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

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Chapter 2

Spatiotemporal variation of plant diversity on ditch banks under different management regimes

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Abstract

Agricultural intensification has led to a loss of biological diversity at various spatial and temporal scales and understanding the mechanisms driving these changes would help target conservation efforts accordingly. In this study we used additive partitioning of diversity and the Jaccard index of similarity to estimate the spatial and temporal patterns of plant diversity on ditch banks under different management regimes. We focused on a total of 118 species, including 18 target species of nature conservation, at 42 sites in three successive sampling periods. For all species taken together, beta diversity contributed most to total species diversity, but was less than expected under random distribution. Target species showed greater beta diversity on a spatial scale compared to all species, but much less so on a temporal scale. Importantly, the differences in target species composition on a spatial scale are probably due to environmental heterogeneity and dispersal limitation, indicating that management strategies should focus on both factors. In agricultural areas, species richness of target species increased significantly, especially between the 1995-1996 and 1997-1998 period, which is just after the start of AES.

Introduction

Over the past few decades, agricultural intensification has led to rapid destruction of natural habitats and loss of biological diversity at various spatial and temporal scales (Benton et al., 2003; Stoate et al., 2009). To date, management practices to restore or conserve biodiversity in agricultural landscapes have sought mainly to conserve remnants of species-rich locations (i.e. nature conservation) or enhance the diversity of agricultural areas (i.e. agri-environment schemes (AES)) (Ferraro and Kiss, 2002; Kleijn and Sutherland, 2003). However, such practices have often yielded disappointing results and the effectiveness of the management regimes concerned has been called into question (Kleijn et al., 2004; Klimek et al., 2007). It is therefore critical to understand the processes driving the spatial and temporal patterns of biodiversity under different management regimes, as this could help to target conservation efforts accordingly.

Recent studies have focused on how species diversity varies at multiple spatial scales in agricultural landscapes, with results suggesting that patterns of species diversity are shaped by processes at multiple spatial scales (Wagner et al., 2000; Gering et al., 2003; Martin et al., 2005). At the regional level of scale, the structural complexity of the surrounding landscape, reflected in the regional species pool, and habitat isolation would affect the local species diversity, while the effect of habitat heterogeneity and dispersal limitation might also influence local species diversity (Roschewitz et al., 2005; Klimek et al., 2008; Hendrickx et al., 2009). However, temporal variation, such as the temporal changes in abiotic and biotic heterogeneity, may also play an important role in overall landscape diversity (Summerville and Crist, 2005; Tylianakis et al., 2005). To our knowledge, there have been far fewer studies focusing on how patterns of species diversity change over time and on the relative contribution of temporal diversity to overall species diversity.

Additive partitioning of species diversity is a promising method in which gamma diversity is partitioned into the sum of alpha (within sites) and beta (among sites) diversity and has been used to estimate landscape patterns of diversity (Wagner et al., 2000) and spatial and temporal patterns of diversity (Gering et al., 2003; Gabriel et al., 2006; Clough et al., 2007). In this method, alpha and beta diversity are expressed in the same measurement units, providing a ready means of quantifying their relative importance in determining total diversity. By including hierarchical sampling levels, moreover, the diversity partitioning model can be applied to investigate how hierarchical levels influence patterns of beta diversity (Veech et al., 2002). However, the beta diversity applied in partitioning model cannot be used to trace trends of similarity in species composition across space and time. Another way

to measure beta diversity is to assess similarity (i.e. the Jaccard index) between pairwise sites; the trend in similarity as a function of distance is known as the distance decay of similarity (Nekola and White, 1999). Ecological factors such as dispersal limitation and habitat heterogeneity have been widely shown to influence alpha and beta diversity in a given landscape (Collins et al., 2002; Legendre et al., 2005; Freestone and Inouye, 2006).

Ditch banks are considered to serve as a refuge for species in grasslands and wetlands (Blomqvist et al., 2003) and are an important feature of the agricultural landscape in the Netherlands (Higler, 1994). In our study, we used diversity partitioning and the Jaccard index to characterize plant diversity on spatial scales (sites) and temporal scales (sampling periods) by investigating ditch banks in 42 plots in three successive sampling periods. First, we focused on a comparison of beta diversity components across spatial and temporal scales to investigate the relative importance of beta sites and beta periods for total observed plant species richness. Secondly, to identify the most appropriate scale for effective conservation management, we focused on beta diversity components across spatial and temporal scales of target species of nature conservation and made a comparison of all species. Thirdly, we were interested whether patterns of species diversity components respond differently between ditch banks in nature reserves and agricultural areas.

Methods

Study region and data selected

Our study region, Krimpenerwaard, is located in the Western Peat District of the Netherlands (51°53'N - 52°01'N and 4°35'E - 4°51'E). Following reclamation and cultivation of the peat bogs formed after the last glacial period, the present-day landscape consists of long, narrow grassland parcels embedded in an extended network of shallow ditches and canals (van Strien, 1991). The area in question currently covers 13,500 ha and is used mainly as pasture for dairy cattle and sheep. The main soil type is peat and peat with clay. The fields vary from 30 to 60 m width and from 400 to 1200 m length and are consistently separated by 1 to 4 m wide ditches. Nature reserves have an average size of 25 ha and have a similar appearance to the agricultural grassland.

The nature conservation strategy applied in this area seeks to conserve plants and meadow birds by ensuring nutrient-poor conditions and limited grazing intensity. In the agricultural areas, AES are in place (van Strien, 1991). AES were introduced as a result of European Union legislation passed in 1992 under which farmers are

eligible for payments if they address environmental problems by implementing “nature-friendly” agricultural practices (i.e. zero fertilizer inputs on ditch banks, postponing of first mowing) on certain parts of their land. In the Netherlands, similar schemes had already been introduced in 1984, although most farmers in Krimpenerwaard only began to implement them in 1994 (Leng et al., 2009).

The data used in the present study were obtained from the vegetation database of the Province of South Holland (the ‘Information System for Vegetation’ (ISV) database). To standardize our sampling from the same location, we eventually selected 42 plots in successive sampling periods 1995-1996, 1997-1998 and 1999-2000, 17 of which plots were located in nature reserves and 25 in agricultural areas. The target species of nature conservation were selected from a list of 25 “ecologically valuable” plants employed by the Dutch government in various contexts, including as criteria for farmer payment in AES. They include formerly common grassland species like *Caltha palustris* as well as internationally rare species such as *Myosotis discolor* (Leng et al., 2009). The presence of each species was recorded in 50 m long relevés varying in width with the width of the ditch bank ($0.87 \text{ m} \pm 0.14 \text{ m}$, average \pm SD).

Data analysis

To quantify the changes in diversity across spatial and temporal scales recorded in our study, we used the additive partitioning model of species diversity in a hierarchical sampling design proposed by Veech et al. (2002). In this model approach, total gamma diversity (γ) is broken down into additive components: alpha (α) and beta (β) ($\gamma = \alpha + \beta$), with γ diversity at a given scale being equal to α diversity at the next scale level. Accordingly, total diversity can be formulated as follows: $\gamma = \alpha_1 + \beta_1 + \beta_2 + \dots + \beta_n$, in which n is the number of scale levels involved. In our study we broke down total diversity into two scales (sites and sampling periods) and it can thus be expressed as: $\gamma = \alpha_{\text{sites}} + \beta_{\text{sites}} + \beta_{\text{periods}}$. Species diversity was calculated using species richness and α diversity was then the average number of species per site per period while γ diversity was the total number of species in the overall body of data. The β diversity represents the average diversity among the sites or periods.

In addition, we applied the null hypothesis of individual-based randomization on spatial and temporal scales to determine whether the observed partition of diversity could be explained by a random distribution of individuals (Crist et al., 2003). The observed diversity was tested against the expected diversity obtained by a random distribution of individuals across any of the samples at the lowest levels. The

randomizations were repeated 1000 times at each level of analysis and statistical significance (p value) was based on the number of expected values greater than the observed estimate. All these analyses were performed using the software PARTITION (Veech and Crist, 2009).

Since the above-described additive partitioning of beta diversity cannot provide information on actual patterns of change in spatial diversity, we examined the distance decay of similarity among sampling periods by using the Jaccard index of similarity (Legendre and Legendre, 1998). The distance decay of similarity is measured as the slope of the linear regression of similarity versus geographical distance separating pairwise sites. Geographic distance was calculated from geographic coordinates, while similarity was log-transformed to normalize regression residuals and to achieve linearity. We applied a randomization test proposed by Nekola & White (1999) to quantify the changes in distance decay between different sampling periods. The test was based on 9999 randomized datasets and performed using the software R 2.9.1 (R, 2009). Species richness (number of species per sites) between different sampling periods was tested using a paired T-test in SPSS 16.

We repeated the above approach for a comparison of all species and target species individually. Additionally, to investigate the effect of management regimes on target species, the complete procedure was conducted separately for 17 plots in nature reserves and 25 plots in agricultural areas.

Results

All species vs. target species

A total of 118 species, including 18 target species, were recorded in the course of our study. In all species, around 22% of the total diversity richness was due to species richness within sites, whereas the β components due to sites and sampling periods contributed most of total species richness of all species (51% and 27%, respectively) (Fig. 1a). In target species, the relative contributions of β components to total diversity was 74% of the β component for sites and only 2% for sampling periods (Fig. 1b). With respect to all species, the observed species richness within sites and the β component for periods was significantly higher than expected ($p = 0.01$ and $p = 0.02$, respectively) and the β component for sites was considerably lower ($p = 0.99$) (Fig. 1a). In contrast, target species showed no significance in the β component for sites ($p = 0.33$) and significantly lower β component for periods than expected ($p = 0.99$) (Fig. 1b).

Among sampling periods, differences in both species richness and distance decay showed no significant difference in all species (Fig. 2a; Table 1a). In target species, however, a considerably higher richness was found in 1999-2000 compared with 1995-1996, while a significant difference in distance decay was found between 1995-1996 and 1997-1998 and between 1995-1996 and 1999-2000 (Fig. 2b; Table 1b).

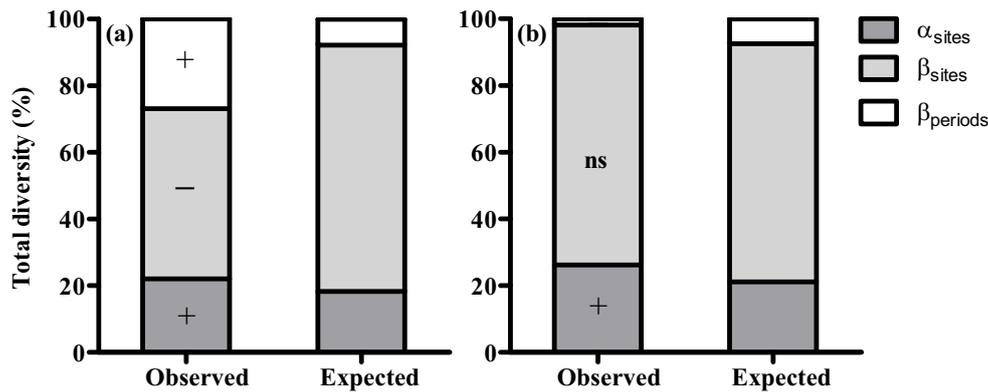


Fig. 1. Observed and expected additive partition of total species richness of (a) all species, (b) target species across two hierarchical levels (sites and sampling periods). Values are expressed as a percentage of total diversity. Observed partitions are compared with expected values from a null hypothesis under individual-based randomization (1000 randomizations). The p values are represented in each bar. A plus (+) indicates that the observed value is significantly higher than expected, a minus (-) that it is significantly lower and ns that there is no significant difference.

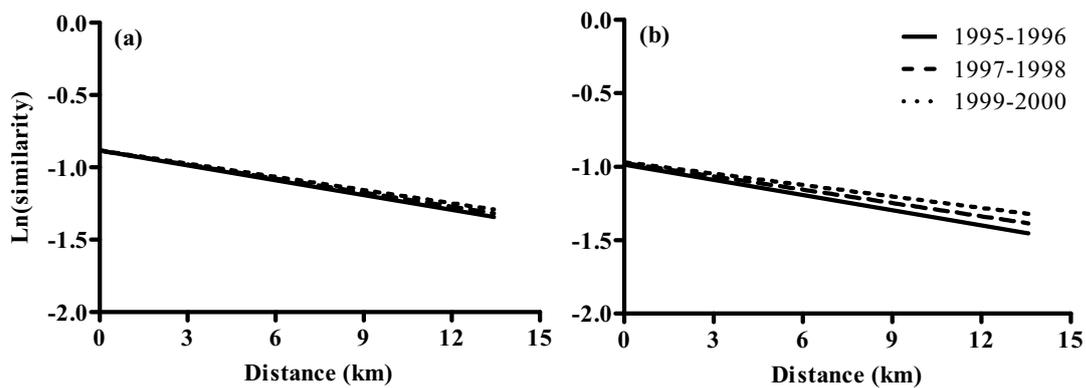


Fig. 2. Distance decay of Ln(species similarity) for all species (a) and target species (b) in the respective sampling periods.

Table 1. Species richness (alpha diversity) and the rate of distance decay of similarity for **(a)** all species and **(b)** target species in three sampling periods. Difference between species richness was tested with a T-test and distance decay with a randomization test (1000 randomizations). * = $p < 0.05$; ** = $p < 0.01$.

No.	Sampling period	Species richness			Distance decay of similarity	
		Mean	SD	p	Slope	p
(a) all species						
1	1995-1996	35.9	1.1	0.88	-0.034	0.89
	1997-1998	36.3	1.1		-0.032	
2	1995-1996	35.9	1.1	0.34	-0.034	0.19
	1999-2000	36.9	1.2		-0.030	
3	1997-1998	36.3	1.1	0.35	-0.032	0.23
	1999-2000	36.9	1.2		-0.030	
(b) target species						
1	1995-1996	4.45	0.31	0.21	-0.034	0.03 *
	1997-1998	4.69	0.33		-0.030	
2	1995-1996	4.45	0.31	0.03*	-0.034	0.008**
	1999-2000	5.02	0.37		-0.026	
3	1997-1998	4.69	0.33	0.17	-0.030	0.39
	1999-2000	5.02	0.37		-0.026	

Nature reserves vs. agricultural areas

All 18 target species were recorded in both nature reserves and agricultural areas. In the nature reserves, the β components for sites and periods contributed 58% and 15%, respectively, to total species diversity (Fig. 3a). The proportion of β components for sites (66%) in agricultural areas is higher than in nature reserves; accordingly, the proportion of β components among sampling periods (9%) is lower (Fig. 3b). Both nature reserves and agricultural areas showed a lower β component for periods than expected ($p = 0.95$ and $p = 0.99$, respectively) (Fig. 3a; Fig. 3b). No species richness and distance decay differences were observed in nature reserves (Fig. 4a; Table 2a), whereas the species richness within plots was significantly higher in 1997-1998 than in 1995-1996 and the distance decay in 1995-1996 was significantly greater than in the 1997-1998 and 1999-2000 sampling periods, respectively in agricultural areas (Fig. 4b; Table 2b).

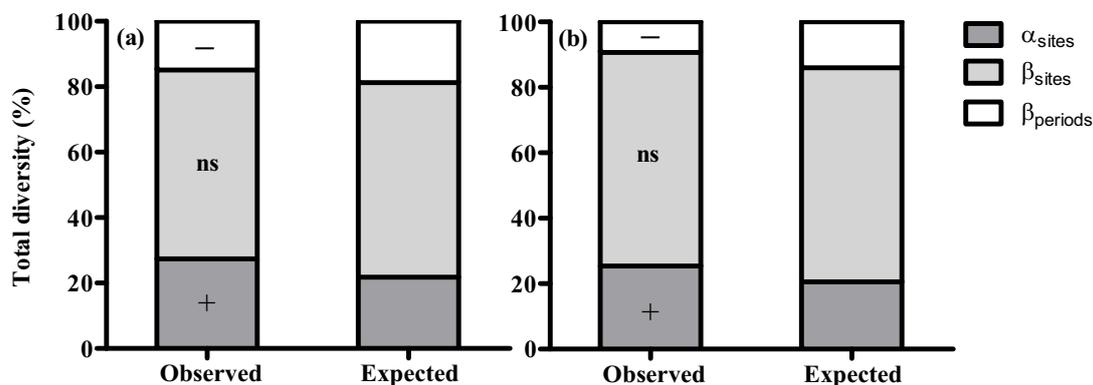


Fig. 3. Observed and expected additive partition of total species richness of target species in nature reserves **(a)** and agricultural areas **(b)** across two hierarchical levels (sites and sampling periods). Values are expressed as a percentage of total diversity. Observed partitions are compared with expected values from a null hypothesis under individual-based randomization (1000 randomizations). The p values are represented in each bar. A plus (+) indicates that the observed value is significantly higher than expected, a minus (-) that it is significantly lower and ns that there is no significant difference.

Table 2. Species richness (alpha diversity) and the rate of distance decay of similarity for target species in nature reserves **(a)** and agricultural areas **(b)** in three sampling periods. Difference between species richness was tested with a T-test and distance decay with a randomization test (1000 randomizations). * = $p < 0.05$; ** = $p < 0.01$.

No.	Sampling period	Species richness			Distance decay of similarity	
		Mean	SD	p	Slope	p
(a) target species in nature reserves						
1	1995-1996	4.82	0.61	0.46	-0.079	0.34
	1997-1998	4.65	0.61		-0.076	
2	1995-1996	4.82	0.61	0.21	-0.079	0.15
	1999-2000	5.41	0.72		-0.058	
3	1997-1998	4.65	0.61	0.06	-0.076	0.49
	1999-2000	5.41	0.72		-0.058	
(b) target species in agricultural areas						
1	1995-1996	4.21	0.31	0.03*	-0.052	0.002**
	1997-1998	4.72	0.39		-0.025	
2	1995-1996	4.21	0.31	0.07	-0.052	0.004**
	1999-2000	4.80	0.37		-0.027	
3	1997-1998	4.72	0.39	0.71	-0.025	0.94
	1999-2000	4.80	0.37		-0.027	

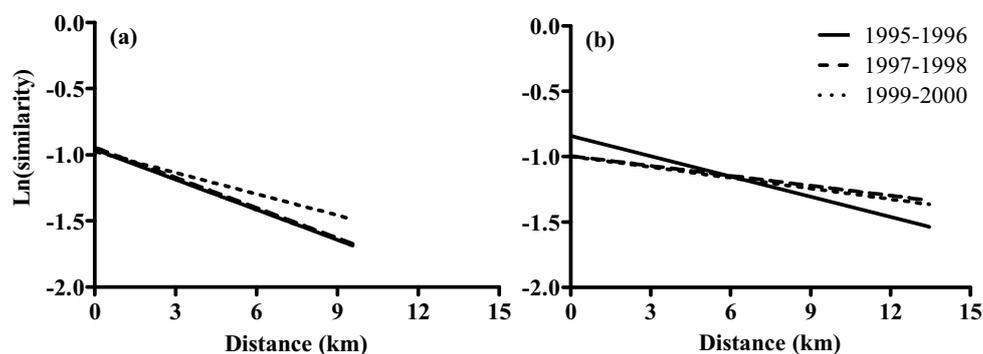


Fig. 4. Distance decay of Ln(species similarity) for target species in nature reserves **(a)** and agricultural areas **(b)** in the respective sampling periods.

Discussion

Spatial and temporal diversity for all species

For all the species considered here, 78% of total species richness was contributed by beta diversity. However, alpha diversity was higher than expected and therefore beta diversity as a whole was lower than expected. This suggests that the vegetation at the different sites comprises largely the same set of species. One explanation for this could be the species loss that has occurred in the past, due to intensification resulting in uniform vegetation on ditch banks, with only those species able to resist high environmental pressure surviving everywhere (Kremen, 2005). The temporal diversity was higher than expected and the diversity increased over time. This could mean the return or appearance of certain common species everywhere. These species are probably not limited by dispersal processes and can survive under all the environmental conditions in Krimpenerwaard (Collins et al., 2002; Freestone and Inouye, 2006; Gabriel et al., 2006).

Spatial and temporal diversity for all species vs. target species

With respect to target species of nature conservation, our results revealed that the diversity of the target species depended more on spatial differences compared with other species, but to a much lesser extent at temporal scales (2%). This is in agreement with the results of our previous study, which proved that target species had a higher rate of distance decay in species similarity due to both environmental heterogeneity and dispersal limitation (Leng, Musters, & de Snoo, accepted). On the

one hand, some research has suggested that these target species are strongly dependent on nutrient levels when it comes to species richness (Blomqvist et al., 2006). Lower nutrient levels apparently improve the germination and establishment of seeds from the seed bank or from other sources. On the other hand, beta diversity among sites was no different from the expected value of the null hypothesis, suggesting that target species may be randomly distributed. However, previous studies have indicated that most of the target species have restricted dispersal capacity or exhibit high specificity to one particular dispersal vector (Benton et al., 2003; Kohler et al., 2008; Leng et al., 2009). These species disperse seeds a few metres by themselves, with less frequent long-distance dispersal events occurring mainly via vectors like water, wind and agricultural machinery (Cain et al., 2000). In our setting, it may be the case that most dispersal is only short-range and limited at larger scales. Further research on species diversity at different spatial scales is required.

Although the beta diversity of sampling periods contributed little to overall species diversity, significantly higher species richness and an accordingly lower rate of distance decay was found in target species in 1999-2000 than in 1995-1996. There are two main hypotheses that might explain the temporal pattern of species diversity (Legendre et al., 2005). One is that species diversity is related to environmental conditions, thus emphasizing environmental site characteristics in landscapes; the other is that species diversity fluctuates in a random, autocorrelated way, thus emphasizing spatially limited dispersal. In our study, improving environmental conditions such as lower nutrient levels, which can increase alpha diversity at the expense of beta diversity might be one explanation. The practices of nature conservation (e.g. reduced nutrient inputs and grazing) and agri-environment schemes (e.g. zero nutrient input and postponed first mowing on ditch banks) applied in our study area suggest an improvement in site conditions for vascular plants (Blomqvist et al., 2006). On the other hand, it is widely evidenced that the dispersal processes of these target species are limited in ditch banks and additional time may be required for small-scale processes to become measurable as landscape-scale patterns and changes in time.

Spatial and temporal diversity in nature reserves vs. agricultural areas

It is important to use diversity partitioning to compare species richness under different management regimes, since the processes determining total species richness may not be captured by alpha diversity alone (Clough et al., 2007). In our study, the proportions of diversity components of target species differed between nature

reserves and agricultural areas, with higher species richness within sites and lower beta diversity among sites in nature reserves. However, the overall species richness, i.e. gamma diversity, in nature reserves and agricultural areas are the same. Previous research has indicated that management regimes such as reduced nutrient inputs and limited grazing intensity should influence the pattern of species diversity (Martin et al., 2005; Klimek et al., 2008). In our study, lower nutrient inputs and grazing intensity in nature reserves may partly explain the higher species richness within sites. This is consistent with previous findings that higher nitrogen inputs reduce plant species richness in temperate grasslands by increasing productivity (Marini et al., 2007; Klimek et al., 2008). The partitioning of diversity in nature reserves and agricultural areas showed a similar tendency: the beta diversity among sites was no different from expected, indicating that the dispersal of plant species in both nature reserves and agricultural areas may tail off with distance, as discussed in the previous section for target species in general.

Among sampling periods, species diversity did not change in nature reserves, while species richness increased and the rate of distance decay of similarity decreased in agricultural areas. In the latter case, species richness increased significantly, especially between the 1995-1996 and 1997-1998 period, which is just after the start of AES. The positive effect of changed environmental conditions under AES may then be the cause of increasing species diversity over time and hence seems to contribute to the changes in the species diversity of target species at the level of the overall landscape. This contradicts our previous finding that AES appeared to be fairly ineffective as a means of enhancing species diversity on ditch banks owing to seed limitation (Kohler et al., 2008; Blomqvist et al., 2009; Leng et al., 2009). However, our study period was at the start of AES implementation and the effect of zero fertilizer inputs on ditch banks would have had a major influence on species diversity during this initial AES period. Other studies in other systems have formed similar effects directly after the establishment of AES (Musters et al., 2009).

Conclusions and implications for conservation

Our findings make it clear that beta diversity at spatial and temporal scales contributed most to total species diversity for all species, but that it is less than expected. Probably this is due to the homogenizing effect of past agricultural intensification. For target species spatial beta diversity was more important. Since environmental heterogeneity and dispersal limitation on a spatial scale seem to play a key role in the pattern of target species diversity compared to that of all species, further management strategies addressing these target species need to focus on

improving environment conditions as well as reducing dispersal limitation among sites. Agri-environment schemes should therefore consider the contributions to diversity from the wider surroundings, rather than focusing entirely on the farm scale.

Furthermore, our study was conducted over a 6-year period of research to investigate patterns of diversity. Since dispersal processes are extremely slow and more time might be needed before the effects of management filter up from small to large scale, it will still remain important to monitor long-term species diversity patterns on ditch banks.

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