< 0.001

Table 2 Significant trait–environment relationships at the community level. Linear regression models were performed with the proportion of species that have access to a given dispersal vector as the dependent variable and the positions of communities along environmental gradients as independent variables. All models are based on 123 terrestrial plant communities. Environmental variables are given in order of entrance into the model. The R^2_{adj} values refer to the total model, while Sig. R^2_{change} refers to the significance of the change in R^2 after entering the variable in the model. Explanatory variables were only included if the proportion of explained variance increased significantly (Sig. R^2_{change}: $P < 0.05$)

Dispersal vector	Environmental variable entered in model	Beta (standardized)	R^2_{adj}	Sig. R^2_{change}
Water	Moisture	0.92	0.84	< 0.001
Wind	Nutrient availability	−0.66	0.38	< 0.001
	Light availability	0.36	0.50	< 0.001
	Moisture	0.14	0.52	0.040
Mammals, externally	Light availability	0.64	0.41	< 0.001
	Nutrient availability	−0.20	0.44	0.005
Mammals, internally	Light availability	0.73	0.53	< 0.001
	Nutrient availability	0.18	0.56	0.004
Birds, internally	Light availability	−0.77	0.57	< 0.001
	Nutrient availability	−0.19	0.61	0.001
Long-distance polychory	Light availability	0.6	0.34	< 0.001
	Moisture	0.55	0.59	0.000
No adaptations	Light availability	−0.50	0.23	< 0.001
	Moisture	−0.47	0.33	< 0.001
	Nutrient availability	0.43	0.48	0.008

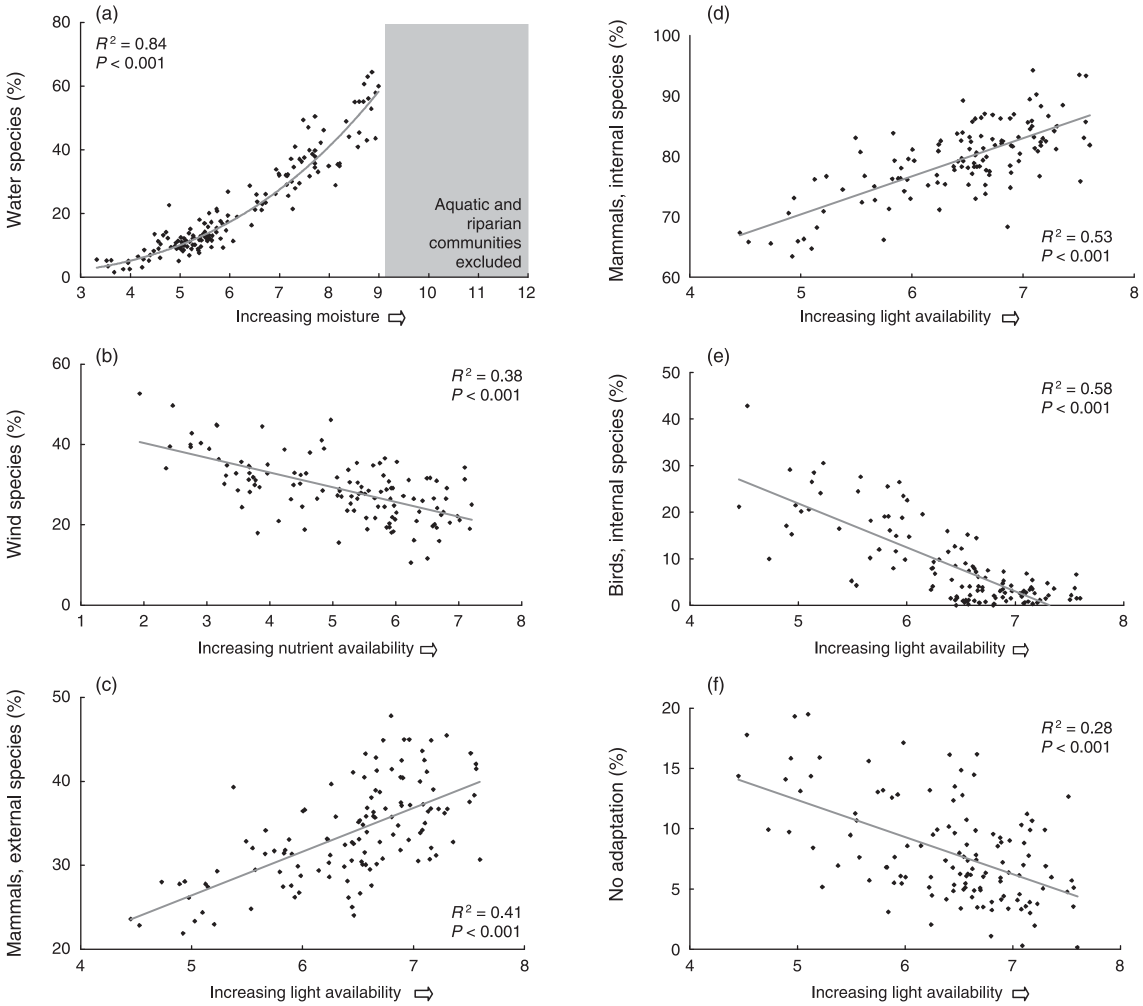

Fig. 2 Overview of relationships between dispersal traits and environmental gradients. All combinations of long-distance dispersal vectors ($n = 5$) and the major environmental gradients ($n = 3$) with a $R^2_{\text{change}} > 0.25$ are given (see Table 2). The graphs show the proportion of species with a high potential for dispersal by, respectively: (a) water, (b) wind, (c) fur of large mammals, (d) dung of large mammals, and (e) birds. Panel f shows the proportion of species without any adaptations for long-distance dispersal vectors. In these panels each point represents a plant community ($n = 123$). The x-axis shows the position of the communities relative to the environmental gradient as indicated by Ellenberg indicator values (mean for communities weighted by the frequency of occurrence of the species). The y-axis shows the percentage of species within each community with a high potential for dispersal by the dispersal vector under consideration.

The variation in the potential for dispersal by water can be largely explained by soil moisture ($R^2 = 0.84$; Fig. 2a). Changes in the potential of wind as a dispersal vector were most closely related to nutrient availability (Fig. 2b) and, to a smaller extent, to light availability. Although some other long-distance dispersal vectors were significantly related to nutrient availability, the increases in the explained variance due to this environmental trait were small ($R^2_{\text{change}} < 0.05$). Despite the differences in relative importance of individual dispersal vectors, all dispersal syndromes are represented in many communities (although sometimes with low proportions; Fig. 2), such that, in 70% of communities, all dispersal vectors are represented by at least 5% of the species.

Many species in the Dutch flora have the potential to be dispersed over long distances by more than one dispersal vector (long-distance polychory). The average number of dispersal vectors per species for all 900 species was 1.57. Weighted by the frequency of occurrence in each community, the average becomes 2.15 vectors per species. The average number of long-distance dispersal vectors per species within the communities (long-distance polychory index) was found to decrease with decreasing availability of light (Fig. 3), thus showing the opposite trend to the proportion of species that have no access to any of the long-distance dispersal vectors (Fig. 2f). The average number of long-distance dispersal vectors per species within a community was not related to nutrient availability (Table 2).

Discussion

ENVIRONMENTAL CONSTRAINTS ON THE AVAILABILITY AND EFFICIENCY OF DISPERSAL VECTORS

The results show clear differences in the potential importance of the various dispersal vectors along the major

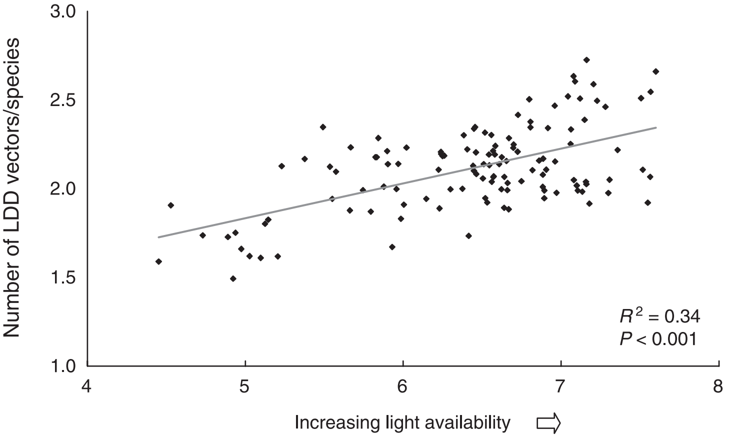

Fig. 3 Mean number of potential long-distance dispersal (LDD) vectors per species within each community (long-distance polychory index) relative to the position along the light availability gradient.

environmental gradients, both at the species level and at the community level. The non-random distribution of dispersal traits along environmental gradients supports the hypothesis that the potential importance of the various dispersal vectors depends on the environmental context. The patterns were much stronger at the community level (higher Beta and R^2-values; Table 1 vs. Table 2). This can be explained by a non-random selection of species assemblages from the regional species pool with regard to dispersal traits. In a complementary study (Ozinga *et al*., 2005) we have shown that species with high dispersal ability are indeed overrepresented in local plots in comparison with a random selection of species from the habitat species pool. In the present paper our main interest is not the difference between the species level and the community level results, but merely the differences in dispersal traits across environmental gradients.

Water

The close correlation ($R^2 = 0.84$) between the position of a plant community along the moisture gradient and the percentage of species with a high potential for dispersal by water indicates that dispersal by water can be important in determining species composition within wet communities. This can be explained by the high efficiency of water as a dispersal vector in frequently inundated sites, in combination with the relatively high gap dynamics in landscapes where parts of the vegetation are regularly destroyed by inundation and/or sedimentation, increasing the availability of safe sites for establishment. These results are in agreement with the findings of Boedeltje *et al.* (2003).

An unexpected finding was that even in communities with intermediate soil moisture levels (mean Ellenberg values 6–8) the percentage of species that can be dispersed by water is still as high as 20–40% (both at the species level and at the community level). This illustrates that, although inundations in these communities may be occasional, the impact on species composition is potentially large. Dry storage of seeds (e.g. remaining attached to the mother plant during winter) increases the floating ability of the seeds of several species (Praeger 1913; Bill *et al.* 1999), probably due to shrinkage of the fruit content relative to the fruit surface, seed coat hardening and increased water-repellency (Baskin & Baskin 1998). Increased impermeability of the seed coat during maturation induces seed dormancy in these species, and might, in dry environments, lead to a correlation between floating ability and seed longevity. This would imply that in medium-dry environments, species with long-lived seeds might profit from occasional inundations.

Wind

The proportion of species with a high potential for dispersal by wind increases with decreasing nutrient availability and increasing openness of the vegetation structure. At least two complementary mechanisms may explain this relationship.

First, the efficiency of wind as a dispersal vector is constrained by the height and density of the surrounding vegetation. Wind can be a very effective long-distance dispersal vector, but is only reliable if the propagules become entrained by turbulence in convective updrafts above the vegetation canopy (Tackenberg 2001; Nathan *et al.* 2002). Within the vegetation, wind speed is inversely related to vegetation density (Grace 1977; Oke 1987), and neighbouring plants may directly intercept propagules (Green & Johnson 1996). In general therefore there is only a chance of effective wind dispersal if propagules are released well above the mean canopy height (Tackenberg *et al.* 2003). Environments with high nutrient availability and low disturbance intensity (correlated with low light availability at ground level) generally have taller and denser vegetation (e.g. Grime 2001), making it increasingly difficult for individual plants to release their propagules above the mean canopy height.

The increase in anemochory along the light availability gradient is presumably also enhanced indirectly by environmental constraints on seed weight. Although there is a huge seed weight variance within communities, median seed weight increases in shaded environments (Salisbury 1974; Thompson & Hodkinson 1998; Bazzaz *et al*. 2000). This may well be related to larger seeds having a higher probability of successful germination and early seedling growth under high levels of competition for light (Grime & Jeffrey 1965; Thompson & Baster 1992; Westoby *et al*. 1996). This advantage is, however, at the expense of the capacity for wind dispersal as, with constant seed morphology, heavy seeds have a lower terminal velocity than light seeds (Augspurger & Franson 1987; Greene & Johnson 1993; Tackenberg 2001).

The combination of these two factors (constraints of nutrient availability on canopy height and seed weight) may, in herbaceous species in productive and shaded environments, lead to a selection pressure against morphological adaptations, such as wings and plumes, for wind dispersal. On a smaller temporal scale, an interesting implication of this trait-environment relationship may be that eutrophication can lead to a decrease in the percentage of wind-dispersed species within local communities. Evidence for this has been provided at the population level for some grassland forbs (Soons & Heil 2002).

Mammals

In many plant communities, a large fraction of herbaceous plants has the potential to be dispersed efficiently by large mammals, externally or internally. Variations between communities in the proportion of both epizoochorous and endozoochorous species are mainly explained by variation in light availability (Fig. 2c,d), but different sets of species and different morphological adaptations are involved in each case. The increase in the potential importance of both epizoochory and endozoochory by mammals along the light gradient probably reflects the higher grazing intensity of large mammalian herbivores in open communities due to a better supply of 'high quality' food. Shade-tolerant species generally have leaves with a high level of compounds offering defence against herbivores and pathogens (Coley *et al*. 1985; Davidson 1993; Reich *et al*. 1999), and communities dominated by these species are thus less attractive to herbivores. Furthermore, herbivore-specific patterns of habitat use at the landscape level may be involved (e.g. shelter and migration in relation to variation in habitat structure), although this behaviour is probably less clearly related to environmental gradients.

Birds

In contrast to endozoochory by mammals, endozoochory by frugivorous birds (ornithochory) is most common in forest and shrub communities. Although ornithochory is a special case of endozoochory, it differs in some important aspects from endozoochory by mammals and is therefore treated separately. The most pronounced difference is the higher degree of specialization in bird-dispersed plant species, which, in temperate regions, include many species with large, fleshy, coloured, nutrient- and sugar-rich fruits. In contrast to tropical regions, such fleshy fruits form only a small fraction of the diet of large mammals (Ridley 1930; Snow & Snow 1988; Willson *et al*. 1989; Herrera 1995). While the capacity for endozoochory by mammals is constrained by seed weight (not fruit weight), due to the higher probability of small seeds escaping destruction by chewing or by the long digestive tract (Janzen 1984; Pakeman *et al*. 2002), this is less the case for bird-dispersed seeds with fleshy fruits. Therefore the trade-off between dispersal capacity and recruitment capacity in shaded environments (Thompson & Baster 1992; Westoby *et al*. 1996) is probably less strong in specialized ornithochorous species with large seeds and fleshy fruits (Herrera 1995; with the exception of extremely large-fruited species, but these are not native in the study area). The higher probability of heavy seeds germinating successfully in shaded environments (Grime & Jeffrey 1965; Westoby *et al*. 1996) is counterbalanced by the need for large investments of resources in the fruit and selective pressure for the development of fleshy fruits is therefore expected to be strongest in shaded environments.

MULTIPLE DISPERSAL VECTORS ARE THE RULE

The relative importance of having multiple dispersal vectors

If we consider the various dispersal vectors together, the results demonstrate that the ability of species to be dispersed by multiple long-distance dispersal vectors is a common phenomenon in many plant communities. The mean number of potential dispersal vectors per species is greatest in communities with a high light availability (Fig. 3). This larger number of potential dispersal vectors does not necessarily mean that dispersal is more effective, but it does at least indicate that, on average, the species in communities with a high light availability have more opportunities for long-distance dispersal and are thus less dependent on the availability of single dispersal vectors (risk spreading). The results confirm the generalization made by various authors (e.g. Harper *et al*. 1970; Connell 1978; Grime 2001) that species with a high dispersal ability will prevail in communities with large-scale or high-intensity disturbances, while adaptations for long-distance dispersal will be less common in late successional stages. This generalization rests on the assumption that, in communities with a severe disturbance regime, a selective advantage is gained by those species that succeed in spreading high densities of propagules across large parts of the landscape (Levin *et al*. 1984; Venable & Brown 1988; Grime 2001).

The increase in the mean number of potential long-distance dispersal vectors per species with increasing light availability is complemented by a decrease in longevity of individual plants (data not shown) and a decrease in the proportion of species with no access to any long-distance dispersal vectors (Fig. 2f). This suggests increased importance of investment in attributes favouring the colonization of new sites (long-distance dispersal) relative to short-distance dispersal and local persistence. This notion is consistent with the existence of a trade-off between dispersal ability and adult longevity, as suggested by Shmida & Ellner (1984), Tilman (1994), Ehrlén & Van Groenendael (1998) and Van Groenendael *et al*. (2000).

Differences in sensitivity to fragmentation between plant communities

The differences between communities in the proportion of species that have access to multiple dispersal vectors probably imply that communities differ in mean rate of long-distance dispersal. These differences may lead to differences in the sensitivity of different plant communities to habitat fragmentation. Moreover, this finding has important consequences for restoration management, because it means that even if the abiotic conditions can be properly restored, communities will probably still differ in the probability of establishment of a representative set of characteristic species from the regional species pool.

It is important to keep in mind that the trait spectra reported here represent only the potential dispersal ability of species. This is no guarantee of actual seed transport, which will be determined by the production of ripe seeds and by the actual availability of dispersal vectors. In the long term, the decline of specific dispersal vectors (e.g. large herbivores) may result in a decline of a subset of species from the regional species pool that depends on these dispersal vectors. This hypothesis, however, remains to be tested. In restoration projects that try to counteract the effects of habitat fragmentation, our results may be used to suggest which dispersal vectors need to be restored when aiming at complete recovery of the 'target communities'.

The effects of habitat fragmentation may be delayed if species with a lower dispersal capacity have higher local persistence, as suggested by Tilman (1994) and Ehrlén & Van Groenendael (1998). The buffering effects of high adult persistence cease to be important after severe disturbance or after the creation of new environments.

Towards multiple vector dispersal models

The observation that, even in relatively stable late-successional communities (e.g. forests), potential dispersal by more than one long-distance dispersal vector is a common phenomenon (Fig. 3), sets limits for the applicability of dispersal models. Whereas most existing dispersal models only consider a single dispersal vector (see Nathan & Muller-Landau 2000), our results emphasize the need for 'mixed dispersal models' (e.g. Clark *et al*. 1998; Higgins & Richardson 1999) based upon multiple dispersal vectors. Furthermore, from the linkages between dispersal traits and environmental conditions, it becomes evident that dispersal models should explicitly include parameters for habitat characteristics in order to integrate niche-based and dispersal-based assembly rules.

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