Restoration of ditch bank plant diversity : the interaction between spatiotemporal patterns and agri-environmental management

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Chapter 3

Spatial variation in ditch bank plant species composition at the regional level: the role of environment and dispersal

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Abstract

Questions: Can patterns of species similarity on ditch banks be explained by environmental and dispersal factors and, if so, to what extent? Does the pattern of distance decay differ among different species groups (all species vs. target species of conservation interest; species of different dispersal type)?

Location: Krimpenerwaard, the Netherlands.

Methods: In 2006-2007 ditch bank vegetation data on 130 terrestrial herbaceous plant species were collected on a total of 72 plots. Species similarity was measured and related to environmental distance (soil type and nutrient level) and dispersal distance (geographic distance and limitation of dispersal by water, wind and agricultural activities) as explanatory factors using multiple regression on distance matrices (MRM). The differences in rates of distance decay in species similarity among different subsets of data (species groups) were investigated by randomization tests.

Results: In all species, patterns of similarity of composition are influenced mainly by variations in dispersal, while for target species these are due to the combined effects of environmental and dispersal variation. Compared with species using other dispersal mechanisms, the water-dispersed species showed only half the rate of distance decay.

Conclusions: For all the species considered here, dispersal limitation seems more responsible for the spatial variation in species composition than environmental determinism. Conservation management focused on the plant species diversity would be more successful to implement in the areas adjacent to those where a similar management regime is already in force. For target species of conservation interest, besides dispersal limitation, environmental determinants like nutrient level are also important. As a means of conserving such target species, therefore, focusing on reducing nutrient levels and facilitating species dispersal will be more effective than the recommendation of current management which mainly focus on simply reducing fertilizer inputs.

Introduction

Patterns of spatial variation in species composition represent one of the central issues in modern ecology. Understanding the relative importance of environmental determinism and dispersal processes in creating differences in species composition between sites (beta diversity) is a major challenge facing ecologists (Whitfield, 2002; Tuomisto et al., 2003). Compared with patterns of species richness, spatial variation in species composition has received far less attention (Steinitz et al., 2006; Qian, 2009). Beta diversity in species composition is a major determinant of species diversity at the regional scale, however, and can be used as a basis for conservation planning (Margules and Pressey, 2000; Ferrier, 2002). It would be very useful to identify a range of sites with maximum representation of regional biodiversity that reveal the processes that create or maintain diversity, an understanding of which is critical for the restoration of plant diversity (Nekola and White, 1999; Gering et al., 2003; Steinitz et al., 2005).

The degree of similarity in species composition between sites ('species similarity') often decreases with increasing distance between sites (Nekola and White, 1999). Environmental determinism may produce a decay in species similarity with geographic distance because environmental conditions tend to be more similar among nearby sites than relative to distant sites owing to spatial autocorrelation (Legendre, 1993). Several lines of evidence support the view that environmental heterogeneity, especially soil factors, contributes to the difference in present-day species composition patterns from local to landscape scale (Condit et al., 2002; John et al., 2007). Dispersal processes may also be a factor in distance decay in species similarity, since dispersal distances are always to some extent limited by spatial factors, like the isolation of habitats and the characteristics of the matrix surrounding them (Shmida and Ellner, 1984; Fleishman et al., 2001). Most plant species can only disperse their seeds a few meters by themselves and are thus effectively dispersal-limited (Cain et al., 2000). At larger spatial scales, rare long-distance dispersal events are considered an important factor in shaping and maintaining metacommunities (Cain et al., 2000). The seeds, aided by vectors like water or wind (Nathan, 2006), have the potential to reach sites that are separated from the source populations by long distances or physical barriers (Levin et al., 2003; Soons and Bullock, 2008).

The last decade has seen a surge in research aiming to explain patterns of distance decay in species similarity in ecological communities (Spencer et al., 2002; Poulin, 2003; Dormann et al., 2007; Nakamura et al., 2009). Recent studies have focused on plant communities in certain natural vegetation types like forests (Tuomisto et al., 2003; Linares-Palomino and Kessler, 2009), but the degree to which the observed patterns hold for man-made agricultural landscapes remains unclear. Furthermore, there has been no research addressing patterns of distance decay in species of specific conservation interest, although any differences in these compared with patterns for other species might be useful for designing management programs. In addition, most research has used geographic distance between sites as a measure to test for dispersal limitation (Condit et al., 2002), with the degree of isolation due to limitation of dispersal by long-distance dispersal vectors like water or wind rarely being tested (Ozinga et al., 2009).

In this paper we explore a model for explaining species composition patterns produced by the combined effects of dispersal and environmental factors using data on the vegetation of ditch banks. Ditch banks, functioning as small-scale landscape elements, serve as a refuge for much of former biodiversity and thus play an important role in the agricultural landscape. Several studies have indicated that seed limitation and site limitation might be important bottlenecks for species diversity on ditch banks (Blomqvist et al., 2003; Donath et al., 2007; Ozinga et al., 2009). Geographic and environmental distance can therefore be considered two fundamental factors governing species composition patterns and were combined in our model. The effect of constraints on long-distance dispersal vectors was also included in the model. Specifically, we addressed the following questions:

1. For all species together, can patterns of species similarity be explained by environmental and dispersal factors and, if so, to what extent?
2. How does the rate of distance decay of all species compare with that of a set of target species of conservation interest?
3. Does the pattern of distance decay differ among plant groups differing in dispersal strategy?

Methods

Study area and selected data

The study area, Krimpenerwaard, is located in the Province of South Holland in the Western Peat District of the Netherlands, a region intersected by an extensive network of ditches and ditch banks. Most of the farmland is used as pasture for dairy cattle and sheep. The soil type is exclusively peat or peat with clay. The fields are long and narrow, varying in width from 30 to 60 m and in length from 400 to 1200 m, and are consistently separated by ditches 1 to 4 m wide. The growing season normally starts in March-April and ends in November. Annual rainfall is 985 mm, with peaks in June-July and in the autumn (KNMI, 2009). The ditch water is maintained at the same level throughout the year.

The vegetation data we used were obtained from the vegetation database of the Province of South Holland. The bulk of the data in this ‘Information System for Vegetation’ (ISV) database derive from the agricultural landscape. As these data had been collected over a period of several years, we took the most recent ditch bank vegetation data, collected during the years 2006-2007. We focused on terrestrial herbaceous plant species, investigating, on 72 plots, a total of 130 species. The presence of each of these species was recorded in 50 m long relevés varying in width with the width of the ditch bank (0.75 m ± 0.14 m, average ± SE). Our basic data set was in binary form, marking the presence or absence of each species in each plot.

Species similarity

Pair wise species similarity between plots was estimated using the Jaccard index (Legendre and Legendre, 1998), which is suitable for our presence-absence data and has been widely used in similar studies (Spencer et al., 2002; Steinitz et al., 2006). For correctly comparing the similarity between groups of species, it is needed that the measure of similarity is independent of species diversity. Jost (2007) has shown that the Jaccard index has that properity when species diversity is defined as species richness, as we do.

Two species typologies were used in our study. The first consists of two plant groups: all 130 species and 25 target species of conservation interest. The latter are not only regarded as valuable by the Dutch government, but also serve as criteria for farmer payment in agri-environment schemes (AES). They include formerly common grassland species like *Caltha palustris* and *Lychnis flos-cuculi* and internationally rare species such as *Myosotis discolor* (Leng et al., 2009). The second typology comprises plant groups of four exclusively different dispersal types based on Grime, Hodgson and Hunt (1988), and, if the dispersal type is not given in this source, on van Dorp (1996): 34 water-dispersed species, 25 wind-dispersed species, 38 species dispersed mainly by agricultural activities (machinery, livestock, etc.) and 33 animal-dispersed species. For each of these species groups we produced separate data on species similarity.

Explanatory variation: dispersal and environmental determinism

Dispersal limitation was estimated by constructing a matrix of geographic distances between study plots and three matrices of limitation of dispersal by long-distance vectors. Pair wise geographic distance (km) between plots was calculated from geographic coordinates. As water, wind and agricultural activities are considered to be the three most important vectors for species dispersal in agricultural landscape (Willson et al., 1990), we explored ways of measuring limitation of dispersal by these three vectors. Dispersal limitation via water was expressed as a categorical matrix using dummy variables, assigning a value of 0 to matrix elements comparing two sites on the same water within which there is free flow of water and a value of 1 to elements comparing two sites in different water systems. The matrices for dispersal limitation via wind and agricultural activities were constructed in a similar fashion. In the study area the wind blows mainly from the south-west to north-east (KNMI, 2009) and we therefore assigned a value of 0 when two plots were aligned south-west or north-east to one another and a value of 1 when they were aligned south-east or north-west. Potential dispersal by agricultural activities was assumed to be restricted to plots managed by the same farmer. Interviews of 18 farmers showed that in our study area, farmers have an average of five connected fields (unpublished data) and we therefore deemed plots located within five fields to belong to the same farmer and assigned these a value of 0, using a value of 1 for plots managed by different farmers. These three categorical matrices were used as proxies for dispersal limitation via long-distance dispersal vectors, because dispersal distances across the field are difficult to measure (Bakker et al., 1996).

Environmental determinism was estimated by constructing environmental distance matrices of soil type and nutrient level, which are considered to be the principal environmental factors affecting ditch-bank plant diversity (Van Strien et al., 1989). The matrices of soil type and nutrient level were constructed similarly to those of dispersal vectors. In nature reserves the amount of fertilizer applied to fields does not exceed 100 kg N ha^{-1} $year^{-1}$, while elsewhere fertilizer dressings may be up to 400 kg N ha^{-1} $year^{-1}$ (Van Strien et al., 1989). We therefore recorded nutrient levels as being associated with nature reserves or not, assigning a value of 0 when two plots belong to the same nutrient level and 1 for plots with different nutrient level. For the soil type, we assigned a value of 0 for two plots with the same type and 1 with different ones. We recognized two soil types, viz. peat, peat with clay.

Data analysis

For the whole dataset, species similarity (S) and geographic distance (D) were calculated, as well as log-transformed similarity and geographic distance. Linear regression was used to estimate geographic distance decay rates and determine which formulation most closely described a linear relationship over distance for all four combinations of untransformed and transformed data. The best linear relationship was found in the model that used the log-transformation of similarity and untransformed geographic distance ($r^2 = 0.042$) compared with others (Ln(S)-Ln(D), $r^2 = 0.024$; S-D, $r^2 = 0.029$; S-Ln(D), $r^2 = 0.023$ individually). We consequently used the equation

$$\mathrm{Ln}(S) = a * D + b$$

in all the regression models presented here, where a indicates the rapidity of the decline of plant similarity with distance between plots and b is the estimated plant similarity of two plots at distance 0.

The differences in rates of distance decay in species similarity as a function of geographic distance between the relevant plant groups (all species vs. species of conservation interest, water-dispersed species vs. wind-dispersed species, etc.) were tested by comparing the slope of regression with that of a randomized dataset (Nekola and White, 1999; Steinitz et al., 2006). The calculation comprised the following main steps: (1) rescaling of the similarity of the two data sets to a common mean, followed by random reassignment to the two data sets in each pair of sites; (2) estimation of slope of regression; (3) repetition of the previous step 9999 times; (4) comparison of the distribution of the differences between the slopes of 9999 randomized datasets with ditto for the slopes based on the original datasets, using these to determine a significance level.

To assess which of all the possible combinations of explanatory (dispersal and environmental) distance matrices best explained species similarity in all species and in species of conservation interest, we used multiple regression on distance matrices (MRM), an extension of the Mantel test. This form of analysis was used because the values of the dispersal and environmental distance matrices are not independent. MRM involves multiple regression of a response matrix on any number of explanatory matrices and has been widely applied to investigate the spatial, environmental and historical factors on the variation of species composition (Lichstein, 2007). The MRM analysis we applied used a model comprising all six matrices, including both dispersal and environmental explanatory matrices, because our research questions focused on the relative importance of these factors.

All calculations were performed using R software and the package Ecodist (Goslee and Urban, 2007). The models were performed with 9999 permutations (Jackson and Somers, 1989).

Results

Distance decay in all species and in species of conservation interest

Pair wise species similarity values of all species calculated between plots ranged from 0.16 to 0.84 (0.41 ± 0.004), while those of the species of conservation interest were between 0.09 and 0.88 (0.42 ± 0.002). For all species as well as for species of conservation interest, species similarity decreased with geographic distance, with a steep decline being found within the first 200-300 m (Fig. 1). In species of conservation interest, distance decay (slope of Ln(S) versus D = - 0.034) was greater than in all species together (slope = - 0.018) and the difference was significant ($p = 0.0009$).

The MRM revealed that species similarity was significantly negatively correlated with limitation of dispersal by agricultural activities and geographic distance in all species and in target species, while limitation of dispersal via water was significantly negative for the target species only (Table 1). The MRM indicated also that the effect of nutrient level was significantly negative in target species only. The model explained only a limited amount of variation in all species as well as in the target species (13% and 5%, respectively).

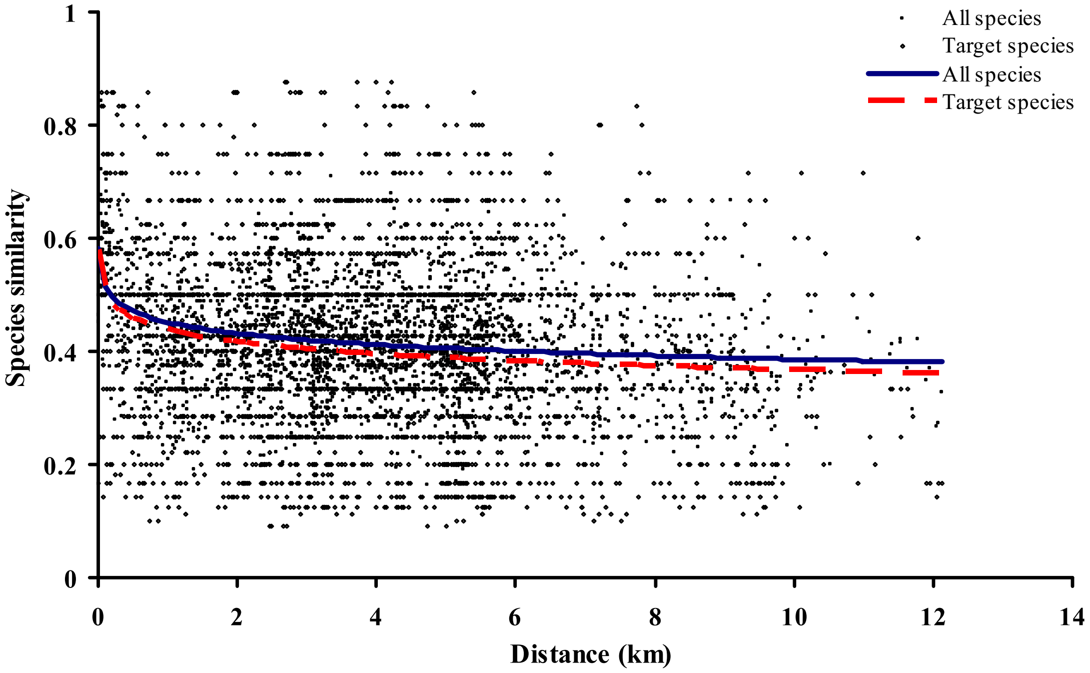

Fig. 1. Distance decay of species similarity in all species (130 species, R^2=0.086) and in target species of conservation interest (25 species, R^2=0.025) on a total of 72 plots, 2556 of pair wise comparisons.

Table 1. Summary of multiple regression on species similarity and possible explanatory (dispersal and environmental) distance matrices for all species and target species of conservation interest. The possible dispersal matrices comprise limitation of dispersal by water (D_{WA}), wind (D_{WI}) and agricultural activities (D_{AG}) and geographic distance (G). The possible environmental matrices comprise soil type (E_S) and nutrient level (E_N). β: Standardized partial regression coefficient. P values are based on 9999 permutations. * p <=0.05; ** p <= 0.01; *** p <=0.001.

Explanatory	All species (130 species)				Target species (25 species)			
matrix	β	P(β)	R^2	$P(R^2)$	β	P(β)	R^2	$P(R^2)$
D_{WA}	-0.006	0.55	0.13	0.0001***	-0.05	0.02*	0.05	0.0001***
D_{WI}	-0.006	0.17			-0.002	0.86		
D_{AG}	-0.13	0.0001***			-0.16	0.0001***		
G	-0.005	0.0001***			-0.013	0.0001***		
E_S	-0.03	0.59			0.005	0.72		
E_N	-0.003	0.36			-0.04	0.0001***		

Distance decay in species groups with different dispersal modes

The rate of distance decay in similarity varied between species groups with different modes of dispersal (Fig. 2). The water-dispersed species exhibited only half the rate of distance decay of other dispersal types, with the differences testing statistically significant (Table 2). The wind-dispersed and animal-dispersed species showed similar rates of distance decay, while the animal-dispersed and agriculturally dispersed species showed a slightly significant difference in decay rate.

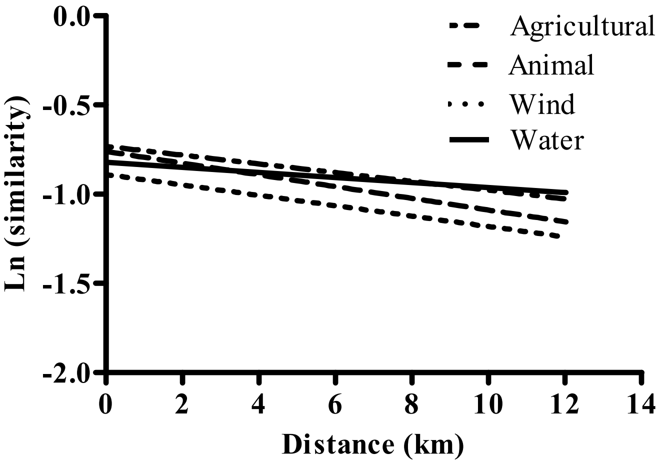

Fig. 2. Distance decay of Ln(similarity) in species of different dispersal type on a total of 72 plots, 2556 of pair wise comparisons. The slope of Ln(similarity) against geographic distance was shown in Table 2.

Table 2. Comparison of slope of Ln (similarity) against geographic distance for species of different dispersal type. P values were determined using randomization tests based on 9999 permutations. * p <=0.05; ** p <= 0.01; *** p <=0.001.

Group	Slope	p value	Group	Slope	p value
Water	-0.019	0.001***	Wind	-0.036	0.36
Wind	-0.036		Animal	-0.04	
Water	-0.019	0.0001***	Wind	-0.036	0.46
Animal	-0.04		Agricultural	-0.029	
Water	-0.019	0.002**	Animal	-0.04	0.03*
Agricultural	-0.029		Agricultural	-0.029	

Discussion

Spatial variation of composition for all species

In our study, similarity decreased with increasing geographic distance between plots for all the species considered, a result that has been frequently demonstrated in previous research (Spencer et al., 2002; Dormann et al., 2007; Nakamura et al., 2009; Qian, 2009). A steep decline in species similarity within the first 200-300 m is in agreement with the finding that species richness declines significantly with increasing distance from seed source (nature reserves), especially within 200 m (Leng et al., 2009). One possible explanation is that seed limitation is more important than site limitation in determining species diversity on ditch banks (Blomqvist et al., 2003; Kohler et al., 2007; Leng et al., 2009).

Our current results show that the effect of limitation of dispersal via agricultural activities was significant in the model comprising only three explanatory dispersal limitation matrices. Including geographic distance in the explanatory model still resulted in a significantly negative effect of agricultural dispersal limitation. This means that the variation of species similarity due to limitation of dispersal via agricultural activities cannot be explained by geographic distance alone. In our model we assumed that dispersal via agricultural activities would occur only on plots belonging to the same farmer, so one possible factor explaining the significance of the effect may therefore be differences in agricultural practices among farmers. In our study area, for instance, some farmers participate in AES and are deemed to adopt certain practices like first mowing at the end of June or beginning of July, zero fertilizer inputs to ditch banks and no deposition of dredged material on ditch bank tops (Van Strien et al., 1989), while other farmers are free in the form of management adopted. Differences in farm management regimes may be of influence on both species dispersal (via differences in mowing time or mowing machinery, for example) and site conditions (via differences in nutrient inputs to ditch banks, for example). This would accord with the results of Dormann et al. (2007), who found significant effects of land-use intensity (e.g. pesticide loads) on plant similarity.

The present study indicates a significant correlation between geographic distance and species similarity. Using a partial Mantel test, separate analysis of this correlation for all possible combinations of the explanatory matrices showed that the effect of geographic distance remained significant even after all other possible factors had been taken into account (Table 1). This emphasizes the need to consider the confounding effects of geographic distance when seeking to establish potential determinants of species composition. The lack of correlation between geographic distance and any environmental condition (p = 0.99; p = 0.98 for soil type and nutrient level individually, Mantel test, permutation = 9999) indicates that geographic distance is more likely to be the result of dispersal limitation rather than environmental heterogeneity in terms of soil type and nutrient level.

Pattern of distance decay in all species versus species of conservation interest

This study demonstrates that, in our setting, the rate of distance decay in species composition is far greater for target species of conservation interest than for all species taken together and the patterns of distance decay differ with respect to both environmental and dispersal dissimilarity among plots. In contrast to the full set of species, the species of conservation interest showed significant correlations with the environmental factor nutrient level. It is well known that these species are highly dependent on nutrient levels when it comes to species richness (Blomqvist et al., 2006) and our analyses confirm this relationship. Lower nutrient levels apparently facilitate the establishment and germination of plant seeds from the seed bank or from other sources. For this group of species a clear relationship was found between limitation of dispersal by water and species similarity, moreover. This finding indicates that constraints on this dispersal vector have a greater impact on species of conservation interest than on other species, possibly due to the limited dispersal capacity of the former. Besides, these species had more than twice the regression coefficient for species similarity and geographic distance, emphasizing the importance of geographic distance for species similarity in species of conservation interest.

Although all six explanatory variables together partly explained the spatial variation observed in all species as well as in species of conservation interest

($R^2 = 0.13$ and 0.05, respectively), these values are quite low, especially for the latter species group, suggesting that there are probably also other factors at work. One possibility is that historical factors play an important part in explaining spatial variation in species composition. Farmland close to the farmhouse was used more intensively in the past than land further away, due to considerations of transportation. The past spatial patterns of farmland use might therefore well be of influence on contemporary species similarity on ditch banks. Further research addressing the influence of such factors is required before a full picture can be obtained of the reasons for spatial variation in the species composition of ditch bank vegetation.

Pattern of distance decay among different dispersal types

In agricultural landscapes, water, wind and agricultural activities are the three most important long-distance dispersal vectors. According to comparative data gleaned from agricultural landscapes (Geertsema et al., 2002), in terms of seed dispersal distance these dispersal vectors rank as follows: wind < water < agricultural machinery. The fact that the distance decay for water-dispersed species was found to be the lowest of all species groups indicates that water dispersal might be the most effective long-distance dispersal vector for ditch bank vegetation in our region. In the context of ditch bank vegetation, long-distance dispersal by water is certainly feasible, since ditches might function as dispersal corridors (Geertsema et al., 2002). In the Krimpenerwaard the ditch water level is kept at a constant level year-round and the permanent presence of flowing water due to water management regimes in this and other agricultural regions might result in widespread dispersal of seeds by water.

Conclusion and implications for conservation

For all the species considered here, the spatial variation in composition has been explained as being due primarily to dispersal processes and, more specifically, to limitation of dispersal via agricultural activities. The results showed that differences in farm management regimes were main reason of dispersal limitation of agricultural activities. Then, conservation management would be more successful to implement in the areas adjacent to those where a similar management regime is already in force. On the other hand, the lower rate of distance decay of water-dispersed species suggests that water dispersal may be a good dispersal vector on ditch banks.

The results for target species of conservation interest indicate that, besides dispersal limitation, environmental determinants like nutrient level are also important for these species. These 25 target species appear to be more sensitive to nutrient levels than other species, suggesting a need for continued reduction of nutrient inputs to ditch banks for effective conservation of these species. Beside the significant effect of geographic distance, dispersal limitation via long-distance dispersal vectors like water and agricultural activity may also play a role in spatial variation. As a means of conserving such target species, therefore, focusing on reducing nutrient levels and facilitating species dispersal will be more effective than simply reducing fertilizer inputs. This is in line with the finding of several previous studies that management efforts to improve ditch bank plant diversity (such as AES) that focus primarily on reducing site limitation while ignoring the issue of seed limitation might explain the disappointing success of such efforts (Blomqvist et al., 2003; Leng et al., 2009).

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