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

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Citation

Leng, X. (2010, May 26). *Restoration of ditch bank plant diversity : the interaction between spatiotemporal patterns and agri-environmental management*. Retrieved from https://hdl.handle.net/1887/15565

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ISBN 978-90-5191-168-8

Thesis Leiden University

Cover design: Di Zhang
Photographs: Xin Leng, Erik Gertenaar
Printed by Wöhrmann Print Service, Zutphen, The Netherlands

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Proefschrift

ter verkrijging van
de graad van Doctor aan de Universiteit Leiden,
op gezag van de Rector Magnificus prof. Mr. P.F. van der Heijden,
volgens besluit van het College voor Promoties
te verdedigen op woensdag 26 mei 2010
klokke 16.15 uur

door

Xin Leng
geboren te Danyang, China
in 1981

Promotiecommissie:

Promotor: Prof. Dr. G.R. de Snoo (Universiteit Leiden)
Co-promotor: Dr. C.J.M. Musters (Universiteit Leiden)
Overige leden: Prof. Dr. H.A. Udo de Haes (Universiteit Leiden)
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This research was financially supported by the Chinese Scholarship Council (CSC).

Contents

Chapter 1

General introduction

Biodiversity in agricultural landscapes

One of the most important types of land use in Europe is agriculture. Agricultural landscapes cover over 45% (180 million ha) of the enlarged European Union, with around 103 million ha of arable land, 65 million ha of permanent grassland and 12 million ha of permanent crops (Verburg et al., 2006). Agricultural landscapes offer a wide variety of conditions, due to a combination of natural factors such as soil condition and water availability, and human factors like differences in land use intensity (Donald et al., 2001; Benton et al., 2002). Agricultural landscapes have thus provided unique habitats for many wildlife species and are of great importance to the conservation of biodiversity. Around 50% of all species in Europe depend on agricultural habitats (EEA, 2004).

During the last decades, however, biodiversity losses have occurred in agricultural landscapes at an unprecedented scale. Agricultural practices have shifted from extensive farming systems to either abandonment of farmland or intensification of land use, both of which are considered to be threatening farmland biodiversity (Fig. 1).

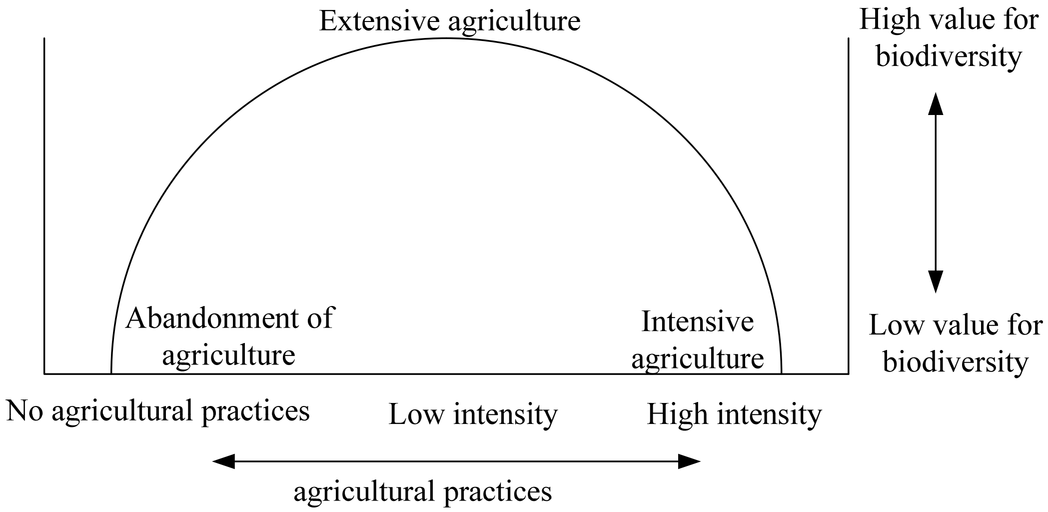


Fig. 1. Relationship between biodiversity in agricultural systems and intensity of agricultural practices (Ostermann, 1998).

Land abandonment is a common phenomenon especially in the regions where agricultural productivity is relatively low (Baldock et al., 1996). The percentage of abandoned arable land in Estonia, for example, was 2% in 1992, and has since dramatically increased to 25% (EEA, 2004). The impact on farmland biodiversity will in most cases be unfavourable (Stoate et al., 2009). At the same time, however, land use intensification is also regarded as one of the most important factors contributing to diversity losses in agricultural areas in Europe (Stoate et al., 2001). Gregory et al. (2000) reported a dramatic decline of bird species in the UK between 1970 and 1998, with Grey partridge (*Perdix perdix*) for instance declining by 82% and Tree sparrow (*Passer montanus*) by 87%. Similar declines in invertebrates and plants have been widely documented in agricultural areas (Petit et al., 2003; Henle et al., 2008).

Land use intensification mainly includes the conversion of complex natural or seminatural ecosystems (grassland) to simplified managed ecosystems (arable fields), and the intensification of resource use, like increasing fertilizer or pesticide input (Tscharntke et al., 2005). Figure 2 shows the effect of landscape complexity on biodiversity at different levels of farming intensity. The biodiversity differences between intensive and extensive farming are most obvious in simple landscapes. Reidsma et al. (2006) assessed land-use intensity change and the related biodiversity loss in the European Union and found that ecosystem quality was lowest in intensively used agricultural areas in lowlands like the Netherlands and northern France.

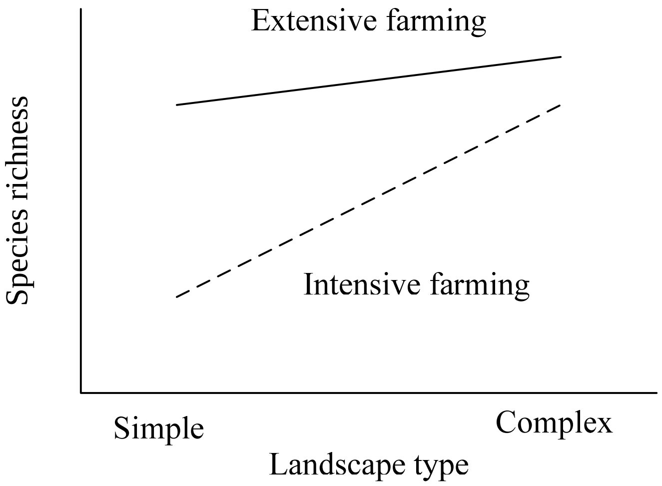


Fig. 2. Diversity of arable land weeds under different management (extensive and intensive) and different types of landscape composition (simple vs. complex) (Roschewitz et al., 2005).

Initiatives to improve biodiversity in agricultural landscape

In order to restore or improve biodiversity, agricultural areas in Europe are now implementing a wide range of strategies at both regional and national levels, including initiatives like the Pan-European Biological and Landscape Diversity Strategy (PEBLDS, 1995), the EU biodiversity action plan for agriculture, and environmental legislation such as the Birds and Habitats directives (79/409/EEC, 92/43/EEC). They mainly focus on either conserving remnants of natural or seminatural areas or enhancing biodiversity in valuable agricultural areas.

Nature protection in the European Union is regulated mainly by the Birds and Habitats directives. It calls for the establishment of a network (Natura 2000) which consists of sites designated under the Habitats directive (Special Areas of Conservation, SACs) and the Birds directive (Special Protection Areas, SPAs). Member States adopt conservation measures on SACs involving appropriate management plans and other measures which correspond to the ecological requirements of the natural habitat types and the species of community interest. SPAs designated under the Birds Directive are managed in accordance with the ecological requirements for bird habitats. The conservation objectives should be met while taking account of economic, social, regional and recreational requirements. It is for the member states to establish the most appropriate methods and instruments to implement the directives and to achieve the conservation objectives for Natura 2000 sites.

Outside protected nature areas, the Common Agricultural Policy (CAP) is the main policy framework affecting conservation of agricultural areas with high ecological value at EU level. Two major relevant elements are agri-environment schemes (AES) and less favoured area payments. AES are considered to be the most important policy instruments to protect biodiversity in agricultural landscapes. They were first introduced by the European Commission (EC), which approved the use of national subsidies for farmers as part of the program. By 1987, countries like England, Germany and the Netherlands had implemented AES. In 1992, the EC adopted the Agri-environmental Regulation EC/2078/92 as part of the Common Agricultural Policy (CAP) reform, and AES became compulsory for member states. Currently, about 25% of all farmland in the fifteen older member states of the EU is covered by some kind of AES (EU, 2005). The main objectives of AES are to counteract the negative effects of modern agriculture on the environment by providing financial incentives to farmers for applying environmentally friendly agricultural practices. Farmers in less favoured areas are eligible for payments per hectare in addition to conventional CAP support, which will generally increase the profitability of farming in marginal areas under natural constraints. As such they are potentially an effective tool for preventing abandonment of ecologically valuable farmland, and may contribute to biodiversity provided they do not create incentives for intensification and particularly overgrazing.

In the Netherlands, the national parliament initiated a new policy called ‘Relatienotabeleid’ in 1975. One purpose was to establish reserves with optimal conditions for plants and other organisms in agricultural areas. In view of the limited area of nature reserves available in the Netherlands, management contracts with farmers were introduced, in which farmers were paid to provide environmental benefits by applying the following treatments: postponement of mowing and grazing, lower fertilizer input and stocking rates and reducing drainage. The first farmer started to participate in the new ‘Relatienotabeleid’ schemes in 1981, and the management measures became substantial after 1990 (Beintema et al., 1997). After the Regulation EC/2078/92 was introduced in 1992, postponement of mowing and grazing became the main agri-environmental measure in the Netherlands. In 2000, a new countryside stewardship subsidy scheme named ‘Subsidieregeling Agrarisch Natuurbeheer’ was introduced. From that time on, farmers implementing ditch bank management were only recommended to use zero fertilizer inputs, low stocking rates, lower ditch cleaning frequencies and extensive mowing and grazing regimes.

Ditch bank vegetation in the Netherlands

In landscapes dominated by agriculture, the former biodiversity is now mostly retained in small-scale landscape elements like ditch banks, field margins and hedgerows (Joenje et al., 1994; Bunce et al., 1998; De Snoo, 1999; Geertsema et al., 2002; Smart et al., 2006). In the Netherlands, ditch banks have a total length of 300,000-400,000 km and are an important feature of the agricultural landscape (Higler, 1994). These ditch banks now function as an important refuge for many formerly common grassland, wetland and hayfield species in terms of survival and diversity (Melman et al., 1991; Blomqvist et al., 2003b). They appear to offer more opportunities to maintain plant diversity, for the following reasons: (1) many ditch banks still harbour species-rich vegetations, including less common species like *Lychnis flos-cuculi* and *Iris pseudacorus*; (2) species-rich ditch banks can be found adjacent to intensively managed fields (Melman et al., 1991; Van Strien, 1991); (3) ditch banks form a economically marginal part of the farm and their grass production is irrelevant on a total farm scale, making it possible to apply extensive management to this habitat.

The peatland areas in the western parts of the Netherlands are among the most intensively exploited areas in Western Europe. The peat bogs that were formed in this area after the last glacial period were later reclaimed and cultivated, causing many changes to the landscape. Long and narrow grassland parcels, separated by shallow ditches or canals, dominate today’s reclaimed peat bog landscape and are used for dairy farming. Although species-rich and flower-rich hayfields and pastures were present in these lowlands for centuries, the intensified agricultural activities in recent years have led to the original vegetation being largely replaced by species-poor pastures with a *Poa-Lolietum* vegetation (De Boer et al., 1982; Jansen et al., 1983). The first cause of this is thought to be dairy farming practices, resulting in a rise in nitrogen fertilization from about 70 kg N $ha^{-1}yr^{-1}$ in 1945 to around 250-300 kg N ha^{-1} yr^{-1} in 1980. From the 1980s onwards, however, several of the intensive farming practices, such as fertilizer applications, have been reduced to the 1960s levels. The second potential cause is that land-use has changed from a varied use of fields to their being used as alternate pastures that are often mown early for silage and grazed afterwards. Furthermore, water tables were lowered by drainage to enable intensive grazing and the use of modern, heavy machinery throughout the year.

Although, as mentioned above, the remnants of the grassland communities can still be found on the Dutch ditch banks, the vegetation of these ditch banks is also becoming more and more impoverished. Records over the past 30 years show that the species diversity on ditch banks has been declining (McNeely et al., 1995; Blomqvist et al., 2003b). Many species that until recently were common in the farming landscape, such as *Caltha palustris* and *Lychnis flos-cuculi,* are now receding (Clausman and Groen, 1987).

Conservation strategies on ditch banks: nature reserves and AES

The nature reserves development approach opts for the conservation and restoration of former farming landscapes with their associated extensive forms of agriculture and diversity of wildlife. These reserves harbour a wider range of plant species than the surrounding area (Kremen et al., 2004). However, nature reserves can only cover a limited area. High land prices and conflicting land user interests are major issues, especially in densely populated areas. Although the National Ecological Network (NEN) in the Netherlands was established to expand the total area of nature reserves to protect wildlife habitats, the conservation areas remain so fragmented that the Netherlands will be unable to meet its international obligations on biodiversity conservation (MNP, 2007), suggesting that the effectiveness of nature reserves is rather limited. Maintenance and increase of biodiversity are thus still hampered by the problem that reserves tend to be small and many dispersal processes have been disrupted in today’s increasingly fragmented landscape (Ehrlen et al., 2006; Kiviniemi, 2008).

As reported above, the AES strategy aims to protect the diversity of species and habitats by offering farmers financial incentives to use “nature-friendly” farming practices on certain parts of their lands. Earlier AES used on ditch banks comprised a regime of zero fertilizer inputs, extensive grazing and postponement of initial mowing and grazing at the start of the season. The latest schemes continue to recommend nutrient reduction, but impose few restrictions on the timing of mowing or grazing (DLG, 2000). Although the evaluation of AES has received more attention in recent years, their efficiency in terms of biodiversity conservation is still questioned (Kleijn and van Langevelde, 2006; Blomqvist et al., 2009). Further studies have shown that colonization was a more important factor determining species richness than extinction (Blomqvist et al., 2003b), so management practices such as lower nitrogen levels and postponed mowing, which focused on extinction, failed to prevent diversity loss on ditch banks (Kohler et al., 2008; Blomqvist et al., 2009).

Factors affecting plant diversity on ditch banks

Traditionally, plant diversity was largely attributed to various environmental (biotic and abiotic) factors, such as nutrients, water supply and intensity of disturbance (Ellenberg, 1996). During the last decades, changes in species composition of plant communities as well as the decline and endangerment of numerous plant species were usually interpreted as the result of the decline of environmental quality due to intensification, abandonment or the complete loss of habitats (Condit et al., 2002). Looking at the conservation strategies on ditch banks, we found that many management practices have focused on restoring soil conditions by refraining from applying fertilizers on ditch banks and adapting mowing and grazing regimes. However, these measures do not to seem increase species diversity (Blomqvist et al., 2003b; Kleijn and van Langevelde, 2006). Although restoration of soil conditions is necessary to maintain species diversity, the management approach will still not be effective if seeds are lacking in the soil seed bank or if dispersal from nearby source populations is limited (Bakker and Berendse, 1999).

Because species richness was found to be low and seed bank composition is dissimilar from the vegetation (Bakker and Berendse, 1999; Blomqvist et al., 2003a; Blomqvist et al., 2006), the enhancement of species richness seems to depend on dispersal from species-rich source populations (Crawley and Brown, 1995; Cousins and Lindborg, 2008; Kohler et al., 2008). Although dispersal was not discussed as an important factor in maintaining diversity up until a few decades ago (Fenner, 1985; Murray, 1986), it has attracted growing attention with the increasing fragmentation of habitats in the agricultural landscape. Much recent theory addresses the processes governing diversity in “meta-communities” or networks of local communities connected by dispersal (Hubbell, 2001; Leibold et al., 2004).

There is widespread evidence that dispersal is a controlling factor for the survival of plant communities and, that it therefore limits species richness and diversity (Eriksson, 1998; Cain et al., 2000; Zobel et al., 2000). In agricultural areas, dispersal distances are always limited by spatial configurations like the isolation of habitats and characteristics of the matrix surrounding the habitats (Fleishman et al., 2001). Moreover, most plant species can only actively disperse their seeds over a few metres and are therefore 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 communities (Cain et al., 2000). The seeds, aided by vectors such as water, wind or agricultural activities (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). It therefore became increasingly obvious that processes and vectors combined with different land-use practices are the key to the dispersal capability of plants. Another important factor is assumed to be the distance between seed source populations and target areas, due to the limited dispersal capacity of most plant species (Fenner, 1985).

Objectives and outline of this thesis

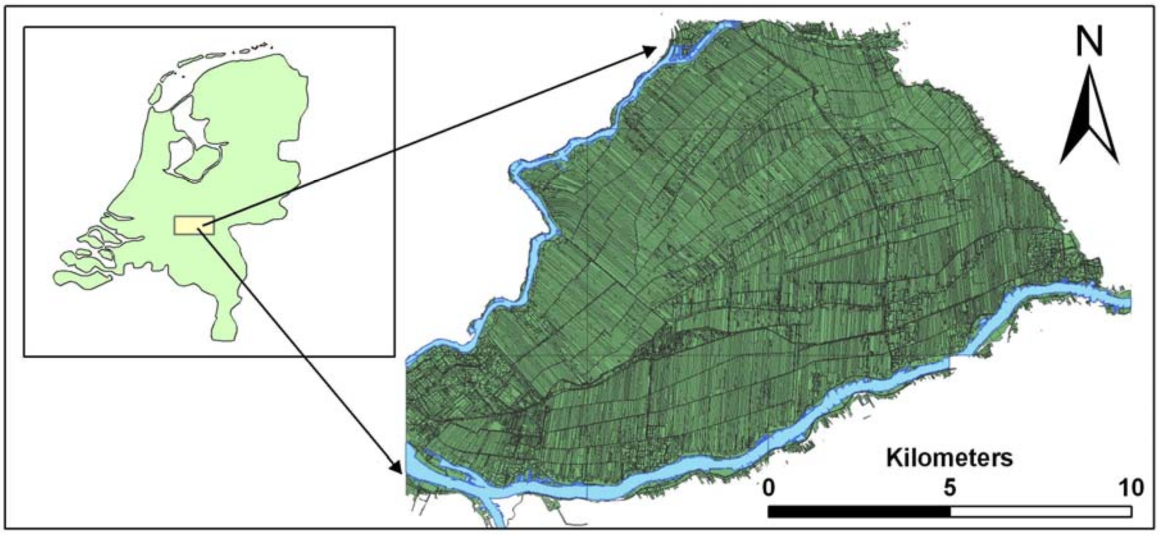
So far, studies of plant diversity on ditch banks have primarily focused either on the effects of ecological mechanisms on individual species (Blomqvist et al., 2003a; Blomqvist et al., 2003b) or on direct management and species richness (Melman et al., 1991; Van Strien, 1991). Initiatives to improve the biodiversity, however, were not as successful as expected (Kleijn and Van Langevelde, 2006; Blomqvist et al., 2009). Effective protection of plant diversity requires more detailed knowledge of ecological mechanisms, especially at larger scale, of plant communities and possible management practices. This study therefore focused on two objectives.

The first objective was to assess *the spatial and temporal patterns of species diversity and the relevant factors on ditch banks*. In recent years, conservation biology has matured and its emphasis has shifted from the management of individual species within habitats to the preservation of entire communities (Whitfield, 2002; Tuomisto et al., 2003). This paradigm shift has required considerable attention to be given to the way patterns of biodiversity vary across spatial and temporal scales. Regional diversity patterns are a result of local processes, underlying environmental heterogeneity and species dispersal among local communities (Collins et al., 2002). Beta diversity, which is the difference in species composition between local communities, is a major determinant of species diversity at regional scale and can be used to measure how variation among local communities contributes to regional diversity (Margules and Pressey, 2000; Ferrier, 2002). We therefore examined how patterns of species diversity change in space and time, as well as the scale dependence of factors that contribute to diversity. Furthermore, since species diversity was poorly protected under management schemes like AES, the selection of additional sites for conservation should be guided by a greater understanding of the species diversity patterns on ditch banks.

The second objective was to explore *possible management for plant diversity restoration based on ecological mechanisms*. Both ecological and economic obstacles often interfere with the creation and maintenance of nature reserves, while the ecological efficacy of agri-environment schemes (AES) is still questioned. A conservation strategy involving integration of nature reserves and agriculture (through AES) has been suggested to improve plant diversity (Steffan-Dewenter and Tscharntke, 1999; Ockinger and Smith, 2007; Cousins and Lindborg, 2008) and we tested whether this strategy can be used on ditch banks. Furthermore, mowing is common practice in grasslands used for dairy farming. In low-intensity farming, it is considered a traditional practice likely to lead to high plant species richness (Huhta and Rautio, 1998). In high-intensity farming, however, it may be regarded as a form of disturbance hampering seed setting in plants. Scientific knowledge about the impact of mowing on seed availability at locations and for dispersal is thus necessary and might help to establish the most effective mowing regime to protect and increase plant diversity.

Research area

Both research questions were addressed by means of analyses of existing data as well as a field study. Our study area encompassed ditch banks in the Krimpenerwaard area, located in the Western Peat District in the Netherlands (51°53’N - 52°01’N and 4°35’E - 4°51’E) (Fig. 3a, 3b). This area can be characterized as a typical Dutch polder landscape and is among the most intensively exploited areas in Europe.



(a)

(b)

Fig. 3. Location of landscapes studied at Krimpenerwaard (**a** and **b**).

The landscape originated about 6000 years B.C. and was formed as a wadden area by the flooding of the lower parts of the Netherlands after the last glacial period. After this area was shut off from the sea by coastal barrier deposits, it transformed into peat bogs. The soil type of the area nowadays consists of peat, while near the rivers, it is bordered by zones of clay and clay-on-peat at greater distances. The current polder land was formed by reclamation of the peat area about 1000 years ago. A network of parallel drainage ditches was created, usually perpendicular to the rivers, resulting in a landscape with long, narrow fields and farmsteads usually near the rivers (Van Strien et al., 1989). Initially, the most distant fields were used extensively, whereas the fields behind the farmhouses near the rivers were used more intensively. As a result of the agricultural intensification process, however, most fields are nowadays exploited intensively (De Boer et al., 1982). The original vegetation types have largely disappeared from the landscape due to the steady lowering of water levels and higher fertilization inputs. The remaining original vegetation types are currently exclusively found on ditch banks and thus serve as a refuge for much of the former biodiversity. The study mainly focused on 25 target species of nature conservation (Appendix in *Chapter 4*). These species were selected because they are not only deemed to be valuable ditch bank plants in Dutch government policy but are also used as criteria for rewarding farmers who implement AES.

In pursuit of the two objectives of this thesis, a series of studies was carried out. The studies relating to the first objective (Part I) are discussed in *Chapter 2* and *Chapter 3*, while those relating to the second one (Part II) are reported in *Chapters 4, 5* and *6* (Fig. 4).

Part I Spatial and temporal patterns of species diversity

Chapter 2

The spatial and temporal patterns of plant diversity on ditch banks under different types of management were examined by means of additive partitioning of diversity as well as analyses of similarity. First, the relative contribution of diversity components to total diversity was estimated for all species, and a similarity index (Jaccard) was calculated for the pattern of species diversity differences in space. Second, we tested whether these patterns differed between all species and the target species. Finally, we studied whether the patterns of target species respond differently between ditch banks in nature reserves and those in agricultural areas.

Chapter 3

Whereas the previous chapter evaluated relative contributions to diversity at different spatial and temporal scales, *Chapter 3* explains spatial patterns of species composition by taking into account the combined effects of dispersal and environmental factors, using multiple regression on distance matrices (MRM). The vegetation data on ditch banks were used to investigate whether and to what extent the species similarity between plots can be explained by the environmental and dispersal factors. Furthermore, the pattern for the target species was also tested and compared with that for all species. Finally, we focused on the patterns for species with different dispersal strategies.

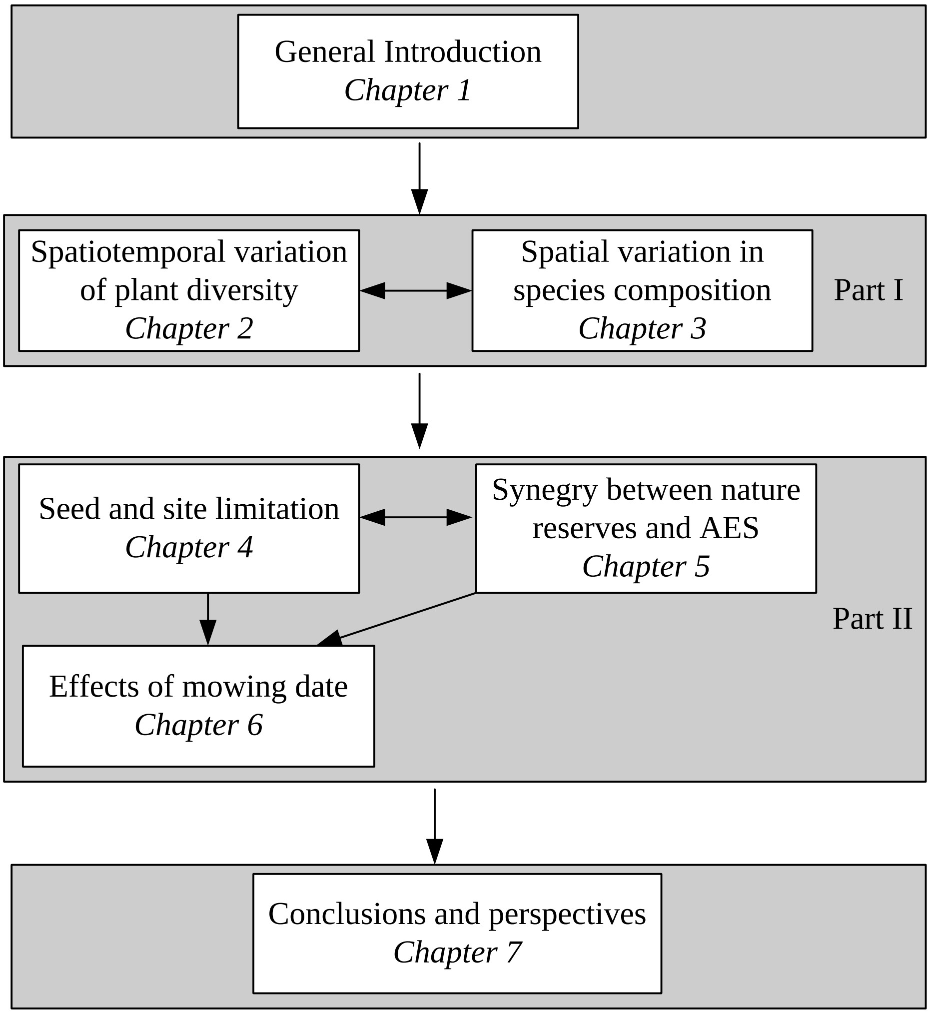


Fig. 4. Structure of the thesis and relation between chapters

Part II Possible managements for plant diversity restoration

Chapter 4

A conceptual model was developed for plant species of ditch banks, to distinguish between site limitation (environmental factors) and seed dispersal limitations.

Studying the restoration sites near species-rich source habitats (nature reserves) enabled us to explore whether dispersal is important to plant diversity restoration. We first tested whether the proximity of nature reserves can improve plant species diversity on the surrounding ditch banks, and then examined whether plant species diversity is higher in ditch banks managed under agri-environment schemes. This was followed by an investigation of the interaction between the presence of nature reserves and AES areas.

Chapter 5

The study reported on in *Chapter 4* thus evaluated the importance of nature reserves for the plant diversity influenced by AES along ditches running transversely from the nature reserve to the farmland. This left unanswered the question of trends in plant diversity along banks running in other directions, to yield an overall picture of how to arrange the nature reserves and AES at the landscape level. This chapter focuses on the effects of the synergy between nature reserves and AES on plant species across a network of ditch banks. We first studied the pattern of plant diversity on successive ditch banks running parallel to a nature reserve, and then made a comparison of the pattern between ditch banks running transverse and parallel to a nature reserve. Finally, we focused on AES and investigated whether ditch banks managed under an AES showed different plant diversity patterns in two directions relative to nature reserves.

Chapter 6

Preliminary studies (*Chapter 4* and *Chapter 5*) revealed that conservation management does not increase connectivity by decreasing seed limitations for plant species. Since mowing might be a measure to increase seed dispersal, we undertook a comprehensive study of the effect of variations in mowing date on seed availability for seed transportation on ditch banks under four different management regimes (nature reserves, AES with long-term management, AES with short-term management and conventional management). Two research questions were addressed, one to check whether the seed-setting of ditch bank plant species is affected by the timing of mowing, the other to assess whether this effect varies with different management regimes.

Chapter 7

This chapter briefly summarizes and discusses the results of the previous chapters. It also proposes guidelines for ditch bank plant diversity conservation and options for future research.

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Chapter 2

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

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Submitted to *Basic and Applied Ecology*

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 m ± 0.14 m, average ± 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: $\gamma = \alpha_1 + \beta_1 + \beta_2 + \ldots \beta_n$, 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: $\gamma = \alpha_{sites} + \beta_{sites} + \beta_{periods.}$ 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).

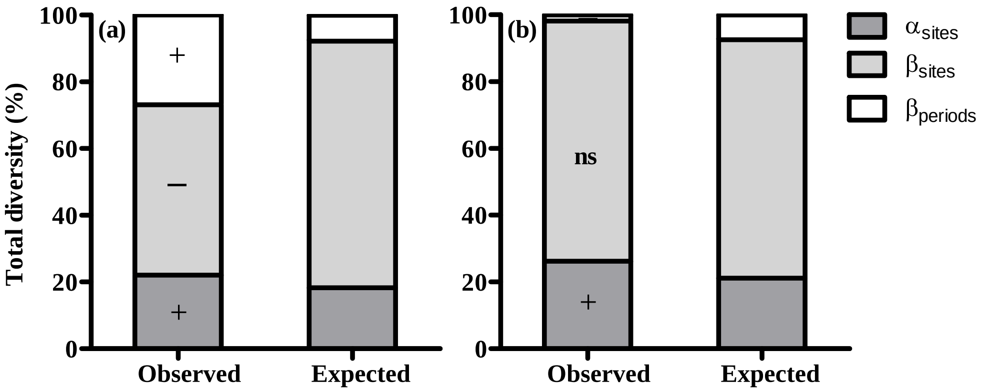

Fig. 1. Observed and expected additive partition of total species richness of **(a)** all species, **(b)** target species across two hierarchical levels (sites and sampling periods). Values are expressed as a percentage of total diversity. Observed partitions are compared with expected values from a 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.

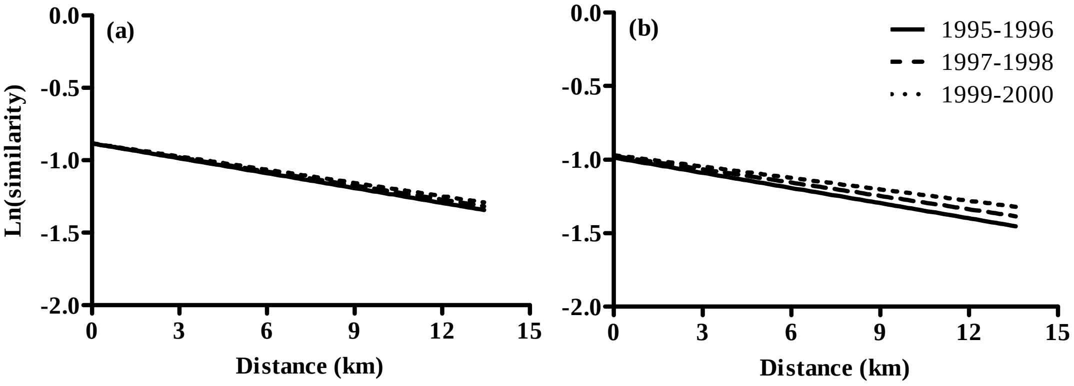

Fig. 2. Distance decay of Ln(species similarity) for all species **(a)** and target species **(b)** in the respective sampling periods.

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).

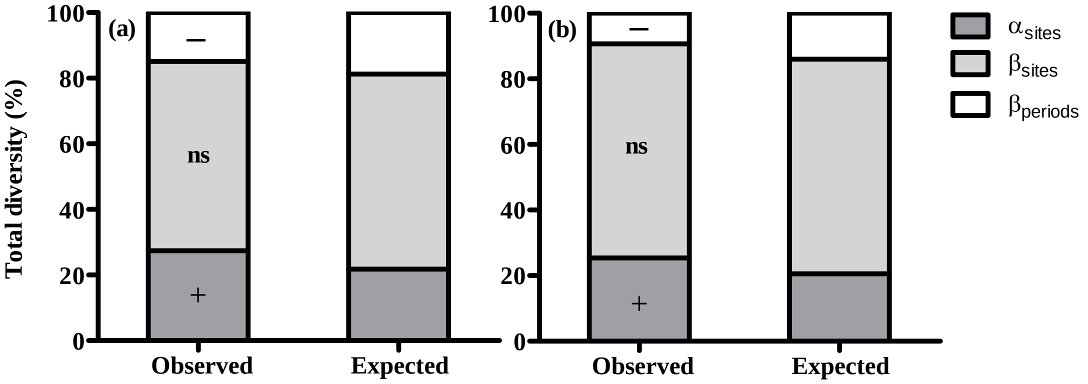

Fig. 3. Observed and expected additive partition of total species richness of target species in nature reserves **(a)** and agricultural areas **(b)** across two hierarchical levels (sites and sampling periods). Values are expressed as a percentage of total diversity. Observed partitions are compared 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	

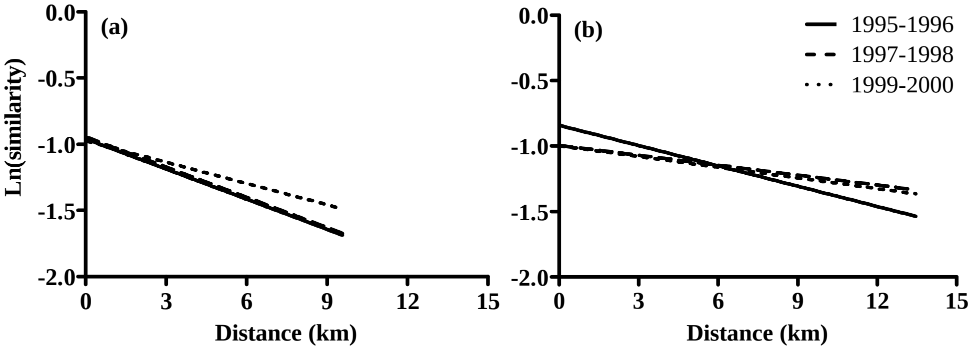

Fig. 4. Distance decay of Ln(species similarity) for target species in nature reserves **(a)** and agricultural areas **(b)** in the respective sampling periods.

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.

Acknowledgements

We thank Rudi Terlouw and Dick Kerkhof of the Zuid-Hollands Landschap for providing data. This research was financially supported by the Chinese Scholarship Council (CSC). We also thank Nigel Harle for improving the English of this article.

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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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In press, *Journal of Vegetation Science*

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).

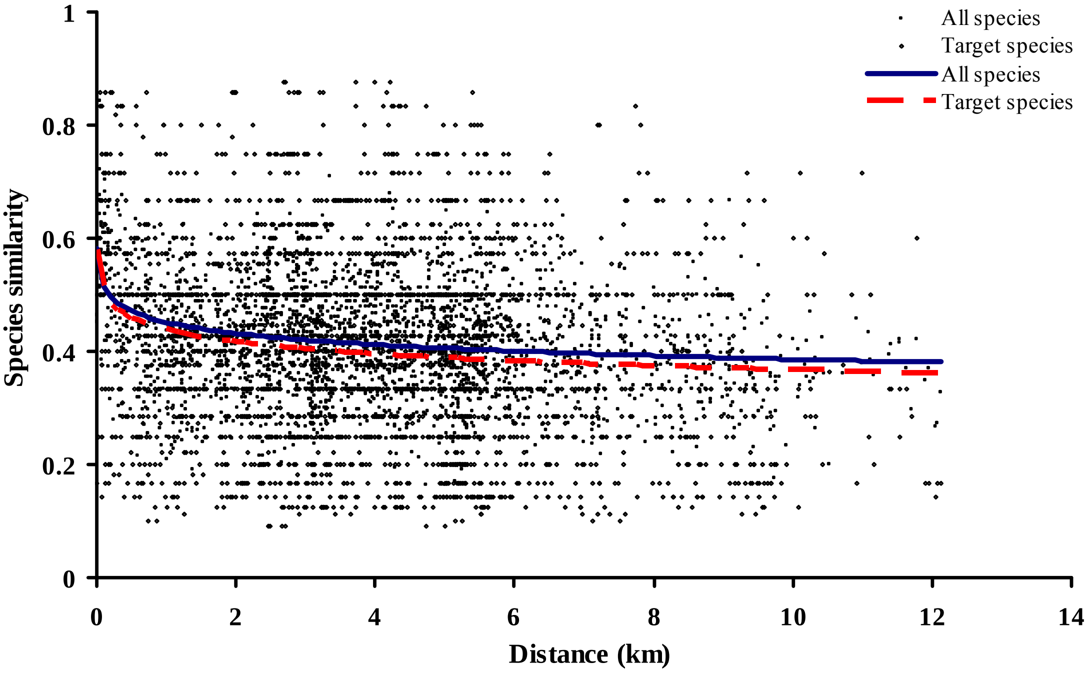

Fig. 1. Distance decay of species similarity in all species (130 species, R^2=0.086) and in target species of conservation interest (25 species, R^2=0.025) on a total of 72 plots, 2556 of pair wise comparisons.

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 matrix	All species (130 species)				Target species (25 species)			
	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.

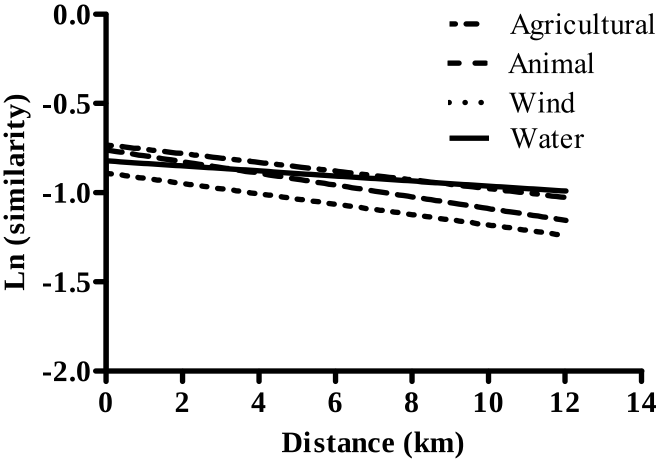

Fig. 2. Distance decay of Ln(similarity) in species of different dispersal type on a total of 72 plots, 2556 of pair wise comparisons. The slope of Ln(similarity) against geographic distance was shown in Table 2.

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).

Acknowledgements

We thank Sarah Goslee for help with programming issues, Jeff Nekola for support with data analysis and Ben A. van Arkel and Xiaofei Zhang for assistance with data collection. We are grateful to Rudi Terlouw and Dick Kerkhof of the Zuid-Hollands Landschap for providing data. We also thank Nigel Harle for improving the English of this article. This research was financially supported by the Chinese Scholarship Council (CSC).

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Chapter 4

Restoration of plant diversity on ditch banks: seed and site limitation in response to agri-environment schemes

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Published in *Biological Conservation* (2009) 142: 1340-1349.

Abstract

Recently it has become clear that seed limitation is probably a much more important factor in plant recovery than has often been recognized. However, in practice, restoration measures that are focussed on decreasing site limitation may actually increase seed limitation. We tried to determine whether the effects of restoration measures affect site or seed limitation or both. An experiment was set up on ditch banks in the Netherlands which applied agri-environment schemes (AES). To investigate whether nature reserves (seed source) can improve species diversity on the surroundings and to what extent AES is improving this function, we studied the plant diversity (presence of individual species and species richness) of ditch bank vegetations in relation to increasing distance from nature reserves. The presence or absence and species richness of 25 target plants were assessed in 26 ditch banks with AES and 36 non-AES at 15 plots each differing in distance to a nature reserve. Data were analyzed using a Hierarchical Generalized Linear Model (HGLM) with species richness and presence of individual species as response variables and distance to nature reserve and application of AES as factors, controlling for possible confounding factors. Results were interpreted as the effects of AES on seed and site limitation of the species. The results showed that plant diversity decreased significantly with distance from source populations. There were considerable differences in species diversity between AES and non-AES ditch banks, with the former showing greater plant diversity especially in the first 200 meters from nature reserves. Presences of all individual species decreased with distance to nature reserve, but the strength of this relationship and the AES effects differed among species. AES ditch banks had lower site limitations for most plant species, but did not affect seed limitation.

Introduction

Agricultural intensification has led to a rapid decrease in plant species in western Europe during last century (Strijker, 2005; Tscharntke et al., 2005). In order to restore plant species diversity, many strategies are available, varying from establishing nature reserve areas to nature friendly management of agricultural areas (Kleijn and Sutherland, 2003). The success of these strategies depends on the ability of the strategy to decrease the limitations of plant recovery. Research provides evidence that the number of plant species would be largely controlled by both site limitation and seed limitation (Nathan and Muller-Landau, 2000; Donath et al., 2007; Ozinga et al., 2009). Site limitation can be defined as a low probability of the presence of a plant species at a microsite due to microsite conditions that determine seed germination, plant growth and plant survival. Seed limitation, on the other hand, can be defined as a low probability of the presence of a plant species at a microsite due to low seed availability. Recently it has become clear that seed limitation is probably a much more important factor in plant recovery than has often been recognized (Blomqvist et al., 2003b; Blomqvist et al., in press; Ozinga et al., 2009). Restoration strategies should therefore not only be focused on decreasing site limitation, but also on decreasing seed limitation. However, in practice, restoration measures that are focussed on decreasing site limitation, such as decreasing nutrient input, restoring water tables, or mitigating disturbances, may actually increase seed limitation, for example if flooding with nutrient rich water is hampered or cattle is kept out of nature reserves (Ozinga et al., 2009). Therefore, it is necessary to be able to assess the effect on seed limitation of restoration measures aimed at decreasing site limitation. Here we present the results of a study in which we tried to separate the effects of restoration management on site and seed limitation. Our study system may serve as a model for other systems in which separation of these effects is needed.

One policy response to improve species diversity in agricultural areas has been the introduction of agri-environment schemes (AES), in which farmers are paid to provide environmental benefits for plants and other organisms by modifying their farming practices. The efficiency of AES on biodiversity conservation, however, has been questioned (Kleijn et al., 2001; Kleijn and Sutherland, 2003). Several studies have furthermore shown that the management failed to prevent the process of diversity loss (Ferraro and Kiss, 2002; Blomqvist et al., 2003a; Klimek et al., 2007). In the Netherlands, for instance, botanical AES was applied mainly on ditch banks which provide an important refuge for common grassland, wetland and hayfield plants (Melman and van Strien 1993; Smart et al., 2006; Blomqvist et al., 2009). The management includes no fertilizers on ditch banks, nor deposition of ditch sediment or plant remains on them, reduced ditch cleaning frequencies and postponed mowing and grazing regimes (Melman and van Strien, 1993). Recent restoration efforts such as a further lowering of nitrogen levels and mowing later in time have not resulted in increased species diversity (Blomqvist et al., 2003b). The problem now is that little is known about which ecological factors and processes may affect the increase and decrease of plant species or why management is not successful.

Many aspects of AES seem to focus on creating infrequently disturbed sites of low fertility which are supposed to lower site limitations. However, some grassland studies found that seed limitation was regulating the size of plant population and might be an important factor behind variation of species richness (Eriksson, 1997, 1998; Zobel et al., 2000; Blomqvist et al., 2003b). Seed limitation of plant species is thought to be determined by seed banks, seed production, as well as dispersal (Bakker and Berendse, 1999; Bissels et al., 2005; Simmering et al., 2006; Blomqvist et al., 2006; Kohler et al., 2008). While species richness was found to be low and seed bank composition dissimilar from the vegetation (Bakker and Berendse, 1999; Blomqvist et al., 2003a; Blomqvist et al., 2006), restoration seems to depend on seed production and colonisation in case of seed limitation. Both colonisation and seed production seem to depend on distance from species-rich source populations, colonisation through dispersal and seed production through pollination (Crawley and Brown, 1995; Coulson et al., 2001; Kohler et al., 2008). Management efforts primarily focussing on lowering site limitation would be one explanation of the disappointing success of AES to restore species diversity (Bakker and Berendse, 1999; Blomqvist et al., 2003a).

By studying restoration sites near species-rich source habitat (nature reserves), it is possible to explore if dispersal and/or pollination is important to plant diversity restoration (Van Dorp et al., 1997; Blomqvist et al., 2003a; Rosenthal, 2006; Kohler et al., 2008). As said, in this paper, we have tried to separate the two forms of limitation and study whether AES, really only decreases site limitation. We investigated the plant diversity on ditch banks in the Western Peat District in the Netherlands which belongs to the most intensively exploited areas of Europe. The purpose of this study was threefold: to test whether nature reserves, regarded as seed source, can improve plant species diversity in the surrounding ditch banks, to test to what extent plant species diversity is higher in AES ditch banks, and to study the interaction between the presence of a nature reserve area and AES. A conceptual model was developed to separate the effects of seed and site limitation on plant species presence from field data.

Methods

Study area

To avoid the confounding effects of inter-regional differences, we selected two study areas, Vijfheerenlanden and Krimpenerwaard, where similar agri-environment schemes have been in place for certain time: between 6 and 12 years, with an average of around 9. Both study areas are situated in the province of South-Holland in the Western Peat District in the Netherlands which belongs to the most intensively exploited areas of Europe (Fig. 1; Maes et al., 2008). Most of the farmland serves as pasture for dairy cattle and sheep. The dominant soil types are peat or peat with clay. Typically, the meadows have 0.8 m - 1.5 m wide field edges (ditch banks) of varying species richness. Ditch bank slopes range from 15º to 20º.

Fig. 1. Study landscape in Krimpenerwaard in the Netherlands. Black frame area is nature reserve named Polder Kattendijksblok. In the middle a small pool is visible.

The nature reserves appear the same landscape as surrounding matrix. Their strategy opts for the conservation and restoration of the former farming landscapes with their associated extensive forms of agriculture and diversity of wildlife in a limited number of areas (Wolff-Straub, 1985). We selected 8 nature reserves for the purposes of our study (Table 1). In Vijfheerenlanden: Huibert, de Waai, de Schaayk and Scharperswijk; In Krimpenerwaard: Kattendijksblok, Middleblok, Bilwijk and Berkenwoude. The size of these nature reserves is between 6 ha and 44 ha and most of them are designed for certain types of biodiversity protection such as flora and meadow birds. The investigation in Vijfheerenlanden was in May 2006 while the surveys in Krimpenwaard were carried out in two successive years, June 2006 and

2007, to trace any systematic differences in species richness between years. We tried to choose three ditch banks with and three non-AES along axes running from each nature reserve. As certain ditch banks under AES in Krimpenerwaard had already been mown and the plant cover removed when we investigated them in 2006, a total of 26 AES ditch banks and 36 non-AES ditch banks were ultimately sampled

Table 1. Number of ditch banks investigated in the study area.

	Vijfheerenlanden			Krimpenerwaard			
	2006			2006		2007	
Reserve	AES	Non-AES	Reserve	AES	Non-AES	AES	Non-AES
De Schaayk	3	3	Kattendijkseblok	2	3	3	3
De Waai	3	3	Middleblok	3	3	3	3
De Huibert	0	6	Bilwijk	3	1	3	3
Scharperswijk	0	6	Berkenwoude	3	2		

Target species, vegetation and habitat variables

The target species selected for study have been assigned status of valuable ditch bank plants by the Dutch government and are used to reward farmers when implementing AES (the whole list see Appendix). These 25 plants are not only easy to recognize, but are also supposed to be indicative for agri-environment schemes management of ditch banks.

Two vegetation variables of target species were used in our study to determine the plant diversity: the presence of individual species and species richness. A large number of possible habitat variables affecting the vegetation of ditch banks were measured. They were selected on the basis of possible relevance for the physical factors and managements of ditch banks (Van Strien, 1989; Geertsema and Sprangers, 2002). Physical factors include ditch bank width, slope angle, slope aspect, ditch water table and ditch water pH. Field managements including the amount of nitrogen applied (kg ha^{-1}year^{-1}) and ditch management involving ditch cleaning frequency were collected from questionnaires distributed to farmers. In addition, the distances of the roads where the farm house are located and which are on the opposite side of farmland than the reserves, as well as the distances of paths which crossed ditch banks and are used for transportation among farms were measured.

To explore which ecological and management factors influence plant seed and site limitation along ditch banks, the ecological traits of each target species were taken into consideration based on Van Strien (1989), Blomqvist (2003a) and Manhoudt et al., (2007) (references in Appendix): nature-value (regional, national and world rarity of species), site requirement (minimum light requirement, moisture, nutrient requirement and acidity values) and ecological strategies (flowering period, germination period, mean plant heights), pollination strategy and dispersal strategy. Since the direction of all ditch banks we investigated is from NW to SE, the wind rose influence is not included.

Sampling

To study the ditch bank vegetation in relation to increasing distance from the adjacent nature reserve, fourteen plots were selected along the ditch banks to form a distance gradient (Fig. 2). Because dispersal distance for most species is limited (Geertsema et al., 2002), we took 2 plots more within the first 200 meters from the reserves to be able to assess a clear distance gradient. In addition, one plot was selected in each nature reserve to represent the source population. To maintain distance parameter coherence and minimize the possible effects of household sewage and non-sewage waste water and possible intense farming activities, all study plots were chosen more than 200 meters from farm houses (Van Strien, 1989).

The vegetation was analyzed in 10 m long plots, the width of which varied with ditch bank (1.25 m ± 0.09 m). This gave a plot size of around 10 m^2, commonly used in ditch bank analysis (Geertsema et al., 2002). The presence or absence of target species was recorded.

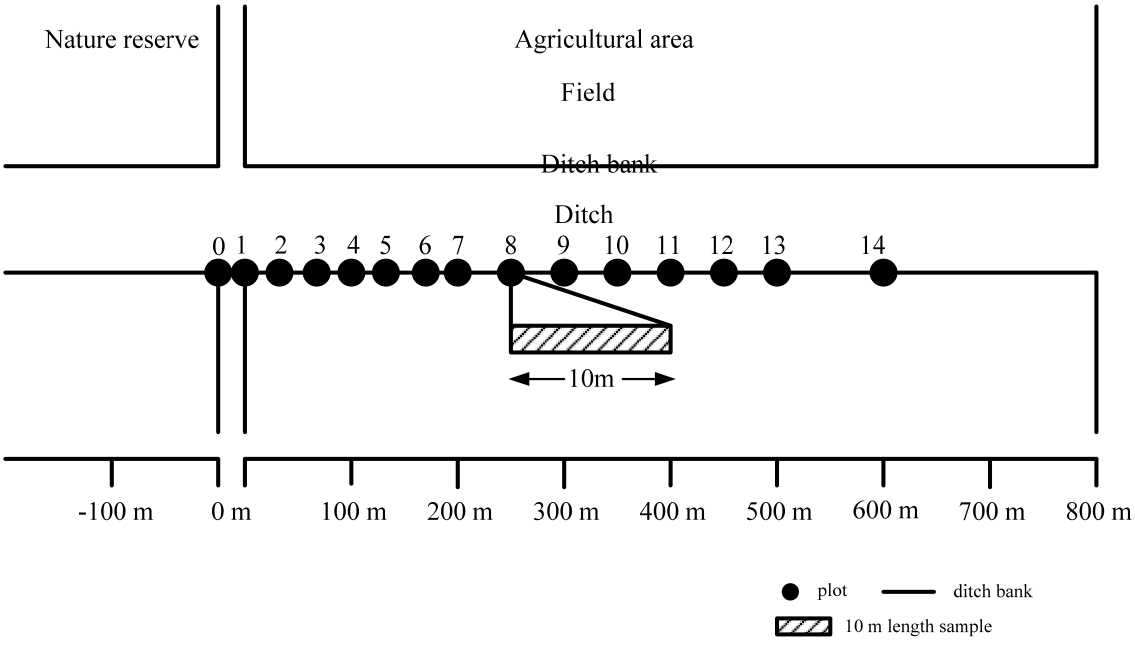

Fig. 2. A sketch of the experimental areas and the surrounding. Each plot is 10 meters length and the width depends on the ditch banks width.

Data analysis

In order to investigate whether site and seed limitation of species influence species diversity, the following conceptual model was adopted. First, we assume that the probability of presence p(P) of a certain ditch bank species in a plot depends on the probability of seeds being present p(S) in that plot times the probability of seeds to germinate, grow and survive p(G) at that plot. We also assume that the probability to germinate, grow and survive depends only on site characteristics. And we assume that the probability of seeds being present depends on the distance to the present seed source. Thus, based on the findings of Blomqvist et al. (2003b), we ignore the relevance of a seed bank in our study area. Like previous authors (such as Willson, 1993; Coulson et al., 2001), we assume an inverse power relationship between seed abundance and distance D to the source. So our model is:

$$p(P) = p(G) * p(S) \qquad \text{and} \qquad p(S) = a * b^D$$

in which a is the probability of seeds being present at distance 0 which we assume to have the maximum probability that is unaffected by either characteristics of the location or distance-dependent mechanisms and in which b is a constant that indicates the rapidity of the decline of the probability with distance from the source. Log-transformation of our model gives:

$$\ln(p(P)) = \ln(p(G)) + \ln(a) + \ln(b)*D$$

Now suppose some form of management that changes the site limitations, that is the microsite conditions of the plots that affect seed germination, plant growth, and plant survival. This would change p(G), but affect neither a nor b. On the other hand, a form of management that would change the distance-dependent mechanisms, like dispersal or pollination, would change b, but neither p(G) nor a. Or, if we replace ln(p(G)) + ln(a) by i and ln(b) by r in our log-transformed model:

$$\ln(p(P)) = i_m + r_m*D$$

in which i_m will change due to management that affects site limitation and r_m due to management that affects seed limitation. So, the effect of management on site limitation becomes visible in the intercept of the regression analyses of the log-transformed probability with distance, and that on seed limitation in the regression coefficient. This gives us in principle a simple field test to separate the effect on site and seed limitation by AES on the presence of individual species (Fig. 3). At one extreme, if neither seed nor site limitation is affected by AES, the species probability will not change due to AES (Fig. 3a). When AES lowers site limitation only, species probability will be higher along the complete ditch bank (Fig. 3b). However, when AES lowers seed limitation only, the species probability will be higher at further distances from source only (Fig. 3c). Figure 3d summarizes a positive effect of AES on both seed and site limitation.

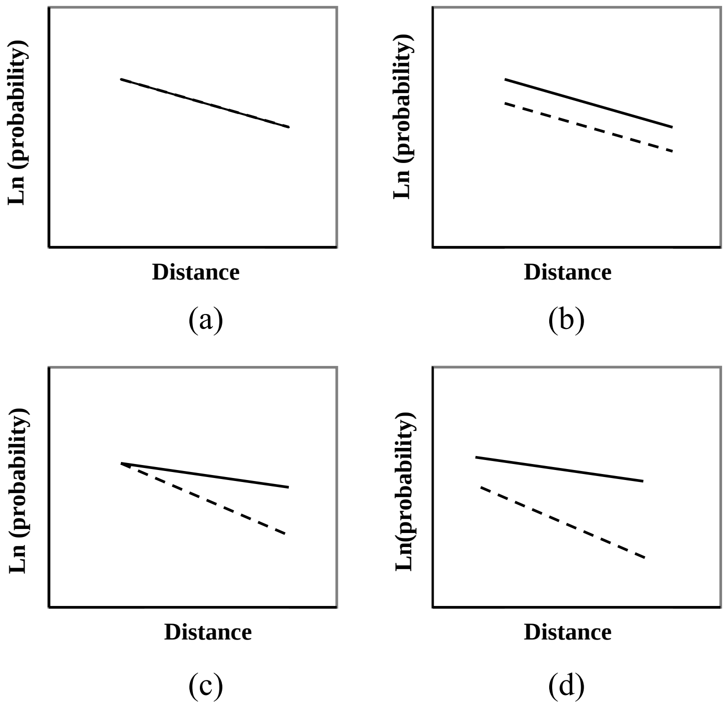

Fig. 3. Possible relationships between log-transformed probabilities of target species presence and the distance to the source in AES and non-AES ditch banks. **(a)** no site or seed limitation effect, species richness is the same in AES and non-AES ditch banks. **(b)** a positive effect on site limitation and no effect on seed limitation, species richness has an equal higher probability in AES ditch banks compared to non-AES ones. **(c)** a positive effect on seed limitation and no effect on site limitation, species richness has higher probability at longer distances from the source in AES ditch banks but no difference at the shortest distances. **(d)** a positive effect on both seed and site limitation, species richness has a combination of higher overall and higher probability at longer distances from the source in AES ditch banks.

The effect of decreasing site or seed limitation on species richness cannot easily be deduced from this. Since species richness is the sum of the plant species present, the expected species richness of a plot is the sum of probabilities of the individual species being present:

$$R_{exp}=\Sigma p_c(P)=\Sigma(p_c(G)*a_c*b_c^D)$$

for species c=1 to n. In this case, log-transformation will not result in a simple linear regression between $\ln(R_{exp})$ and D. However, simulation of species richness based on 15 individual species differing in site and seed limitation over the complete scale of 0.9 to 0.1 showed that the regression line between $\ln(R_{exp})$ and D is very close to linear. Changes in site limitations did affect the intercept of the regression line strongly, but hardly affected the regression coefficient. On the other hand, changes in the seed limitation changed both the regression coefficient strongly and the intercept moderately. This seems to suggest that in case of a change of intercept only, this can be interpreted as a change in site limitation, while a change in intercept and regression coefficient could be the result of either a change of seed limitation only, or a change of both site and seed limitation. However, these results may depend on the simulation applied. Therefore, the interpretation of changes in the regression line between $\ln(R_{exp})$ and D should be done very carefully and not without studying the changes in the individual species.

Of course, our response variable is not really a direct measurement of probability, but either the presence or absence of a species or the count of the number of species in a plot. These variables are assumed to have respectively a binominal and a Poisson distribution. Therefore, General Linear Model’s were applied. In order to be able to control for confounding variables, species presence and species richness under different management regimes were analysed with a Hierarchical Generalized Linear Model (HGLM, GENSTAT 10.0). The fixed part of the model included distance from nature reserve, management and their interaction. We considered our study locations each year as random samples, therefore location was added as a random factor, nested as year/region/reserve in case of individual species and nested as year /region /reserve /ditch number in case of species richness. In case of species richness, we added as confounding variables, all habitat variables that reflect the habitat quality along ditch banks, distance from the path crossing the ditch banks (Distance middle) and distance from the farm roads (Distance road). Due to inability of resolving the models, this was not possible in case of the individual species. We used the HGLM to test the impact of distance, AES, and their interaction on respectively the presence of individual species and species richness. We also used the models to predict species probability and species richness over a range of distances. We used these predictions to calculate the intercept and regression coefficient of the regression line between distance and ln(species probability) and species richness.

If our conceptual model is correct in that the effect of changed site limitation on probability of a species' presence is manifested in a change in the intercept of the regression line between ln(p(P)) and D, whereas change in seed limitation is manifested as a change in the regression coefficient, then differences between species in the change of either intercept or regression coefficient can be expected to correlate to species ecological traits related to site or seed limitation respectively. Relationship between species ecological traits and management effect on intercept and regression coefficient was explored using linear regression analysis in case of ordinal traits. Quadratic terms were included to check for non-linearity. If not significant ($p<0.05$), the quadratic term was dropped. ANOVA was used in case of nominal traits.

Results

Presence of individual species

Of the 25 target species, a total of 17 were found in the ditch bank vegetation. All 17 species were found at 45 m distance and, of these, 13 species were found at 205 m distance, while the following 10 species could be found further away than 405 m: *Cirsium palustre*, *Galium palustre*, *Iris pseudacorus*, *Lotus pendiculatus*, *Lycopus europaeus*, *Lysimachia thyrsiflora*, *Lythrum salicaria*, *Myosotis*, *Ranunculus flammula* and *Vicia cracca*. All species showed a significant negative relationship with distance, while 11 out of 17 species had significantly higher presence in AES ditch banks, one species had a significantly lower presence in AES ditches, viz *Lathyrus pratensis*. Six species showed a significant interaction between distance and management (Table 2).

The intercept of regression between distance and log-transformed species probability was higher in AES ditch banks in significantly more species than expected in case of chance, viz. 15 out of 17 species (Table 3; p-value chi-square test: 0.002). But about an equal number of species showed a higher regression coefficient in AES ditch banks as did a lower regression coefficient (8 out of 17 species increased).

Table 2. Results of HGLM analysis of effect of distance (from nature reserves), management (AES vs. non-AES) and interaction per target species. *=p<0.05.

Species name	distance		management		interaction	
	estimate	t	estimate	t	estimate	t
Caltha palustris	-0.43	-4.92*	0.34	1.36	0.24	2.65*
Cirsium palustre	-0.06	-8.62*	0.02	0.06	-0.02	-1.8
Filipendula ulmaria	-0.22	-12.45*	-2.33	-8.2*	-0.003	-0.06
Galium palustre	-0.07	-9.27*	-1.08	-2.92*	0.02	1.64
Iris pseudacorus	-0.06	-7.44*	-0.99	-3.91*	0.02	1.93
Lathyrus pratensis	-0.04	-2.99*	0.54	2.01*	-0.07	-3.72*
Lotus uliginosus	-0.06	-3.95*	-0.14	-0.43	-0.002	-0.29
Lychnis flos-cuculi	-0.07	-8.88*	-1.64	-6.02*	0.01	0.82
Lycopus europaeus	-0.06	-7.89*	-0.33	-1.35	0.004	0.32
Lysimachia thyrsiflora	-0.12	-10.81*	-0.89	-3.31*	0.005	0.38
Lythrum salicaria	-0.04	-6.23*	-1.09	-3.88*	-0.018	-1.34
Mentha arvensis	-0.38	-11.78*	-17.51	-1.7	0.38	1.18
Myosotis	-0.09	-12.12*	-2.21	-3.06*	0.02	1.09
Pedicularis palustris	-0.36	-9.47*	-3.87	-13.95*	0.34	8.74*
Ranunculus flammula	-0.03	-4.87*	-1.94	-5.11*	-0.42	-4.66*
Veronica beccabunga	-0.26	-11.63*	-2.32	-9.11*	0.17	6.82*
Vicia cracca	-0.09	-11.17*	-2.68	-8.91*	0.03	2.21*

Table 3. Intercept of the regression analysis of the log-transformed probability with distance (i) and regression coefficient (r) based on results of HGLM analysis of effect of distance (from nature reserves) and management (AES vs. non-AES) per target species.

Species name	Management				Differences	
	$i_{\text{non-AES}}$	$r_{\text{non-AES}}$	i_{AES}	r_{AES}	D_i	D_r
Caltha palustris	-4.22	-0.18	-2.73	-1.21	1.49	-1.03
Cirsium palustre	0.14	-0.03	0.016	-0.02	-0.124	0.01
Filipendula ulmaria	-1.59	-0.21	-0.55	-0.16	1.04	0.05
Galium palustre	0.01	-0.013	0.085	-0.014	0.075	-0.001
Iris pseudacorus	-1.01	-0.029	-0.76	-0.028	0.25	0.001
Lathyrus pratensis	-0.84	-0.11	-3.91	-0.04	-3.07	0.07
Lotus uliginosus	-0.38	-0.02	-0.17	-0.01	0.21	0.01
Lychnis flos-cuculi	-1.38	-0.05	-0.59	-0.06	0.79	-0.01
Lycopus europaeus	-0.64	-0.05	-0.53	-0.04	0.11	0.01
Lysimachia thyrsiflora	-0.19	-0.07	-0.05	-0.08	0.14	-0.01
Lythrum salicaria	-1.91	-0.05	-1.05	-0.03	0.86	0.02
Mentha arvensis	-12.57	0	-1.29	-0.11	11.28	-0.11
Myosotis	0.006	-0.0006	0.03	-0.003	0.024	-0.0024
Pedicularis palustris	-4.69	-0.02	-2.29	-0.24	2.4	-0.22
Ranunculus flammula	-1.83	-0.38	-1.29	-0.02	0.54	0.36
Veronica beccabunga	-2.43	-0.08	-1.58	-0.15	0.85	-0.07
Vicia cracca	-1.01	-0.057	-0.04	-0.062	0.97	-0.005

Species richness

The results of the HGLM on species richness are given in Table 4. A significant non-linear relationship was found between distance and number of target species in the vegetation, indicating that the species richness of the vegetation declines with increasing distance from nature reserve, both in AES and non-AES ditch banks. The effects of agri-environment schemes were found to be significant (Table 4). On average, the mean number of species in the AES ditch banks (5.05 ± 2.41) was 9% higher than in the non-AES ones (4.58 ±1.82).

Table 4. Results of HGLM analysis for the effect of distance from nature reserve, management (AES vs. non-AES) and habitat variables. *nitrogen supply on the adjacent field (class 1: 0-200 kg $ha^{-1}year^{-1}$; 2: 200-300 kg $ha^{-1}year^{-1}$; 3: 300-400 kg $ha^{-1}year^{-1}$; 4: 400-500 kg $ha^{-1}year^{-1}$). Lambda estimates represent the random part of the model. *=p<0.05, **=p<0.01, ***=p<0.001.

	Species richness		
	estimate	s.e.	t
Constant	2.26	0.17	13.4***
Distance	-0.04	0.003	-16.8***
Management	-0.26	0.04	-6.59***
Management*Distance	0.01	0.003	4.08***
Square Distance	0.0004	0.00004	9.03***
Management*Square distance	-0.0001	0.00006	-2.5*
Distance road	0.005	0.002	2.75**
Square Distance road	-0.00004	0.00001	-4.41***
Distance middle	0.0003	0.00007	3.76***
Square Distance middle	-6.6E-08	9.9E-08	-0.66
Ditch bank width	-0.02	0.12	-0.17
Ditch water table	-0.18	0.13	-1.35
Aspect 2	-0.087	0.084	-1.03
Aspect 3	-0.013	0.079	-0.17
Aspect 4	-0.055	0.084	-0.65
Slope	0.002	0.008	0.18
pH	0.01	0.009	1.06
Cleaning frequency	0.12	0.12	1.00
Nitrogen supply*	-0.12	0.06	-1.86
Estimates from the dispersal models:			
phi	-1.34	0.048	-27.68***
Lambda year	-8.15	4.26	-1.85
Lambda year* region	-5.38	1.63	-3.3***
Lambda year* region* reserve	-5.76	0.81	-7.1***
Lambda year*region*reserve * ditch bank	-4.07	0.22	-18.4***

Figure 4 shows that differences between the two management types were found up to 200 meters from the reserves but no significant management effect remained at distances over 200 m. The regression lines of log-transformed richness against distance show a relationship with AES on both the intercept and the regression coefficient: the intercept is higher in AES ditch banks, while the regression coefficient is lower (Fig. 5).

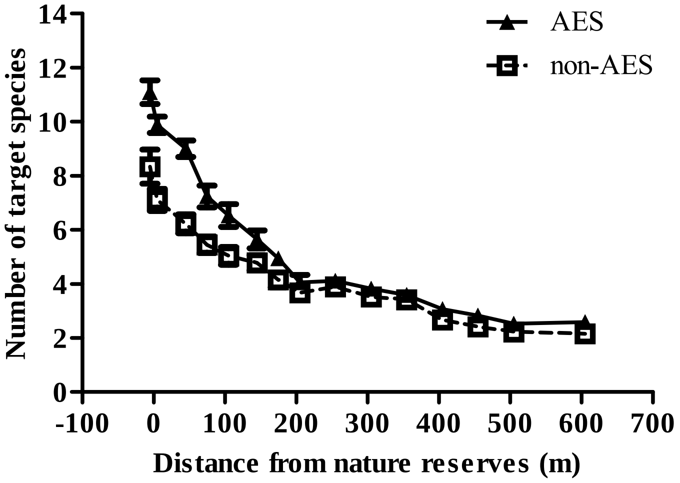

Fig. 4. Relationship between species richness and distance from nature reserves on AES and non-AES ditch banks. Vertical bars are standard errors.

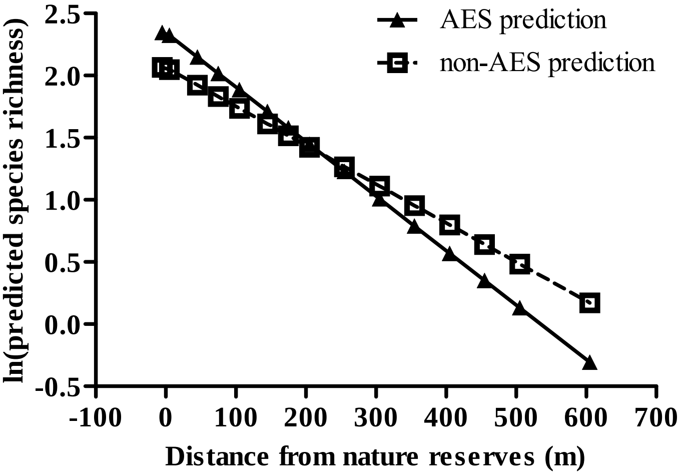

Fig. 5. Relationship between predicted species richness and distance using results of HGLM.

A non-linear relationship between distance from farm roads and species richness was found, while the distance from the path and species richness showed a linear correlation. The average road distance to the nearest study plot is 360 m (SD=226.6 m). For all other habitat variables, no significant effects were found on species richness.

Ecological traits

Flowering time and mean plant height are the only factors that seem to affect the impact of distance on plant presence (Table 5). The relatively strong relationship between initial flowering time and the effect of distance is an inverse U-shape, showing an optimum between May and June. So, species beginning to flower earlier or later in the season seems to be more strongly negatively affected by distance than species beginning to flower in May and June. Species that end flowering in July show a significantly less negative effect of distance than those that flower later in season. In addition, species with lower mean plant height show significantly stronger negative effects of distance than do higher ones.

The initial flowering time is the only ecological trait that seems to have a relationship with the difference in the intercept of the regression between species presence and distance between AES and non-AES ditch banks (Table 5). A strong inverse U-shaped relationship was found, with plants that flower in the middle of May showed the highest intercept in AES ditch banks. No relationship could be found between any ecological trait and the difference in regression coefficient between AES and non-AES ditch banks (Table 5).

Table 5. Relationship between plant species characteristics and estimated distance and management parameter from HGLM. Regression analyses were used for ordinal characteristics, one-way ANOVAs for nominal characteristics. N=16; *=p<0.05; **=p<0.01. ^{2}=quadratic term was significant and included.

Regression	Distance			Management					
				D_i			D_r		
	F	df	p	F	df	p-value	F	df	p
Nature value	0.06	1	0.81	0.32	1	0.58	1.15	1	0.31
Moisture (F)	0.001	1	0.98	0.14	1	0.72	0.03	1	0.87
Minimum light requirement (L)	0.16	1	0.69	0.29	1	0.59	1.85	1	0.19
Nutrient requirement (N)	0.84	1	0.37	2.75	1	0.12	0.002	1	0.96
Acidity (R)	0.98	1	0.34	1.93	1	0.19	0.29	1	0.59
Begin flowering time	11.28^2	2	0.01**	49.8^2	2	0.001**	0.69	1	0.42
End flowering time	5.05	1	0.04*	0.44	1	0.52	2.73	1	0.12
Self-pollination	0.08	1	0.78	0.97	1	0.34	1.61	1	0.23
Mean plant height	4.88	1	0.04*	0.9	1	0.36	0.045	1	0.84
ANOVA									
	F	df	p	F	df	p	F	df	p
Germination period	0.25	4	0.9	1.19	4	0.37	1.35	4	0.31
Dispersal type	0.43	3	0.74	0.59	3	0.64	0.78	3	0.53

Discussion

Species abundance and distance from nature reserve

Our results show clearly that density of each individual species as well as species richness decreases with distance from nature reserves. This is in concordance with recent findings of Kohler et al. (2008). Both studies show that distance from species-rich areas is crucial in the presence of plant species with linear landscape elements like ditch banks.

For most grassland plants, it is only within the first 50 m that colonization is likely to occur within one generation (Melman et al., 1991; Geertsema et al., 2002). Species that can germinate on ditch banks but cannot set seed there will be unable to "move" along the entire ditch banks. These species can be recognized by being absent at distances over 50 m. In our study this might be the case for *Caltha palustris* and *Pedicularis palustris*. All other species can be divided into two groups: those that occur along the entire banks and those that are no longer present on banks after a certain distance. In the first group, presences of each species decreased significantly with increasing distance from nature reserves but the trends differed. In our study, the species of the second group are *Filipendula ulmaria, L. pratensis, Lychnis flos-cuculi, Mentha arvensis* and *Veronica beccabunga*.

Our results showed that richness significantly decreased with increasing distance from the nature reserves. No important habitat variables, such as ditch bank width, ditch bank slope or nitrogen supply from adjacent field, which are supposed to influence species diversity, were found to be of significance in species diversity of the ditch banks. Some research has indicated possible farm house waste water effects on ditch bank vegetation (van Strien, 1989). The significant impact of farm roads and paths on species diversity we found confirmed the importance of human disturbance. All the farms and roads were located at the opposite end of the ditch banks from the nature reserves. However, because we included both distance from the nature reserve and distance to these places of human disturbance in our model, the gradient we found in species richness from nature reserves is not confounded by distance to farms roads and paths. Therefore, we conclude that the vicinity of a source population does enhance the species diversity on ditch bank vegetation and that, on the other hand, human disturbance has an independent influence on species diversity. The dependence of species richness on source populations in itself shows that the presence of plant species is at least partly limited by seed availability.

Species abundance and AES

Previous studies have found that it is difficult to enhance plant species diversity under AES (Cameron, 2001; Kleijn et al., 2001; Critchley et al., 2003). This conclusion is in contrast to our results that ditch banks under AES management were found to have a higher presence of most target species and a considerably higher species richness of (about 9%). A recent study showed that ditch banks under AES already had higher species richness at the beginning of AES implementation (Blomqvist et al., 2009). These results seem to suggest that a selection bias may exist, because farmers that have relatively high species diversities in their ditch banks may more readily join AES (Blomqvist et al., 2009). However, when comparing the differences between AES and non-AES ditch banks in relation to distances, we found the difference being clear only over the first 200 metres from the nature reserve. This means that, if a selection bias exists due to the higher plant species diversity in the ditch banks, it can only be based on the 200 metre nearest the nature reserves (i.e, on the 200 metres at the far end of the farms). But of course, farmers motivation also could be important, resulting in higher nature values on the farm in general, even long before AES were available.

Interaction between distance and AES: seed or site limitation

For studying the effect of the interaction between distance and AES on species presence and species richness, we calculated the difference in intercept and regression coefficient of the regression of distance on log-transformed probability of species presence or species richness between AES and non-AES ditch banks. This was based on a simple conceptual model describing seed abundance as having an inverse power relationship to distance. Willson (1993) found that in 85% of the species he studied, this power law described the relationship adequately. Visual check of our results also showed that in most cases (about 80%) the power law resulted in an almost straight line between ln(probability) and distance. We could have chosen for a complicated, but more general model (Le Corre et al., 1997; Nathan et al., 2001). However such models have many more parameters and the interpretation of these parameters in terms of site or seed limitation would have been problematic, if not impossible. For this reason, we kept our simple model and accepted that in some cases the relationship between presences and distance may not have been described adequately.

We found that the intercept of the relationship with distance was higher in AES ditch banks in all but one target species (Table 3), as well as in species richness

(Fig. 5). Our interpretation of this is that in general, site limitation is less in AES ditch banks. This is also supported by current management recommendations such as nutrient reduction are focussing on decreasing site limitation (Blomqvist et al., 2006). Species that start flowering in May seem to be less limited by site (Table 5). This suggests that the mechanism behind site limitation is the flowering time and time of seed setting. An obvious mechanism could be that plants can only survive in a ditch bank when they are able to set seed within that ditch bank. It is possible that plants that start flowering in May are the ones that are able to flower and set seed within the period between the first and second mowing (Blomqvist et al., 2006). The ecological mechanisms involved require further study.

Regression coefficients per species did differ in AES ditch banks, but no general pattern could be detected (Table 4). The differences in the regression coefficient should be regarded as the outcome of random processes, which is confirmed by our results of the analysis of the ecological traits (Table 5). We therefore conclude that AES does not change seed limitations for the species, and that the lower regression coefficient of species richness we found in AES ditch banks is not a sign for increased seed limitation, but an artefact of the log-transformation of an additive model. Our results confirm that, although seed limitation is an important factor in the species richness of ditch bank vegetation, Dutch AES for ditch banks in peat areas only affects species richness through site limitation, if it affects species richness at all.

Implications for conservation

Our results support the idea of the importance of nature reserves beside AES for ditch banks plant species richness (Blomqvist et al., 2003a; Soons et al., 2005; Maes et al., 2008; Kohler et al., 2008). Spatial planning of nature reserves and AES management would be helpful for plant restoration and the presence of nature reserves should therefore be given greater consideration in implementing management policy. On the other hand, the obvious limited distance of influences from nature reserves to surrounding, also found by Kohler et al. (2008), showed that seed limitation is still a problem. Further work addressing how to effectively arrange the spatial pattern of ditch banks in nature reserves and AES management is needed to determine the extent to which the ditch banks provide species refuge in a landscape of grassland fragments. Investigating the surrounding AES and non-AES ditch banks in the other direction of source population (parallel to nature reserves) might help to show the possible plant pattern on the whole mixed landscape.

The results suggest a potential benefit of the approach of increasing landscape connectivity through improving matrix quality using delivery systems such as AES (Donald and Evans, 2006; Maes et al., 2008). However, at the same time we found that present AES do not increase connectivity through decreasing seed limitation. AES should therefore be changed in such a way that they could decrease seed limitation. Since machines and cattle may transport seeds (Strykstra et al., 1997), they may be used for that: mowing could be such that machines are first used in nature reserves and then, without cleaning, in conventional ditch banks; the same animals could be let grazing in nature reserves as well as conventional fields. Another possibility is that mowing periods are changed such that all plants are able to set seeds. These plants could then function as sources of seeds for secondary or Phase II dispersal, which might greatly affect dispersal distances (Nathan and Muller-Landau, 2000), although the effects on pollination distances might be limited (Kohler et al., 2008).

Acknowledgements

We are grateful to the farmers who allowed us to carry out the experiments: F. Bakker, M. Boele, K. Both, W.S. Both and N. Both-de Jong, C. Bruynes, A. den Besten, K. de Vor, S. de With, T. de With, J. Kon, A. Kool, G. Kool, W. Markus, A. Noorlander, D. Terlouw, A.H. Tober, P.C. van den broek, A. van der Stouwe, T. van Es, P.M. van Leeuwen, A. van Weverwijk, P. Verhoef, J. Verkaaik, and A. Voogd. We wish to thank N. Brouwer and L. van Hoven of the farmers' collectives 'Den Hâneker' and 'Weidehof', respectively, and R. Terlouw and D. Kerkhof of the Zuid-Hollands Landschap for providing us with the necessary information and licenses. We also thank E.R. Gertenaar, M. Bok, T. Hofman and J. Maes for helping carrying out the experiments. And finally, we thank N. Harle for correcting and improving the English of this article.

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Appendix. Overview of target species with their characteristics. Nature value: Clausman and van Wijngaarden (1984). L, F, N, R from Ellenberg et al. (1992); Wiertz (1992); Hill et al. (1999). L: shade tolerant(6), intermediate(7), light demanding(8); F: indifferent(×), dry(4-6), moist(7-8), wet(9); N: indifferent(×), oligotrophic(1-4), mesotrophic(5-6), eutrophic(7-9); R: indifferent(×), acidneutral(2-6), neutralalkaline(7-9). Dispersal type: Grime et al.(1988); Van Dorp (1996); Pakeman et al. (2002). All other characteristics from Biobase (CBS, 2003). Flowering period: month number. Lumped taxa * *Myosotis arvensis* and *Myosotis discolor*.

Species name	Nature value	Minimum light Requirements (L)	Moisture (F)	Nutrient Requirement (N)	Acidity (R)
Achillea ptarmica	42	8	8	2	4
Caltha palustris	36	7	9	×	×
Centaurea jacea	35	7	×	×	×
Cirsium palustre	37	7	8	2	4
Filipendula ulmaria	31	7	8	4	×
Galium palustre	35	6	9	4	×
Hydrocotyle vulgaris	40	7	9	2	3
Hypericum perforatum	31	7	4	3	6
Iris pseudacorus	40	7	9	7	×
Lathyrus pratensis	32	7	6	6	7
Leucanthemum vulgare	39	7	4	3	×
Lotus uliginosus	40	7	8	4	6
Lychnis flos-cuculi	44	7	7	×	×
Lycopus europaeus	29	7	9	7	7
Lysimachia thyrsiflora	37	7	9	3	×
Lythrum salicaria	31	7	8	×	6
Mentha arvensis	37	7	8	×	×
Myosotis[*]	40	7	9	6	4
Pedicularis palustris	60	8	9	2	×
Potentilla palustris	41	8	9	2	3
Prunella vulgaris	31	7	5	×	7
Ranunculus flammula	43	7	9	2	3
Rhinanthus angustifolium	44	7	6	2	7
Veronica beccabunga	39	7	10	6	7
Vicia cracca	25	7	5	×	×

Germination period	Mean plant height	Self-pollination	Dispersal type	Begin Flowering time	End Flowering time
Spring	60	Non-self	wind	7	8
Late spring	32.5	Non-self	water	4	11
Late Summer	65	Self	wind	6	9
Early summer	105	Self	wind	6	8
Late spring	90	Self	water	6	8
Autumn	27.5	Self	water	5	9
Spring	15	Non-self	water	7	9
Spring	50	Self	water	6	8
Early summer	80	Non-self	water	5	9
Autumn	75	Non-self	unassisted	6	7
Late summer	45	Self	unassisted	5	8
Spring	65	Non-self	unassisted	6	9
Direct	60	Self	wind	5	11
Early summer	60	Self	animals	6	10
Late spring	45	Self	water	5	9
Spring	90	Non-self	water	6	7
Late spring	30	Non-self	water	7	7
Spring	25	Self	animals	5	9
Late spring	32.5	Non-self	wind	5	11
Late spring	60	Non-self	unassisted	6	11
Early autumn	26	Self	animals	5	9
Direct	27.5	Self	water	6	8
Spring	45	Non-self	animals	5	7
Late spring	37.5	Self	animals	5	11
Direct	115	Non-self	unassisted	6	10

Chapter 5

Synergy between nature reserves and agri-environment schemes in enhancing ditch bank target species plant diversity

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In press, *Biological conservation*

Abstract

The issue of what conservation strategies to apply in agricultural landscape for the most effective protection of biodiversity has been debated for some years. The creation and maintenance of nature reserves is often hampered by both ecological and economic factors, while the ecological effectiveness of agri-environment schemes (AES) still being queried. Our study examined how the spatial pattern of nature reserves and AES affects the diversity of 25 target species of conservation interest in ditch banks and how this information might be used to develop a strategy resulting in synergy between protected areas and enhanced matrix quality. We studied target species plant diversity on 92 ditch banks under AES and on 102 banks not under such a regime; all of them running parallel to nature reserves. We compared the results with those obtained from a previous study which focused on ditch banks running transverse. On non-AES ditch banks running parallel to nature reserves, there was a significant decline in species richness with increasing distance from the nature reserve while this was not the case for AES ditch banks. The effect of AES differed between the two directions, with a significant effect beyond 200 m in the parallel direction and within 200 m in the transverse direction. Our results indicate that synergy between nature reserves and AES can enhance plant diversity and, since the AES effect was different in different direction due to wind direction and nitrogen input to adjacent fields, location of AES should be chosen carefully.

Introduction

In the last few decades there has been a dramatic decline in the biodiversity of agricultural landscapes (Stoate et al., 2001; Gregory et al., 2004), with increasingly intensive agricultural practices leading to substantial losses of natural habitats and species diversity (Benton et al., 2003; Duelli and Obrist, 2003; Tscharntke et al., 2005). In an attempt to conserve diversity, the creation of protected areas has become a fundamental element of conservation strategies (Richardson et al., 2006). One of the key problems faced in all efforts to maintain and enhance biodiversity by establishing such areas is how their spatial arrangement can be designed most cost-effectively (Andelman and Willig, 2002; Drechsler et al., 2007; Wikberg et al., 2009). One important factor in this context is obviously the distance between protected areas. The optimum distance will depend on the quality of the intervening matrix: a landscape with greater permeability for species will allow protected areas to be spaced further apart. In examining the issue of spatial arrangement, this study focused on the potential interplay of the two main conservation strategies employed in modern agricultural landscapes: *nature reserves*, i.e. protected areas, and *agri-environment schemes* designed to improve the quality of the matrix for plant species.

Nature reserves, which in agricultural landscapes harbour a broader range of plant and animal species than the surrounding area (Kremen et al., 2004), are a potential source of biodiversity for the wider matrix (Soons et al., 2005; Kohler et al., 2008; Leng et al., 2009). However, it is obviously out of the question to designate an entire farming region as nature reserves. High land prices and conflicting land user interests are the main issues, especially in densely populated areas. In the Netherlands, for instance, the conservation areas still remain so fragmented that the effectiveness of nature reserves is fairly limited (MNP, 2007). The maintenance and enhancement of biodiversity is still hampered by the small area of many reserves and by the fact that in today's fragmented landscapes many plant dispersal processes have been disrupted (Ehrlen et al., 2006; Kiviniemi, 2008; Ozinga et al., 2009).

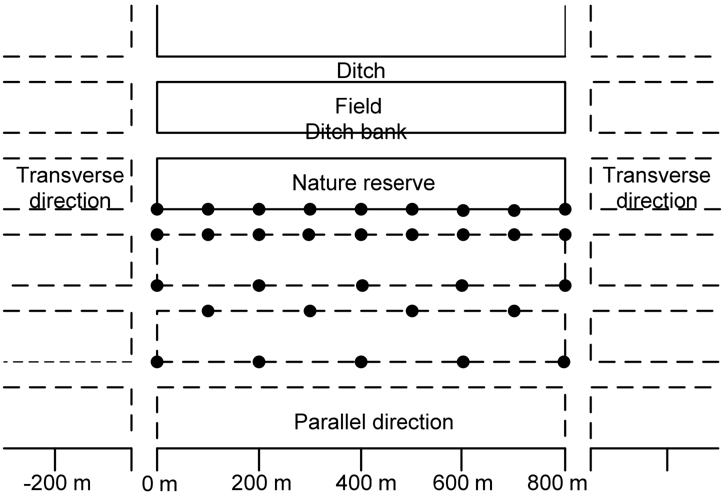
Agri-environment schemes (AES), introduced in many European countries in the 1990s, are to protect the diversity of (farmland) species and habitats by offering farmers financial incentives to use 'nature-friendly' agricultural practices on certain parts of their land (Whittingham, 2007). Their effectiveness is still being debated (Kleijn and Sutherland, 2003; Musters et al., 2009). One important impediment to improve plant diversity on farmland might be seed limitation (Zobel et al., 2000; Blomqvist et al., 2003). At locations where the seeds of many species have been lost from the seed bank (Bissels et al., 2005), seed influx from nearby species-rich source habitats like nature reserves appears to be an essential precondition for restoring plant diversity (Rosenthal, 2006; Kohler et al., 2008; Leng et al., 2009).

In the Netherlands ditch banks with a total length of 300,000-400,000 km are an important feature of the agricultural landscape (Higler, 1994). AES are often implemented on these banks, with mandatory provisions including no fertilizer use, no deposition of ditch sediment or plant remains on the banks, reduced ditch-cleaning frequency, postponed mowing and a grazing regime at the start of the season (Kleijn et al., 2004). Leng et al. (2009) has evaluated the importance of nature reserves for the plant diversity of ditch banks influenced by AES along ditches running transversely from a nature reserve to the farmland, with positive effects being found within the first 200 m. This leaves unanswered question of trends in plant diversity along banks running in other directions, a common feature in the Netherlands, so that there is still no clear picture of the impact of the entire network of nature reserves, AES and ditch banks (Fig. 1a).

In this research we test a set of hypotheses concerning whether there might be synergistic effects of nature reserves and AES on plant species within a network of ditch banks in the Western Peat District of the Netherlands, a country with an extensive network of ditches and one of the most intensively exploited regions in Europe. By focusing on plant diversity on AES and non-AES ditch banks running parallel to the edge of nature reserves and comparing the results with the findings of research on transverse ditch banks (Leng et al., 2009), we attempted to identify the aggregate influence of the entire mixed landscape of nature reserves and AES.

Specifically, we tested the following hypotheses. First, because of its association with seed limitation, we predicted that the plant diversity on successive ditch banks running parallel to a nature reserve might exhibit a declining gradient according to distance from the reserve. Given the effect of lower nutrient input (Blomqvist et al., 2003), we also predicted that ditch banks under AES would have higher plant diversity than those under non-AES. Second, human disturbance and wind direction might be important factors contributing to plant diversity (Leng et al., 2009). In the ditch banks with less human disturbance and suited on the downwind direction of a seed source, the plant diversity is expected to be high. We thus predicted that the association between plant diversity and distance to nature reserve might differ between ditch banks running transverse and parallel to a nature reserve and AES might show different pattern of plant diversity in the two directions. We focused on 25 target species that have been designated as valuable ditch bank plants by the Dutch government.

(a)



(b)

Fig. 1. (a) Landscape of Middelblok Polder in the Western Peat District of the Netherlands, with the nature reserve delineated in black (from Google Earth). **(b)** Sketch of the Middelblok polder, with ditch banks in the reserve and surrounding area depicted as solid and dashed lines, respectively; the sampled plots were ditch bank sections with a length of 10 m and a width depending on ditch bank width.

Methods

Study area

The study area Krimpenerwaard is located in the Western Peat District of the Netherlands. Most of the farmland here is grassland used either for hay-making or as pasture for dairy cattle and sheep. The soils are mainly peat or peat with clay. The fields are long and narrow, varying in width between 30 and 60 m, and are all separated by ditches 1-4 m wide. The field edges (ditch banks) are 0.8-1.5 m wide, with slopes ranging from 15º to 20º. The nature reserves in this region are mainly grassland and have been chose to protect plant diversity and meadow birds in nutrient-poor habitats (Fig. 1a). Ten nature reserves (Table 1) were selected, with a size of 42 ± 48 ha (average ± SE). On the surrounding farmland we investigated ditch banks managed under AES (n = 92) and those that were not (n = 102). The duration of AES management varied, with a mean of 10 ± 3 years. A total of five nature reserves had only AES ditch banks in its surrounding in the parallel direction, four reserves had only non-AES ditch banks, and one reserve had both.

Table 1. Number of ditch banks investigated in Krimpenerwaard in 2007. In the Middelblok, Kattendijksblok and de Nesse polders two nature reserves were selected, in one of which both the downwind and upwind direction were investigated.

Reserves	Parallel to nature		Transverse to nature	
	AES	non-AES	AES	non-AES
Bilwijk	4	11	3	3
Polder Middelblok 1	14			
Polder Middelblok 2, upwind		17	3	3
Polder Middelblok 2, downwind		12		
Polder Kattendijksblok 1	20		3	3
Polder Kattendijksblok 2, upwind	14			
Polder Kattendijksblok 2, downwind	9			
Polder de Nesse 1	15			
Polder de Nesse 2, upwind		16		
Polder de Nesse 2, downwind		12		
Polder Krommer		16		
Polder Berkenwoude		18		
Berkenwoudse Driehoek	16		3	3
Total	92	102	12	12

Study design

Data were collected from the ditch bank boarding the nature reserve and from successive ditch banks parallel to the nature reserve. The sample size we used is commonly applied in ditch bank analysis (Leng et al., 2009): bank width x 10 m long plots. Bank width is on average 1.15 ± 0.07 m. On the ditch bank bordering the nature reserve as well as on the first following ditch bank we marked off nine replicate plots at regular intervals of 100 m from one end (Fig. 1b). From the second ditch, we defined the two ditch banks of the same ditch as one since our previous study indicated that there was no significant effect of the different sides of the ditch on species richness. Therefore, four or five replicate plots on each side of a ditch were investigated at regular intervals of 200 m, marking nine replicate plots per ditch to represent each distance from nature reserves (Fig. 1b). Sampling was carried out from May 15th to July 15th, 2007.

Target species surveys and habitat variables

As stated, we focused on all 25 target species that based on a list of valuable plants used by the Dutch government. These species are easy to recognize and their presence is used in rewarding farmers for AES implementation. On each plot the vegetation variables recorded were the presence of each individual target species and the total number of target species (species richness). Of the 25 target species, 19 species were found in our study. Nine of them are water-dispersed species: *Caltha palustris*, *Filipendula ulmaria*, *Galium palustre*, *Hydrocotyle vulgaris*, *Iris pseudacorus*, *Lysimachia thyrsiflora*, *Lythrum salicaria*, *Mentha arvensis*, *Ranunculus flammula*; three are wind-dispersed species: *Cirsium palustre*, *Lychnis flos-cuculi*, *Pedicularis palustris*; four are animal-dispersed species: *Lycopus europaeus*, *Myosotis* (*Myosotis arvensis* and *Myosotis discolor* were lumped), *Prunella vulgaris*, *Rhinanthus angustifolium* and the last three are unassisted-dispersed species: *Lathyrus pratensis*, *Lotus uliginosus*, *Vicia cracca* (Grime et al., 1988; Van Dorp, 1996).

A large amount of habitat variables relative to habitat parameters and management which potential influence on plot vegetation were measured (Van Strien et al., 1989; Geertsema and Sprangers, 2002). Habitat parameters include ditch bank width, ditch water level below the field surface and ditch bank slope. On non-AES ditch banks, farmers were free to choose the kind of management adopted, while on all types of AES ditch banks a similar management regime is recommended or applied, as described in the Introduction. Management indicators such as mowing time and nitrogen supply to adjacent fields were established in interviews with farmers. The distances to the roads where the farm houses are located were also measured due to possible human disturbance. As plant diversity is possibly influenced by wind direction, which in the Netherlands is mainly from south-west to north-east, we categorised nature reserves as being either on the south-west side (upwind location) or north-east side (downwind location) of the plot under consideration. Beside nature reserves, the other seed sources such as woodlots were also considered.

Statistical analysis

The relationships between the vegetation variables per plot (species richness and the presence or absence of individual species) and possible variables affecting plot vegetation were tested by HGLM (Hierarchical Generalized Linear Model; GENSTAT 10.0). HGLM was used in our study since the vegetation variables are assumed to have a Poisson (richness) or Binominal (individual species) distribution, and our ditch banks and neighbouring nature reserves were assumed to be a random sample of all possible locations (Lee and Nelder, 2001). In all HGLM analyses, ditch bank nested within reserve was thus added as a random factor.

For each plot on the successive ditch bank parallel to the nature reserve, the variables and factors listed in Table 2 were used in a HGLM (analysis 1) to test changes in species richness as a function of distance from the reserve. Species richness was taken as the dependent variable, while distance, management, their interaction, and other variables of potential influence on species richness were taken as independent variables and included in the fixed part of the model. To detect non-linear relation, quadratic terms of each distance variable were also included. Because of inability of resolving the models, only the independent variables that were found to be significant in the previous analysis of species richness was tested on presence of individual species using HGLM (analysis 2). For that, the presence or absence of each species was regarded as response variable and the fixed model consisted of the independent variables mentioned above. Because *C. palustris*, *H. vulgaris*, *P. vulgaris* and *R. angustifolium* were rare in our study area, they were not analysed in the model, so that finally 15 individual species were tested. Wald test in HGLM was used to test a fixed effect on individual species by leaving out this fixed variable from the HGLM. The results of these two analyses enable us to test whether plant diversity decreased with increasing distance from nature reserves, to what extent plan diversity was higher under AES, and whether individual species differed in these aspects (Hypothesis 1). We further used Mann-Whitney U-test to investigate whether species richness was significantly different in different distance categories (we defined each 100 m from nature reserve as a category).

Whether plant diversity differs between AES and non-AES ditch banks running transverse and parallel to the nature reserve (Hypothesis 2) were also tested in HGLM. To avoid the influence of time as well as regional differences, we used only the 2007 data of the Krimpenerwaard from our previous study on ‘transverse’ ditch banks (Table 1). For species richness (analysis 3), the variables found to significantly affect species richness in the transverse and parallel direction individually were added as fixed factors. As ditch water level might also potentially affect ditch bank biodiversity (Van Strien et al., 1989), this was also included as a fixed factor. For the presence or absence of species (analysis 4), the variables found to significantly affect species richness in analysis 3 were added as fixed factors. The Mann-Whitney U-test was again used to compare the species richness per distance category and independent variables between transverse and parallel direction.

Results

Species diversity pattern on parallel ditch banks

Of the 25 target species considered, 19 were observed on the ditch bank bordering nature reserves and 18 on the surrounding ditch banks. *P. vulgaris* was found only bordering nature reserves. The mean species richness bordering reserves was 6.95 (SE = 0.28). The mean species richness on AES ditch banks was found to be 6% lower (6.57 ± 0.18) and on non-AES banks 11% lower (6.16 ± 0.23) than the ditch bank bordering nature reserves.

On non-AES ditch banks parallel to the nature reserve, species richness declined significantly with distance from the reserve, over and against no significant relationship for AES banks (Fig. 2, analysis 1, significant management x distance interaction in Table 2). Presence of most individual species also declined with distance (data not show, analysis 2). The differences between AES and non-AES ditch banks tended to increase with distance from the reserve. On AES ditch banks considerably higher species richness was found at distances of 200-300 m and 300-400 m.

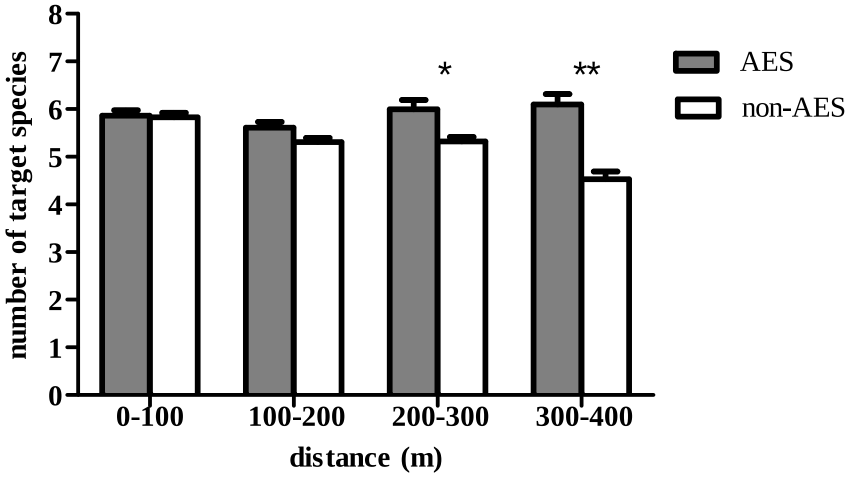


Fig. 2. Relationship between distance and species richness on AES (closed bars) and non-AES (open bars) ditch banks running parallel to a nature reserve. Bars indicate mean values ± SE; * = p<0.05; ** = p<0.01 (Mann-Whitney U-test).

Table 2. Results of HGLM analysis for the effect of distance, management and habitat variables on ditch banks running parallel to a nature reserve. Management (class 1: AES; class 2: non-AES); Nitrogen supply on the adjacent field (class 1: 0-200 kg $ha^{-1}year^{-1}$; 2: 200-300 kg $ha^{-1}year^{-1}$; 3: 300-400 kg $ha^{-1}year^{-1}$; 4: 400-500 kg $ha^{-1}year^{-1}$); Reserve location (class 1: nature reserve suits on the south-west side of parallel ditch banks (downwind parallel direction); class 2: nature reserve suits on the north-east side of parallel ditch banks (upwind parallel direction)); Other seed source (class1: no other seed source; class 2: seed source such as woodlots). Lambda estimates represent the random part of the model. * p<0.05; *** p<0.001.

	Species richness		
	estimate	SE	t
Constant	2.54	0.65	3.92***
Distance from nature reserve	0.005	0.0052	1.05
Square distance	0.0001	0.0001	-0.22
Management	0.039	0.049	0.78
Management*Distance	-0.012	0.003	-3.59***
Distance from farmhouse	0.0003	0.0008	-0.34
Square distance from farmhouse	0.0001	0.0001	0.23
Ditch bank width	0.81	1.06	0.76
Ditch bank slope	-0.096	0.11	-0.91
Ditch water level below field surface	0.23	0.14	1.75
Mowing time	0.031	0.044	0.71
Nitrogen supply	-0.069	0.015	-4.67***
Reserve location	-0.11	0.042	-2.37*
Other seed sources	0.048	0.045	1.07
Estimates from the dispersal models:			
phi	-1.23	0.045	-27.57***
Lambda reserve	-5.78	0.55	-10.51***
Lambda reserve*ditch bank	-5.45	0.18	-30.48***

Higher species richness was correlated to lower nitrogen input to the field adjacent to the ditch bank (analysis 1, Table 2), while mean species richness was significantly higher within 100 m when the nature reserve was on upwind location compared to downwind location (Fig. 3, analysis 1, Table 2). A significantly positive effect of upwind nature reserves location was found on two water-dispersed species *F. ulmaria* and *L. salicaria* (p = 0.009 and p = 0.03, respectively; Wald test) and one wind-dispersed species *L. flos-cuculi* (p = 0.03; Wald test) (analysis 2).

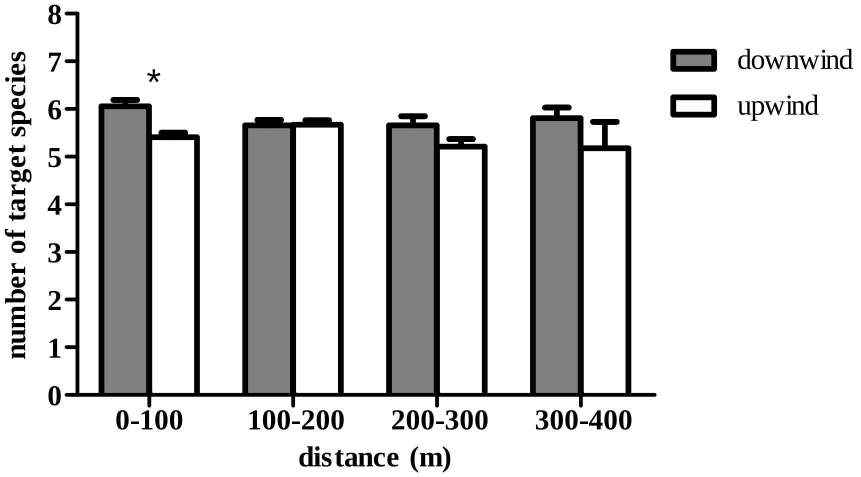


Fig. 3. Relationship between distance and species richness in the downwind (closed bars) and upwind (open bars) parallel direction. Bars indicate mean values ± SE. Differences between**)** downwind and upwind parallel direction were tested with Mann-Whitney U-test; * = p<0.05.

Species diversity on parallel and transverse ditch banks

The transverse ditch banks showed a significantly greater number of species between 0 and 100 m from the reserve than parallel ditch banks. From 100 m onwards, however, species richness was lower, becoming significantly lower at a distance of 200 m. In the parallel direction, the decline in species richness was far less pronounced than along ditches extending in the transverse direction (Fig. 4). Both AES and non-AES ditch banks showed a significantly different change of species richness with distance from nature reserve according to whether they were transverse or parallel (analysis 3, Table 3).

A significant difference in correlation between species richness and distance from the farmhouse between the transverse and parallel direction was found: in the transverse direction the correlation was lower than in the parallel direction (analysis 3, Table 3). Nitrogen input, which showed no change along the transverse ditch banks but a significant change along the parallel banks, was found to have a significant effect on species richness. The level of the ditch water below the field surface, which showed no changes in either the transverse or parallel ditches, had a significant effect on species richness when the two directions were included in the model. In the parallel ditches the distance between ditch water level and field surface was found to be significantly greater (0.58 ± 0.07) than in the transverse ditches (0.49 ± 0.11) ($p < 0.01$, Mann-Whitney U-test). Moreover, 8 of 15 species had significant effects of ditch water level, two were positive (*Myosotis* and *P. palustris*) and six were negative (*C. palustre*, *I. pseudacorus*, *L. pratensis*, *L. uliginosus*, *M. arvensis* and *R. flammula*) (data not show, analysis 4).

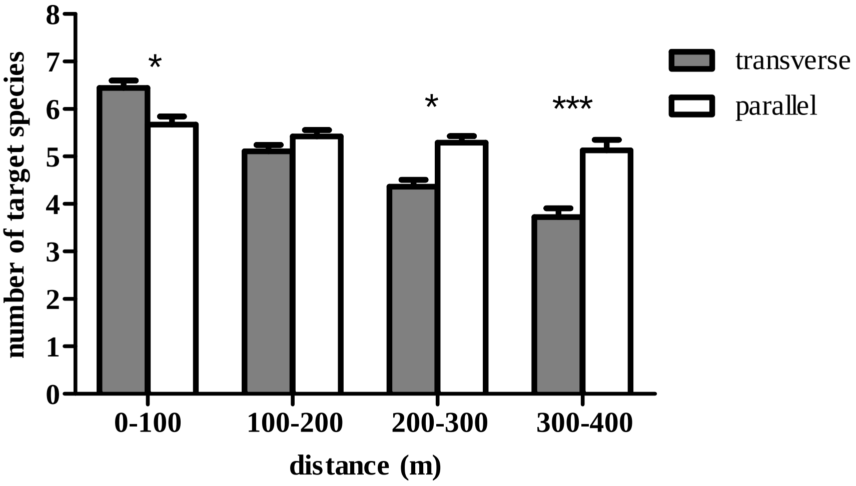


Fig. 4. Relationship between distance and species richness on ditch banks transverse (closed bars) and parallel (open bars) to a nature reserve. Bars indicate mean values ± SE. Differences between transverse and parallel direction were tested with Mann-Whitney U-test; * = p<0.05; *** = p< 0.001.

Table 3. Results of HGLM analysis for the effect of distance, management and potential habitat variables on ditch banks transverse and parallel to a nature reserve. Management (class 1: AES; class 2: non-AES); Nitrogen supply on the adjacent field (class 1: 0-200 kg ha^{-1}year^{-1}; 2: 200-300 kg ha^{-1}year^{-1}; 3: 300-400 kg ha^{-1}year^{-1}; 4: 400-500 kg ha^{-1}year^{-1}). Lambda estimates represent the random part of the model. * = p<0.05; ** = p<0.01; *** = p<0.001.

	species richness		
	estimate	SE	t
Constant	2.22	0.08	26.37***
Distance from nature reserve	-0.01	0.004	-3.15**
Square distance	0.0002	0.00005	4.57***
Distance*Management	-0.009	0.0038	-2.49*
Distance*non-AES* upwind parallel	0.008	0.0044	1.74
Distance*non-AES*transverse	-0.02	0.0039	-4.44***
Distance*AES* upwind parallel	0.01	0.0031	4.43***
Distance*AES*transverse	-0.005	0.0025	-2.02*
Distance from farmhouse	0.002	0.00049	-4.22***
Distance from farmhouse*direction	0.0017	0.00041	4.09***
Ditch water level blow field surface	-0.18	0.075	-2.37*
Nitrogen supply	-0.063	0.011	-5.68***
Estimates from the dispersal models:			
phi	-1.31	0.039	-32.91***
Lambda reserve	-4.61	0.45	-10.31***
Lambda reserve*ditch bank	-5.29	0.15	-34.94***

Predicted species diversity on parallel and transverse ditch banks

With respect to the predicted species richness indicated by HGLM, for non-AES ditch banks we found a different pattern of species diversity on the surrounding of nature reserves (Fig. 5; Fig. 6a). In particular, species richness was greater in the downwind parallel direction. For example, six species were predicted up to 425 m in the downwind parallel direction. The same number of species was found up to 87 m in the transverse direction and up to 186 m in the upwind parallel direction. Figure 6b shows the difference in species pattern between AES and non-AES ditch banks running transverse and parallel to the nature reserve. In the transverse direction this difference between AES and non-AES ditch banks becomes smaller further from the reserve, while in the parallel direction it increases. Comparison of species richness downwind and upwind parallel direction indicated that the effects of differences in management regime extended further in the downwind direction.

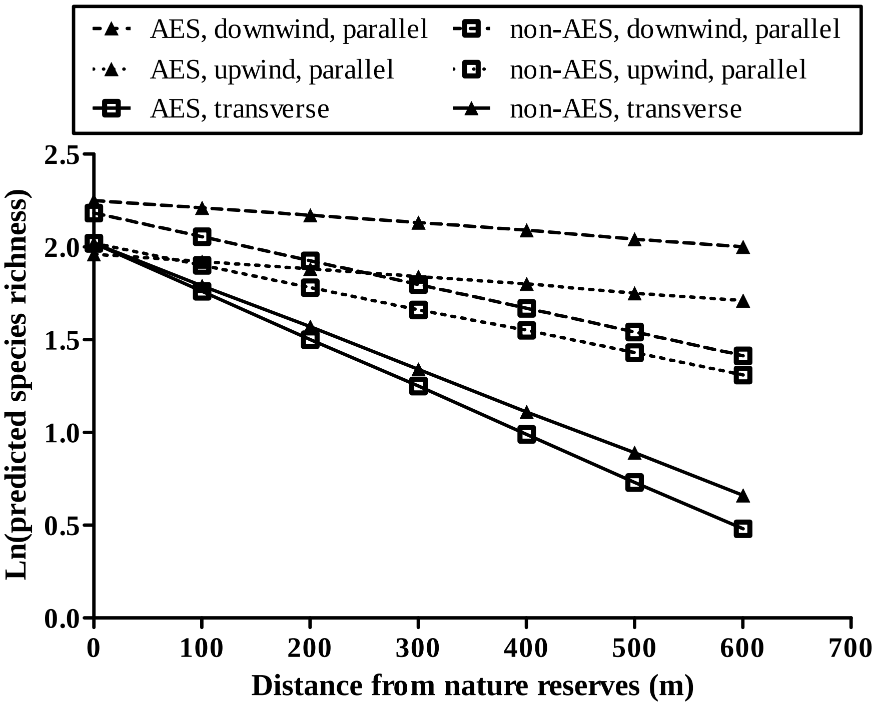


Fig. 5. Relationship between distance from nature reserve and species richness as predicted by HGLM.

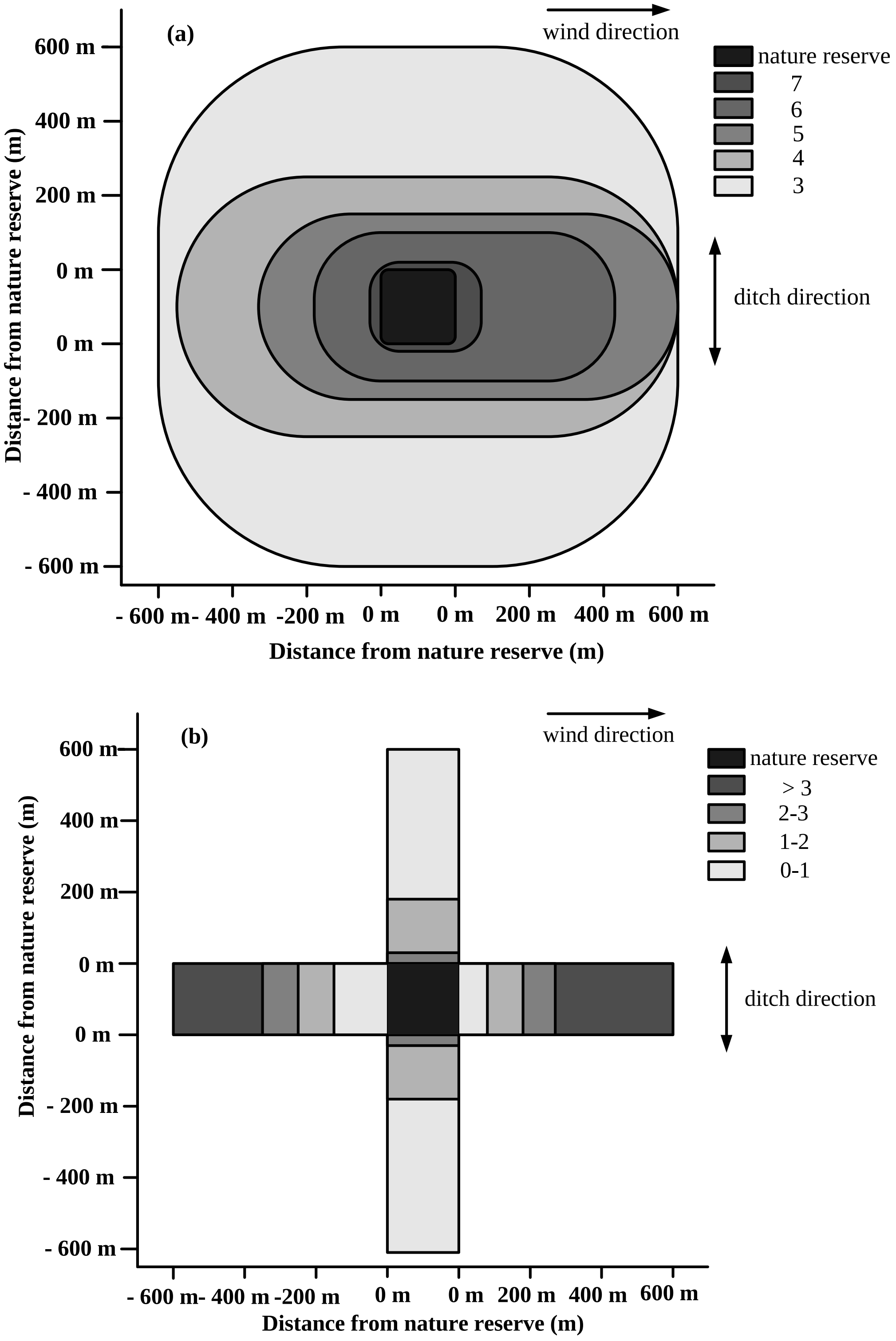


Fig. 6. (a) Relationship between distance and HGLM-predicted species richness on non-AES ditch banks; numbers in legend = number of target species. **(b)** Relationship between distance and HGLM-predicted difference in species richness between AES and non-AES ditch banks transverse and parallel to a nature reserve; numbers in legend = difference in number of target species between AES and non-AES ditch banks.

Discussion

Pattern of plant diversity parallel to a nature reserve

In the Western Peat District of the Netherlands within nature reserves, lower nutrient levels and limited grazing intensity are being applied in order to enhance plant diversity. Our results show that species richness on the ditch bank bordering nature reserves is higher than on the other ditch banks, whether these are under an AES regime or not, and that a species like *P. vulgaris* was found only bordering nature reserves. Nature reserves might therefore act as a source of plant diversity for nearby ditch banks. The precise contribution of nature reserves to regional plant diversity is generally hard to assess, however, as little is known about the dispersal capacities of individual plant species (Duelli and Obrist, 2003). We, therefore, further investigated plant diversity on AES and non-AES ditch banks parallel to the nature reserves to test for possible effects in this respect. As we hypothesized, on non-AES ditch banks species richness declined significantly with increasing distance from the reserve, thus confirming that species-rich sites (nature reserves) can serve as a source for the surrounding area. This is in agreement with the results of Kohler et al. (2008) and Leng et al. (2009), who demonstrated that distance from species-rich sites is an important determinant of species diversity in linear landscape features like ditch banks.

However, Geertsema (2005) suggested that colonization distances of most of the target species considered here is no more than 150 m from source (e.g. *G. palustre, I. pseudacorus, L. vulgaris* and *L. flos-cuculi*). The ditch banks parallel to the nature reserves are separated by fields with a width of 30-60 m, and species growing on the bank directly bordering the reserve may have difficulty moving to the next bank. Even if nature reserves can function as a seed source for the immediate surroundings, then, these seeds may fail to reach locations further away. Our results indicate that upwind nature reserve location has a distinctly positive impact on plant diversity. The parallel ditch banks situated downwind of a nature reserve were richer in species than those upwind, especially within the first 100 m. This might suggest that wind direction amplifies the effect of a nature reserve, by increasing seed dispersal distances. However, the positive effect of the downwind direction was not only found in wind-dispersed species. Two water-dispersed species showed the same positive relation to the wind direction. One possible explanation is that the downwind direction helped water flow and thus increasing dispersal distance of water-dispersed species. Nitrogen supply to adjacent fields had a negative impact on plant richness, confirming the results of several previous studies (Melman and van

Strien, 1993; Manhoudt et al., 2007; Blomqvist et al., 2009). Lower nitrogen inputs on these fields induce greater plant diversity by reducing site limitation pressure on certain species. On the ditch banks parallel to the nature reserve, other key habitat variables such as ditch bank width and slope were found to have no significant impact on plant diversity.

An effect of ditch bank management on the correlation between species richness and distance from nature reserves was found. At distances of over 200 m from the nature reserve, species richness was higher on AES than on non-AES ditch banks. In other words, the positive effects of agri-environment schemes appear to be relatively pronounced in the parallel direction, even at a considerable distance from the nature reserve. However, the higher diversity under AES observed in our study might also be due to a ‘selection effect’, for several studies report that some farmers may opt to apply AES management on fields with a high species diversity (Kleijn and van Langevelde, 2006; Matzdorf et al., 2008; Blomqvist et al., 2009).

Pattern of plant diversity parallel and transverse to a nature reserve

On the parallel ditch banks, a lower decline in species richness with distance from the nature reserve than on the transverse banks was observed, which supports our second hypothesis. Plant diversity in the parallel direction was influenced by distance to the reserve, while in the transverse direction it was also related to distance to the farmhouse (Leng et al., 2009). In the latter case, human disturbance around the farmhouse may be the cause of lower species richness. Ditch water level below the field surface was different for the parallel and transverse ditches. Ditch banks with a greater distance between water and surface level tended to have more species, which contrasts with the findings of Van Strien et al. (1989). Their study investigated the whole vegetation while our study only focused on 25 target species, which might also explain the discrepancy. Furthermore, in Van Strien’s paper, ditch water level was categorized according to a wider scale as 15-40 cm, 40-50 cm and 50-80 cm. In our study, the difference in ditch water level between the two directions was only 10 cm on average, however, falling within 50-80 cm category of Van Strien et al. in both cases. Our differences in water level are thus on a completely different scale to those studied by Van Strien et al. The effect of ditch water level differed among species and was not depending on dispersal strategy. It has been demonstrated in numerous studies that seed dispersal is related to water levels in certain types of vegetation (Andersson and Nilsson, 2002; Boedeltje et al., 2004). Whether our results indicate a causal relationship between water level and species richness is an issue requiring further study.

The effect of AES management was markedly different in the transverse and parallel direction. In the transverse direction it is limited to 200 m, while in the parallel direction it was significant at this distance. The effect of AES appears to be greater in the parallel direction. If the ‘selection effect’ is indeed the cause of the AES effects, this would still mean that parallel ditch banks differ more markedly in species richness than transverse banks. These two directions showed different effects of nitrogen input to the adjacent field. Nitrogen supply had no effect on species richness on the transverse ditch banks but a significantly negative effect on the parallel banks, suggesting greater differences in land use intensity in the parallel direction. Although the ditch banks themselves were not fertilized directly and relatively lower fertilizer inputs were applied in the field under AES, it is unclear to what extent nutrients applied by neighbours could have an impact through joint use of drainage ditches (Kleijn et al., 2004; Smits et al., 2008). In our study it was observed that the areas with AES ditch banks in the transverse direction were seriously fragmented, generally involving clusters of 5-6 together, while all the AES ditch banks parallel to the nature reserve were in clusters of at least 14-15, except in Bilwijk. The relatively greater fragmentation of AES management may impede its efficacy (Geertsema, 2005; Soons et al., 2005; Donald and Evans, 2006; Gabriel et al., 2006; Smits et al., 2008). Several studies have shown that application of AES cannot alleviate the pressure of seed limitation, which plays an important role in species richness (Zobel et al., 2000; Blomqvist et al., 2003; Leng et al., 2009). Further studies on the process of seed dispersal would help elucidate the process behind the patterns of species diversity observed in our study.

Implications for management

The results of this study provide new insights of relevance for the design and implementation of conservation networks for plant diversity on ditch banks. First, our results suggest that plant diversity may be enhanced by the synergy between species-rich grasslands and AES. On the ditch banks running transverse to a reserve the impact was relatively minor and limited to a distance of 200 m, while on the banks running parallel the effect appears to be greater at distances of over 200 m. Priority should therefore be given to implementing AES on the banks of parallel ditches at some distance from a nature reserve. Second, species richness also appears to be affected by several other factors, such as location relative to wind direction and nitrogen input on adjacent fields. Downwind parallel direction as well as fewer nitrogen fertilizer applications on adjacent fields may consequently lead to conservation of a wider diversity of plant species by means of AES. Third, we observed that AES ditches running parallel to a nature reserve had greatly enhanced plant diversity even 400 m from the reserve. The underlying ecological mechanism requires further study. It is worth investigating whether the effects of AES adjacent to nature reserves would be enhanced by expanding the size of the AES area, as several studies have demonstrated that fragmentation would be a problem for nature reserves and our study found greater species diversity in larger stretches of AES areas (Geertsema, 2005; Gabriel et al., 2006; Smits et al., 2008). In our view, then, farmers implementing AES would be more successful if they selected ditch banks adjacent to those where a similar management regime is already in force.

Figure 6a shows the species diversity pattern around nature reserves based on our predicted species richness, while Figure 6b shows the effect of AES on ditch banks transverse and parallel to a nature reserve. Together, these figures provide an impression of species diversity in a network of nature reserves and AES areas. For spatial planning purposes we recommend that AES be preferentially implemented in the parallel direction, especially downwind of nature reserves. Since the impact of AES in this direction was greater beyond a distance of 200 m from the reserve, we suggest management plans should target ditch banks beyond this distance.

Acknowledgements

We are grateful to the farmers J.M. Oudenes, J.P. Verkaik, Th.A. Holierhoek, M. Verzuilen, G. de Groot, D. Leede, J. Anker, G. de Jong, M. Verkaik, M.C.M. Gille, P.G. Blanden, I. Halling, H. Hogendijk, A. Hogendijk, V. Noordergraaf, K.A. Anker, J. Rehorst and V. Erk and nature reserve manager R. Terlouw from Zuid-Hollands Landschap for granting access to their land. We thank the regional water boards of Schieland en Krimpenerwaard for providing information on changes in water tables and L. van Hoven of the ‘Weidehof’ farmers’ collective for data on AES. We gratefully acknowledge the help of E.R.Gertenaar in carrying out the experiments. We thank Nigel Harle for revising our English.

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Chapter 6

Effects of mowing date on the opportunities of seed dispersal of ditch bank plant species under different management regimes

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To be submitted

Abstract

Mowing and plant removal is a traditional practice in low-intensity farming and likely to lead to high plant species richness. Even today, scientific knowledge on the impact of mowing on seed availability is still very limited. We studied whether the seed availability of ditch bank plant species was affected by the timing of mowing and, if so, whether the effect varied according to management regime (nature reserve, agri-environment scheme (AES) with long-term management, AES with short-term management, conventional management). Our focus was on seed availability for transportation, because restoration of ditch bank vegetation is known to be limited by seed dispersal. The presence and seed-setting of 25 target species in 384 plots were recorded at the mowing date, under four management regimes. A Hierarchical Generalized Linear Model (HGLM) was used to analyze the effects of mowing date and management on the number of species setting seed. It suggests that when the mowing is twice annually, mowing on July 1st and on Sept. 1st will result in a maximum number of species of which the seeds are available for transportation and, therefore, create largest opportunities for seed dispersal on ditch banks in the western peat area of the Netherlands. The effect of mowing date differs among species, with certain rare species like *Caltha palustris* and *Lythrum salicaria* in particular differing from the commoner species. A flexible mowing regime varying from year to year would therefore help to protect these rare species. The later peak in seed-setting found in nature reserves and long-term AES suggest a postponed mowing compared to conventionally management and short-term AES.

Introduction

With loss of biodiversity continuing apace, the restoration, development and conservation of endangered plant communities have become important aims of nature conservation authorities (Edwards et al., 2007; Ozinga et al., 2009). The success of such efforts depends very much on the ability to provide suitable site conditions and seed sources (Pywell et al., 2002; Donath et al., 2007). Mowing, with subsequent removal of cuttings, is a traditional practice in low-intensity farming and likely to lead to high plant species richness (Huhta and Rautio, 1998). In recent years it has been discussed as a possible restoration measure and its practicability tested in a range of ecosystem including fens, meadows, semi-natural grassland and field margins (Hansson and Fogelfors, 2000; Stammel et al., 2003; Middleton et al., 2006; Musters et al., 2009).

On the one hand, it is postulated that mowing promotes favourable site conditions. It extends the space available for plant establishment by increasing light availability at ground level (Schaffers, 2002; Billeter et al., 2007). It also mitigates the negative effects of nutrient enrichment on plant species diversity by removing accumulated litter from the system (Hovd and Skogen, 2005). On the other hand, the mowing equipment may function as a vector for long-range seed dispersal within and between fields and is therefore thought to be important for the re-establishment of rare species (Strykstra et al., 1997). Until now, many studies have examined the influence of mowing on changes in site conditions that favour target species (Stampfli and Zeiter, 1999; Maron and Jeffries, 2001; Stammel et al., 2003; Billeter et al., 2007). However, only a handful of studies have directly compared the effect of mowing on seed dispersal (Strykstra et al., 1997; Coulson et al., 2001).

Mowing before species have set seeds strongly diminishes the seed sources for re-establishment (Kleijn et al., 2004; Geertsema, 2005; Leng et al., 2009). Appropriate timing and intensity of mowing may therefore have a substantial effect on seed availability at the location. However, it also affects the amount of seeds available for transportation by mowing equipment. It is possible to explore the effect of mowing time on seed availability for transportation by investigating the number of seed-setting species and the percentage seed set per species at the moment of mowing. We illustrate the pattern of number of seed-setting species and its consequences of seed availability in Fig. 1. We assumed that the number of seed-setting species would increase in time until it reached a maximum. The number will then decrease due to shedding of seed in certain species (Fig. 1a). Accordingly, the seed availability for both the location and transportation will increase up to the maximum number of seed-setting species. After the maximum, the seed availability on the location will be constant (seeds in the plants plus seeds on the ground), but the seed availability for transportation will decrease as seeds in the plants decrease (Fig. 1b). The percentage seed set per species will show a similar pattern as the number of seed-setting species.

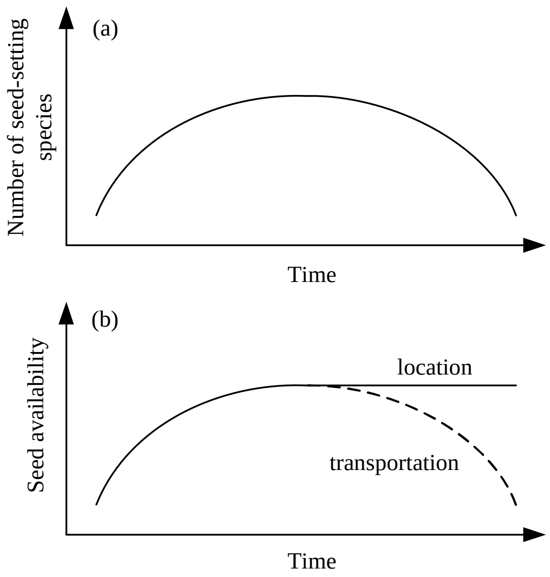

Fig. 1. Concept of the pattern of number of seed-setting species **(a)** and seed availability for the location and transportation **(b)**.

In landscapes dominated by agriculture, ditch banks provide an important refuge for plant species in terms of survival and diversity (Smart et al., 2006). Over the past 30 years, however, the species diversity of ditch banks has been in decline (McNeely et al., 1995; Blomqvist et al., 2003). One of the main policy initiatives to conserve the plant diversity of ditch banks has been the introduction of agri-environment schemes (AES), which were first implemented in England, Germany and the Netherlands in 1987. Earlier Dutch AES comprised a regime of zero fertilizer inputs, extensive grazing and later initial mowing and grazing at the start of the season. The latest schemes continue to recommend nutrient reduction, but impose few restrictions on the timing of mowing or grazing (DLG, 2000). The effectiveness of AES, however, is still being questioned (Kleijn and van Langevelde, 2006; Blomqvist et al., 2009). Seed limitation might be a important factor of variation in species richness (Zobel et al., 2000; Blomqvist et al., 2003; Leng et al., 2009). It is therefore important to test a range of mowing strategies, which might influence the seed availability for transport to establish the regime most effective for increasing the chances of plant dispersal.

In this paper we report a comprehensive study of the number of seed-setting species and the percentage seed set per species of ditch banks at the time of mowing under different management regimes. Mowing is at least twice a year in our study area. We hypothesized that the number of seed-setting species and seeds per species would increase with postponement of first mowing to later in the growing season. We further hypothesized that the number of seed-setting species and seeds per species would increase as the time between first and second mowing was extended. Finally, we hypothesized that the effects of mowing treatments would be different under different management regimes, because of differences in environmental conditions such as nutrient availability between nature conservation and agricultural areas. Because seed dispersal seems crucial for restoration of ditch bank plant diversity, we are looking for the combination of first and second mowing time that optimizes the opportunities for seed transportation, i.e. on the highest sum of the first and second mowing time number of seed-setting species and seeds per species, while the seeds are still in the plants (Fig. 1).

Materials and methods

Study site and species

The study took place from May to October 2008 on a network of ditch banks at Krimpenerwaard (province of South Holland, The Netherlands) in an area of farmland used as pasture for dairy cattle and sheep. The soils here are mainly peat or peat with clay. The ditch banks are 0.8-1.5 m wide, with slopes ranging from 15º to 20º. The vegetation is dominated by *Agrostis stolonifera*, *Holcus lanatus*, *Glyceria maxima*, *Glyceria fluitans* and *Cardamine pratensis* (Blomqvist et al., 2009).

As experimental sites, ditch banks under four types of management were chosen, nature conservation, AES with long-term management, AES with short-term management and conventional management (control). The nature conservation strategy in this area aims to conserve biodiversity such as plants and meadow birds by providing relatively nutrient-poor conditions and limited grazing intensity. For AES with long-term management we chose sites where AES had been in place for more than 16 years, and for AES with short-term management sites initiated less than 6 years ago. In AES, a ‘no cure, no pay’ system is in force whereby farmers are free in their choice of management regime, but are recommended to apply the following treatments: first mowing at the end of June or beginning of July, zero fertilizer inputs, low stocking rate and deposition of dredged material on the top of ditch banks (van Strien, 1991). Conventional management is the regime implemented by farmers when choosing freely. The first mowing is usually around June 1st, second mowing around Aug. 1st and fertilizer inputs, ditch sediment deposition are applied on ditch banks (personal observation).

We used a set of 25 target species of dual interest, species deemed to be valuable ditch bank plants under Dutch government policy, on the one hand, and species the presence of which are used as criteria for rewarding farmers implementing AES, on the other. A list of the species along with their salient characteristics which might be related to the seed-setting is provided in Table 1.

Table 1. Overview of target species with their characteristics. Lumped taxa * *Myosotis arvensis* and *Myosotis discolor*. Nature value, Clausman and van Wijngaarden (1984). Minimum light requirement (L), Nutrient requirement (N) from Ellenberg et al., (1992); Hill et al., (1999), shade tolerant(6), intermediate(7), light demanding(8); N, indifferent(×), oligotrophic(1-4), mesotrophic(5-6), eutrophic(7-9). Flowering period, month number. All other characteristics from Biobase (CBS, 2003).

Species name	Nature value	Germination period	L	N	Mean plant height	Begin flowering	End flowering
Achillea ptarmica	42	Spring	8	2	60	7	8
Caltha palustris	36	Late spring	7	×	32.5	4	11
Centaurea jacea	35	Late Summer	7	×	65	6	9
Cirsium palustre	37	Early summer	7	2	105	6	8
Filipendula ulmaria	31	Late spring	7	4	90	6	8
Galium palustre	35	Autumn	6	4	27.5	5	9
Hydrocotyle vulgaris	40	Spring	7	2	15	7	9
Hypericum perforatum	31	Spring	7	3	50	6	8
Iris pseudacorus	40	Early summer	7	7	80	5	9
Lathyrus pratensis	32	Autumn	7	6	75	6	7
Leucanthemum vulgare	39	Late summer	7	3	45	5	8
Lotus uliginosus	40	Spring	7	4	65	6	9
Lychnis flos-cuculi	44	Direct	7	×	60	5	11
Lycopus europaeus	29	Early summer	7	7	60	6	10
Lysimachia thyrsiflora	37	Late spring	7	3	45	5	9
Lythrum salicaria	31	Spring	7	×	90	6	7
Mentha arvensis	37	Late spring	7	×	30	7	7
*Myosotis**	40	Spring	7	6	25	5	9
Pedicularis palustris	60	Late spring	8	2	32.5	5	11
Potentilla palustris	41	Late spring	8	2	60	6	11
Prunella vulgaris	31	Early autumn	7	×	26	5	9
Ranunculus flammula	43	Direct	7	2	27.5	6	8
Rhinanthus angustifolium	44	Spring	7	2	45	5	7
Veronica beccabunga	39	Late spring	7	6	37.5	5	11
Vicia cracca	25	Direct	7	×	115	6	10

Experimental design

In order to include a wide range of ditch banks in our study, for each of the four management regimes six ditch banks were selected in different polders. Each of these banks was assigned to 16 plots on which four different first-time mowing treatments (FT I - FT IV) and four second-time mowing treatments (ST I - ST IV) were combined in all permutations (Fig. 2). A total of 384 plots were thus investigated. Each plot was 10 m long, with its width depending on the steepness of the ditch bank (average, 0.96 m ± 0.12 m).

Just before each mowing, biomass samples were clipped. In each plot, two replicates were sampled by cutting the vegetation in a 20 × 50 cm square (0.1 m^2) 3 cm above grade. These were dried at 70 °C for 72 h and weighed. Biomass calculated as g dry weight/m^2 was then used as a measure of productivity. Habitat variables of potential influence on ditch-bank vegetation were measured, including ditch bank width, slope angle and ditch water table (van Strien, 1991). In each plot, both the presence of the species and the species with ripe seeds in all the individual target species were recorded just before mowing.

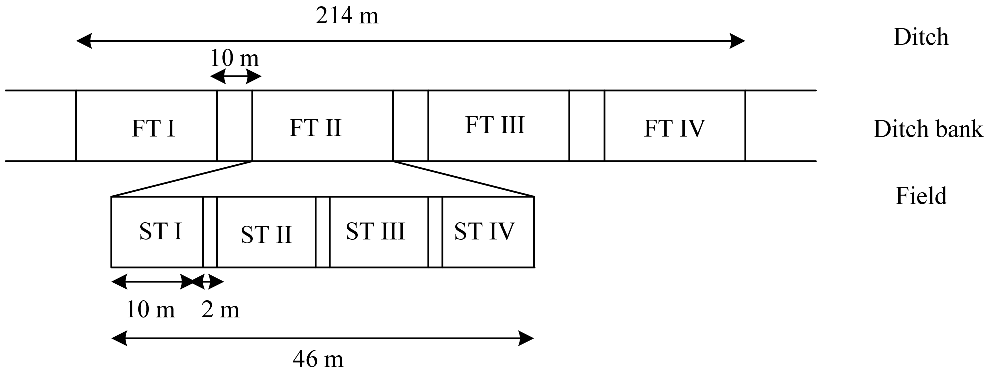

Fig. 2. Experimental set-up comprising sixteen plots on each ditch bank (FT I - FT IV= experimental first mowing; ST I - ST IV= experimental second mowing).

We applied double mowing regimes on each plot. Both the first and second mowing date was categorized as four mowing treatments with regular intervals of two weeks from May 15th to July 1st and Aug. 1st to Sept. 15th individually. Mowing was carried out with a brush-cutter, the action of which is equivalent to typical cutting with a disc mower. The vegetation was mown to a height of 5-10 cm. All the cut plant material was removed immediately after mowing and throughout the experimental period no deposition of ditch sediment was permitted.

Data analysis

To analyze the effects of treatments and management regimes on total target species, we used a Hierarchical Generalized Linear Model (HGLM), taking as dependent variables the total number of species setting seed and the percentage of species with seed at both first and second mowing time. HGLM was used because the two dependent variables in the sampled plot are assumed to have a normal distribution and the sample locations were assumed to be a random sample of all possible locations (Lee and Nelder, 2001). The time of first mowing, the time of second mowing, their interaction, the management regime and variables of potential influence on ditch-bank vegetation were included in the fixed model. We considered our study locations as random samples of all ditch banks, therefore ditch-bank was treated as the random model. A normal distribution and an identity link function were used. Additionally, we used T-test to compare the number of seed-setting species under different mowing time and used Mann-Whitney U-test to test species characteristics differences among species.

To investigate the effect of four different managements on number of seed-setting species, Mann-Whitney U-test was again applied to compare biomass, species richness under different management regimes. The HGLM was run using the statistical program GENSTAT 11.0, while all other calculations were performed with SPSS 16.

Results

Seed set at first and second mowing time

The average number of species per location setting seed at the first mowing time rose significantly as the time of first mowing was delayed (Fig. 3a). Figure 4a shows that on May 15th *C. palustris* was the only species seeding. On June 1st or June 15th this was the case for seven species and the percentage seed set per species tended to be greatest on July 1st except for *Cirsium palustre*. *Galium palustre*, *Lathyrus pratensis*, *Lotus uliginosus* and *Vicia cracca* had seed set by July 1st, while no seeds of *Lythrum salicaria* were found at first mowing, regardless of mowing date.

The average number of species with seed at second mowing was highest when first mowing was on May 15th and second mowing on Sept. 1st (Fig. 3b). At the species level, seven out of 11 species showed maximum seed set when first mowing was on May 15th, while the percentage seed set for these 11 species differed considerably at the second mowing date (Fig. 4b). *C. palustris* and *Rhinanthus angustifolius* had no seed set at second mowing.

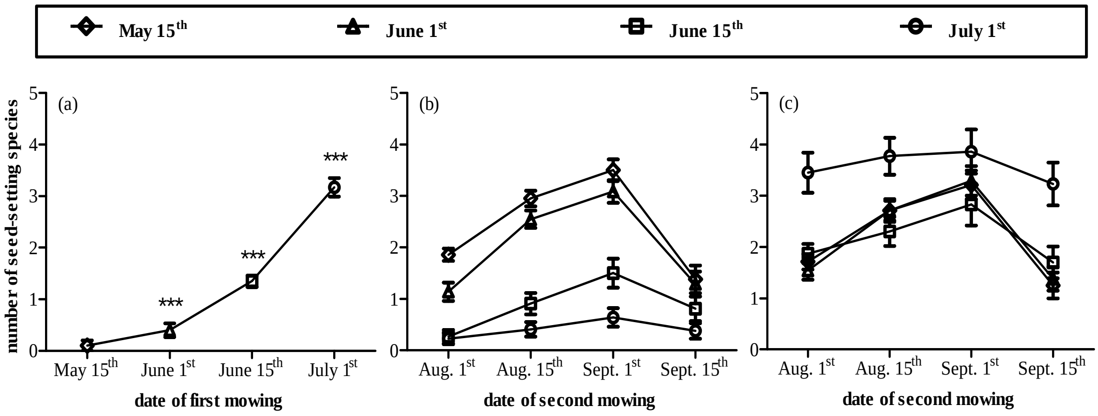

Fig. 3. Number of species setting seed at first **(a)**, second **(b)** mowing and under double mowing regimes **(c)**. Significant differences between May 15th and other first mowing dates on number of seed-setting species are indicated by asterisks (*** = $p<0.001$, T-test). Vertical bars are standard errors.

Seed set under double mowing regimes

A significant relationship was found between mowing date and total number of seed-setting species at mowing under double mowing regimes (Table 2). Considerably higher numbers were observed with first mowing on July 1st and second mowing on Aug. 15th or Sept. 1st. The greatest number of seed-setting species was found when mowing was on July 1st and Sept. 1st (Fig. 3c). The average number (3.86 ± 0.43) was 126% higher than the number of seed-setting species when mowing on June 1st and Aug. 1st, the conventional mowing regime (1.71 ± 0.15). None of the habitat variables was found to have a significant effect on the relationship between mowing date and number of seed-setting species.

There are large inter-species differences with respect to percentage seed set under double mowing regimes. Generally speaking, species can be assigned to one of five groups, the first three of which have been reported on in Figure 4. Group A comprises those species in which the peak in the percentage plants with seeds is independent of second mowing date. The six species in this category are *C. palustris, G. palustre, Iris pseudacorus, L. flos-cuculi, R. angustifolius* and *V. cracca*. With the exception of *C. palustris*, all these species had the highest percentage seed set on July 1st. Group B are those species in which maximum seed set occurs during a prolonged interval between the first and second mowing. In *L. pratensis* and *L.*

uliginosus this maximum occurred over a period of 10 to 12 weeks, while in *Lysimachia thyrsiflora* and *L. salicaria* it was 16 weeks. Group C comprises species in which maximum seed set occur during a short interval between the two mowing dates. In *C. palustre, Myosotis* and *Ranunculus flammula* maximum seed set was recorded over a 6-week period. Group D are those species that were present but in which no seeding was observed, such as *Filipendula ulmaria*, *Hydrocotyle vulgaris, Lycopus europaeus* and *Mentha arvensis*. Group E, finally, comprises the eight species of the 25 target species that were not found. They are *Achillea ptarmica*, *Centaurea jacea*, *Hypericum perforatum*, *Leucanthemum vulgare, Pedicularis palustris*, *Potentilla palustris*, *Prunella vulgaris*, *Veronica beccabunga*. When compared species characteristic differences in all possible combination of pairwise species group, only group A and group D showed significant first flowering time differences (P=0.02, Mann-Whitney U-Test).

Table 2. Results of HGLM analysis of impact of first and second mowing date, their interaction, management regimes and habitat variables on total number of seed-setting species and percentage of species with seed under double mowing regimes. * = p<0.05; ** = p<0.01; *** = p<0.001.

	Total number		Percentage	
	Estimate	t	Estimate	T
Constant	5.54	1.99	-0.05	-0.13
June 1st	-0.33	-0.91	-0.12	-1.79
June 15th	0.04	0.11	-0.06	-0.93
July 1st	1.64	4.57***	0.24	3.69***
Aug. 15th	1.09	3.02**	0.13	1.98*
Sept. 1st	1.63	4.55***	0.16	2.51*
Sept. 15th	-0.38	-1.05	-0.15	-2.33*
June 1st * Aug. 15th	0.16	0.34	0.11	1.09
June 1st * Sept. 1st	0.32	0.63	0.09	1.01
June 1st * Sept. 15th	0.41	0.79	0.13	1.41
June 15th * Aug. 15th	-0.59	-1.16	-0.04	-0.48
June 15th * Sept. 1st	-0.59	-1.16	-0.06	-0.67
June 15th * Sept. 15th	0.24	0.47	0.12	1.28
July 1st * Aug. 15th	-0.77	-1.52	-0.07	-0.74
July 1st * Sept. 1st	-1.22	-2.41*	-0.21	-2.21*
July 1st * Sept. 15th	0.08	0.16	0.03	0.36
AES, short-term	0.25	0.77	-0.11	-1.46
AES, long-term	0.01	0.02	-0.05	-0.74
Nature reserve	0.75	2.02*	0.02	0.25
Ditch-bank width	-1.48	-1.57	0.04	0.29
Ditch-water level	1.54	0.56	-0.06	-0.23
Ditch-bank slope	-0.13	-1.71	0.03	1.44
Estimates of parameters				
Phi	0.25	3.35	-3.16	-42.37
Lambda ditch-bank	-1.59	-3.88	-7.82	-7.87

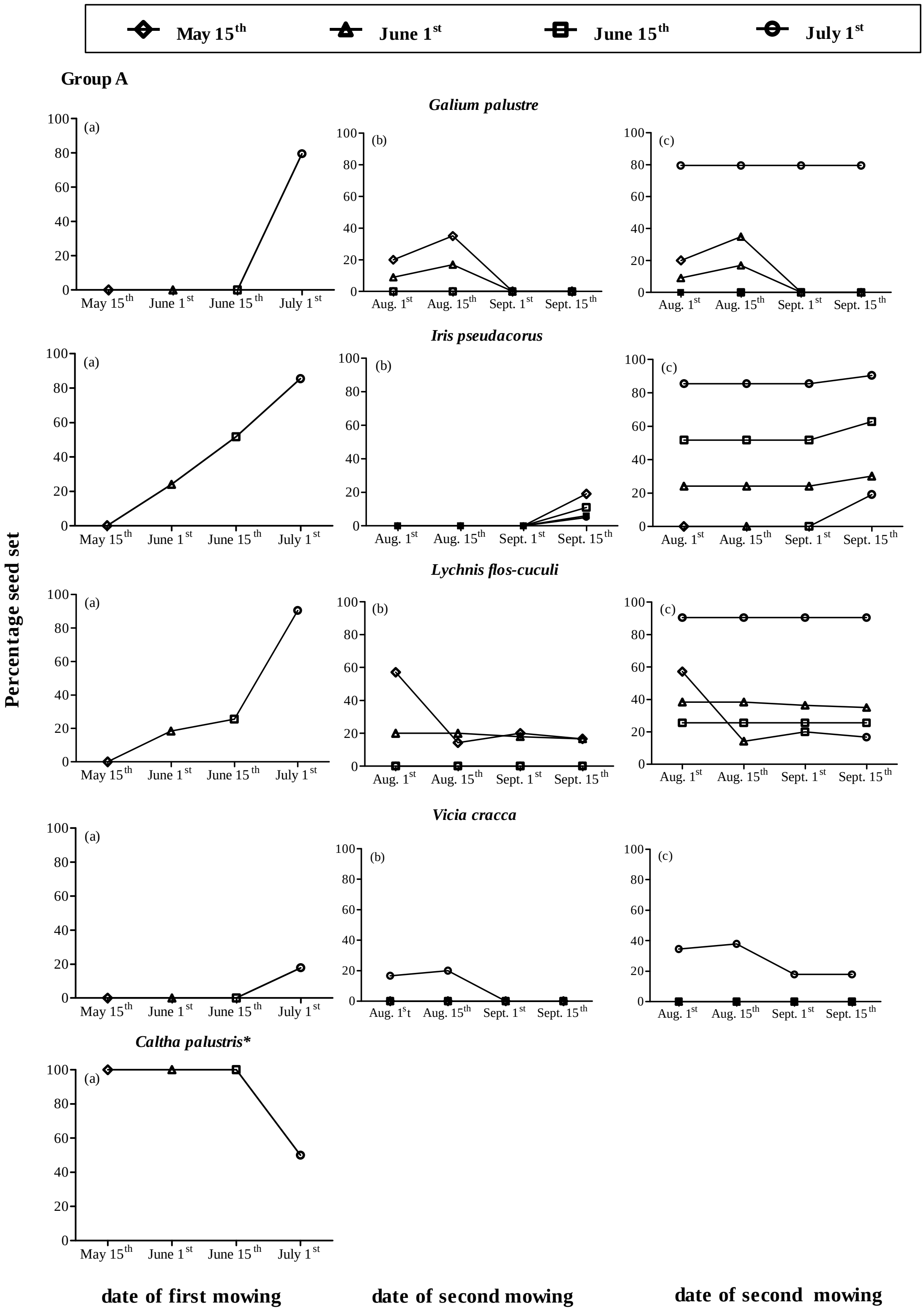

Fig. 4. Percentage seed set per species at first **(a)** and second **(b)** mowing and under double mowing regimes **(c)**. * species found only at first or at second mowing. The species not shown in the figure were those that did not produce seeds.

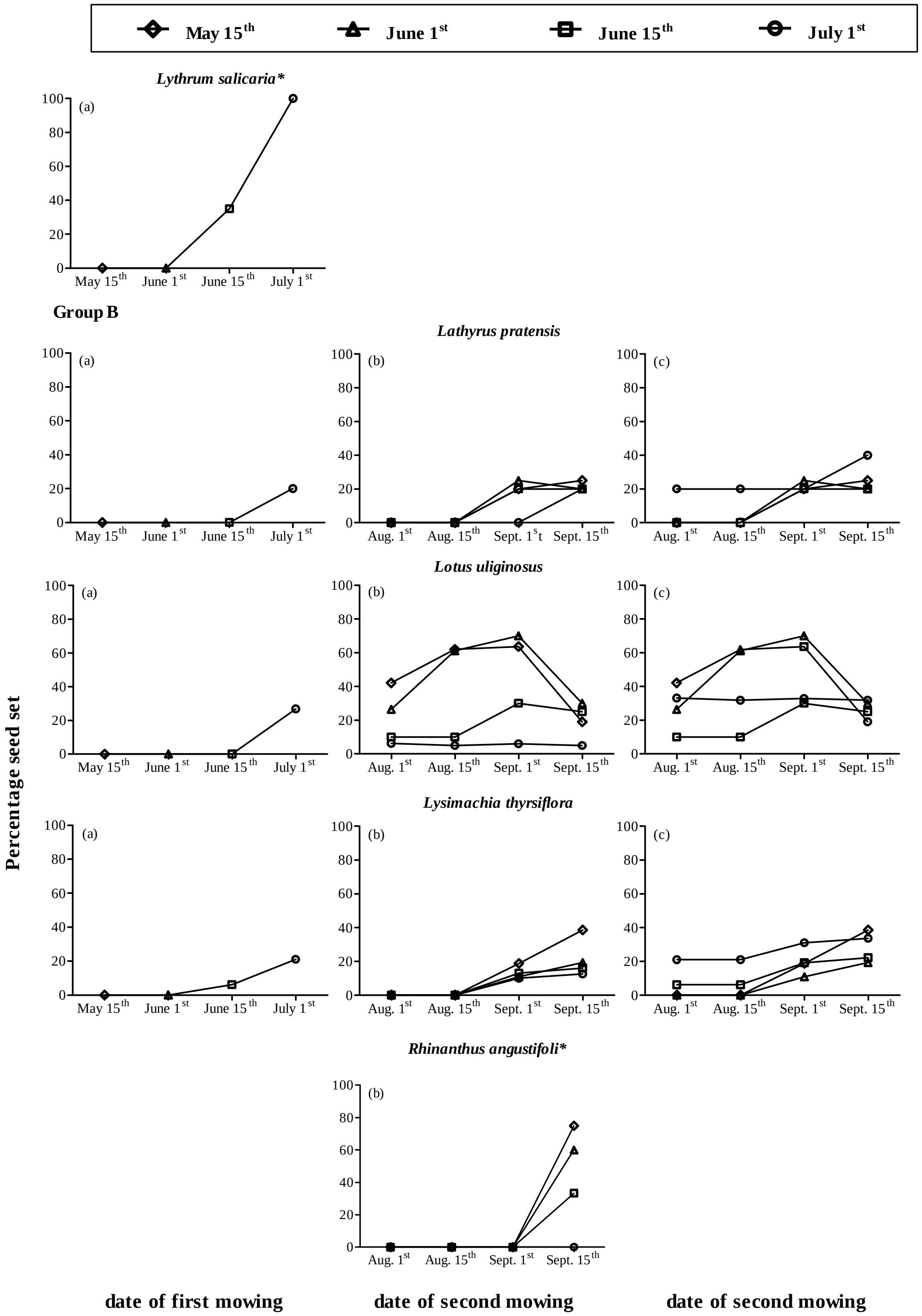

Fig. 4. Continued.

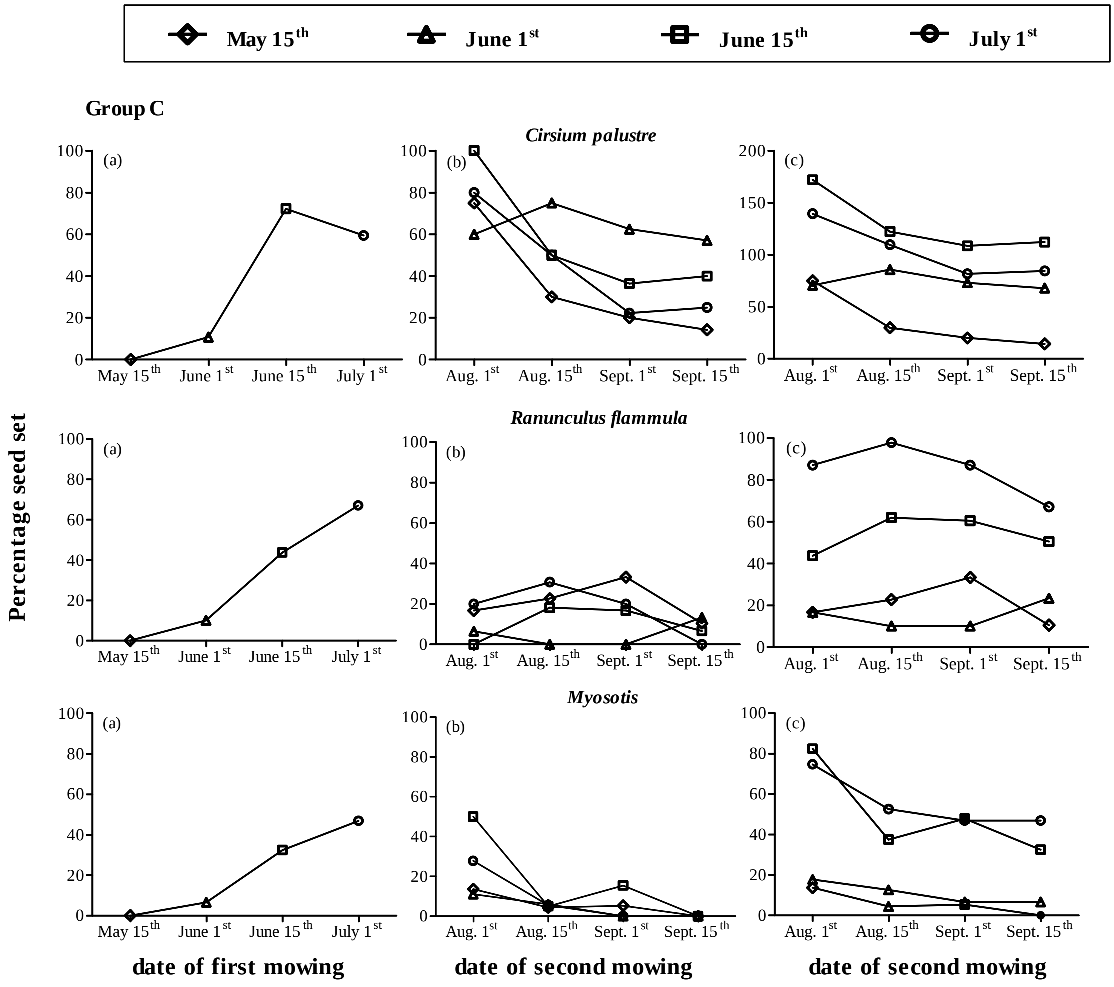

Fig. 4. Continued.

In 12 out of 13 species, the highest percentage seed set was at least twice compared to mowing on June 1st and Aug. 1st, the conventional mowing regime (Fig. 4c). Five species, such as *L. pratensis*, *L. thyrsiflora*, *L. salicaria*, *R. angustifolius* and *V. cracca*, can not be found setting seeds when mowing first on June 1st and later on Aug. 1st.

Effect of management

Biomass varied depending on management regime and was highest on plots under conventional management and lowest in nature reserves. On the other hand, species richness was lowest under conventional management and significantly higher in nature reserves (Fig. 5).

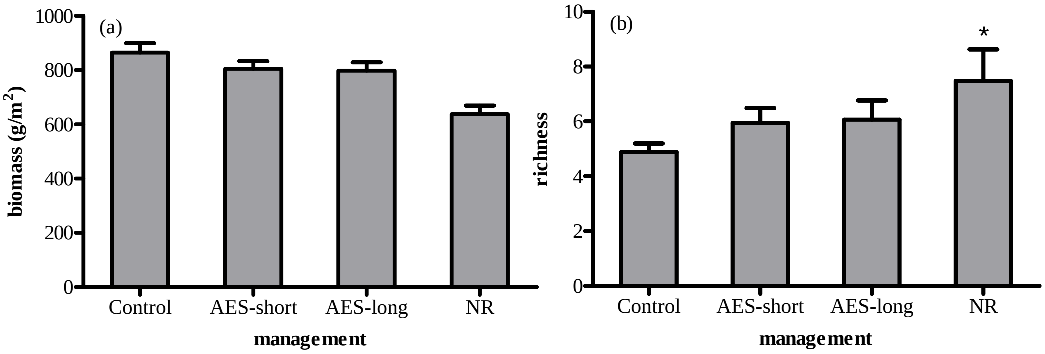

Fig. 5. Total biomass production (**a**) and species richness (**b**) under different management regimes. Significant differences between conventional management and other regimes are indicated by an asterisk (* = $p<0.05$, Mann-Whitney U-test). Vertical bars are standard errors.

The HGLM analysis showed a significant effect of management on the total number of species setting seed, with significantly higher numbers being found in nature reserves compared with conventional managed plots (Table 2). No difference in percentage of species with seed was found between conventionally managed and other plots. On plots under short-term AES and on conventionally managed plots, seed set peaked on Aug 15th, while in nature reserves and on long-term AES plots this was on Sept. 1st (Fig. 6).

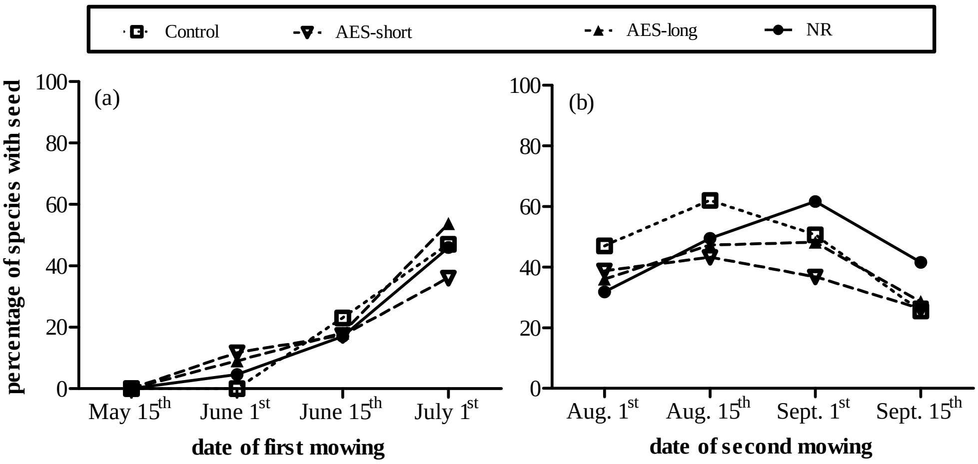

Fig. 6. Percentage of species with seed on date of first (**a**) and second (**b**) mowing under different management regimes.

Discussion

Seed set at first and second mowing time

Our first hypothesis, that higher number of seed-setting would correlate positively with later mowing date, was supported by the results. As first mowing was delayed, the number of species setting seed rose. The target species considered in our study vary widely in terms of seed-setting phenology and later first mowing would give many species like *G. palustre*, *L. pratensis*, *L. uliginosus* and *V. cracca* an opportunity to set seed prior to mowing.

Our second hypothesis, that the number of seed-setting would be enhanced by extending the interval between first and second mowing, was also supported by the results. That the highest number of seed-setting species was recorded with the first mowing on May 15th and a late second mowing on Sept. 1st is in line with Blomqvist et al. (2006) who found enhanced species reproduction with May and autumn mowing. Seven species showed maximum percentage seed set at the second mowing when the first mowing was on May 15th and *G. palustre*, for instance, had seeds at the second mowing only if first mowing was on May 15th or June 1st. This result indicates that in some species earlier first mowing might enhance flowering and seed-setting opportunities in the period prior to second mowing. For eleven of the target species, the percentage seed set at the time of second mowing differed considerably. When aggregated, however, the total number of species setting seed was found to peak on Sept. 1st, regardless of the date of first mowing. After September the number of species with seed declined, which can be attributed to the shedding of seeds during this period. This is further confirmed by investigations in the field, where in most common species (*G. palustre* and *Myosotis*) no seed-setting individuals were found after September.

Effect of mowing date on seed set under double mowing regime

The highest total number of seed-setting species was found with a combination of first mowing on July 1st and second mowing on Sept. 1st. Moreover, it has a 126% higher number of seed-setting species compared to mowing under conventional mowing regime, a combination of June 1st and Aug. 1st. As a consequence, under a twice mowing regime, mowing on July 1st and Sept. 1st would result in a maximum seed availability for transportation, and therefore in maximum opportunity for seed dispersal. Although it is possible that earlier first mowing might enhance target-species seed-setting by reducing competition (Collins et al., 1998; Hovd and Skogen, 2005; Williams et al., 2007), this potential effect seem to be outweighed by the positive effect of late first mowing on late seed-setting species. That half the target species exhibited maximum seed set when first mowing was on July 1st also corroborated the importance of a later date for first mowing. None of the habitat variables deemed to potentially affect plant diversity proved to influence the effect of mowing date on the number of seed-setting species.

At the species level, the six species in group A showed no impact of second mowing on maximum seed set. Some species like *L. flos-cuculi* have low germination rates or have difficulty establishing, especially under high-biomass ditch banks according to Blomqvist et al. (2006), and in *C. palustris* and *R. angustifolius* no seeds at all were observed after first mowing. For these species, then, the appropriate mowing regime should be a single mowing at the occurrence of maximum seed set to obtain highest seed availability for transportation or a single mowing later on to achieve highest seed availability for the location. The species in group B and C that showed an impact of both first and second mowing on maximum seed set were categorized based on the interval between the two mowing dates. In group B, maximum seed set was recorded over an interval of over 10 weeks between mowing. A later date for second mowing is therefore needed to obtain a high percentage of seed-setting individuals. *L. salicaria,* for instance, should be mown in September if viable seeds are to be formed to get highest seed availability for transportation and mown after September for the location. The species in group C showed maximum percentage seed set over a 6-week period, with the timing of second mowing seemingly not that important, compared with group B. All the species in group C were found to belong to the commonest species considered in our study. In this group, moreover, the time between the beginning and end of flowering (3 to 6 months) is much longer than in group B (2 to 3 months). This suggests that the mechanism behind the effect of second mowing date might lie in the duration of flowering. For species in this group, a combination of later date for first mowing and earlier date for second mowing is necessary to obtain maximum seed availability for transportation and a single later date for first mowing is needed to obtain maximum seed availability for the location. In the species in group D no seed set was observed and significant differences in the start of flowering were found compared with group A. Most of the species in group A begin flowering in May, while those in group D do not start flowering until June. This indicates that first mowing should take place later for group D than for group A and that in the present study mowing too early may be one explanation for the lack of seed set in the species of group D.

When comparing the percentage seed set differences between optimal and conventional mowing regime, we found that 12 out of 13 species have more than two times higher percentage seed set and 5 species can only be found under optimal mowing regime. This means that mowing regime in conventional management seriously hampers seed availability for plant species in ditch banks, both for transportation and for the location.

Effect of management (nutrient availability) on number of seed-setting species

Our final hypothesis was that the number of species setting seed is influenced by differences in nutrient availability among management regimes. Although the number of seed-setting species found on conventionally managed plots was considerably lower than in nature reserves, there was no difference in the percentage seed set per species. The relatively low species richness on conventionally managed plots leads to fewer species setting seed compared to nature reserves. This possibility lends support to earlier findings that species diversity in grassland tends to decline when total annual biomass production exceeds 600-700 g/m^2 (Oomes, 1992). The hypothesis is further supported by the earlier timing of the peak in seed set on conventionally managed plots compared with nature reserves. With greater nutrient availability, species are presumed to grow faster.

Implications for conservation

Current management in ditch banks does not address the issue of seed availability for transportation, and, therefore, ignores the opportunities for seed dispersion by mowing equipment. This study showed clearly that seed availability for transportation, measured as percentage seed set per individual species as well as number of seed-setting species, was significantly lower under a conventional mowing regime compared to the optimal one. Land managers and farmers therefore need to select appropriate mowing times for increasing opportunities for dispersal of the species being targeted. Our result shows that when mowing twice annually, on July 1st and on September 1st, respectively, may in principle be a useful strategy for maximizing seed transportation by mowing equipment on ditch banks in the western peat area of the Netherlands. For increasing seed availability at the location, mowing on July 1st and not before September 1st would be helpful.

The impact of mowing date differs from species to species. Certain species like *C. palustris* and *L. salicaria*, in particular, are thought to be affected by early mowing via germination and competition (Blomqvist et al., 2006; Williams et al., 2007). From this perspective early mowing might be good for certain species. To protect these rare and internationally valued species it would therefore be useful to establish flexible mowing regimes that vary from year to year.

The higher number of seed-setting species found in nature reserves combined with the later peak in seed-setting highlights the need to take different management into consideration. Our results suggest it may be necessary to mow later in nature reserves and long-term AES than on conventionally managed and short-term AES plots. At the same time, though, this conflicts with the idea that the higher number of species producing seed in nature reserves, and mowing machines as dispersal vectors, make it possible to enlarge opportunities for species dispersal outside nature reserves by first mowing in nature reserves and then, using the same equipment, mow the agricultural surroundings.

Acknowledgements

We thank the farmers J.M. Oudenes, Th.A. Holierhoek, M. Verkaik, P.G. Blanden, I. Halling, H. Hogendijk, V. Noordergraaf, K.A. Anker and M. van Zuijlen and nature reserve manager R. Terlouw from Zuid-Hollands Landschap for granting access to their land. We thank L. van Hoven of the ‘Weidehof’ farmers’ collective for data on AES. We gratefully acknowledge the help of E.R.Gertenaar in carrying out the mowing during the experiments. Finally, we are grateful to Nigel Harle for revising our English.

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Chapter 7

Conclusions and perspectives

Conclusions

Over the last decades, intensification of agricultural practices has led to a rapid destruction of natural habitats and loss of biological diversity at various spatial and temporal scales (Benton et al., 2003; Stoate et al., 2009). However, current management practices such as the creation of nature reserves (aiming at conserving remnants of species-rich sites) or agri-environment schemes or AES (aiming to enhance the diversity of agricultural areas) often produce mixed results and the effectiveness of these management methods is still being questioned (Ferraro and Kiss, 2002; Kleijn and Sutherland, 2003; Kleijn et al., 2004; Blomqvist et al., 2009).

Ditch banks in grasslands and wetlands are considered an important feature of the agricultural landscape in the Netherlands and are assumed to serve as a refuge for plant species (Blomqvist et al., 2003b). Over the past 30 years, however, the plant species diversity of ditch banks has been in decline. In Dutch grassland areas, the maintenance and enhancement of plant diversity is hampered by the small area of nature reserves and by the fact that many plant dispersal processes have been disrupted in today’s fragmented landscapes (Soons et al., 2005; Kohler et al., 2008). On the other hand, the effect of agri-environment schemes might be hampered by seed availability limitations (Zobel et al., 2000; Blomqvist et al., 2003b).

The research reported on in this thesis focused on two main objectives: (1) understanding the processes behind the spatial and temporal patterns of plant diversity on ditch banks; (2) identifying options for the conservation and restoration of plant species diversity on ditch banks. The most important findings are summarized below.

Part I Spatial and temporal patterns of species diversity

Spatiotemporal pattern of species diversity

For all species considered in our study, the observed spatial beta diversity was lower than theoretically expected, suggesting that the vegetation of the Krimpenerwaard research area is currently homogeneous, i.e., that more or less the same set of species is found at the different sites. The temporal diversity was higher than expected, and plant diversity increased over time, indicating the return or appearance of certain common species everywhere in the sample plots. These species are probably not limited by dispersal processes and can survive under the different environmental conditions in the Krimpenerwaard area.

For the target species of nature conservation, spatial species diversity was not different from the theoretically expected value, but the temporal beta diversity was lower than expected. Moreover, the diversity of the target species depended more on spatial differences than that of other species, probably due to both environmental heterogeneity and dispersal limitation, especially at a larger spatial scales. Significantly lower differences were found between sampling periods, although species richness increased significantly. One possible explanation might be the improved environmental conditions, while at the same time, more time may be required for these small-scale processes to influence landscape-scale patterns.

The proportions of diversity components of target species differed: in nature reserves, species richness within sites was higher and beta diversity among sites was lower than in agricultural areas. The higher species richness in nature reserves may be explained by lower nutrient input and limited grazing intensity, which may facilitate colonization by various species. Furthermore, the null hypotheses for nature reserves and agricultural areas showed a similar tendency, in that the beta diversity among sites was not different from the expected values. This might indicate that the dispersal of plant species is not a limiting factor in either nature reserves or agricultural areas. An alternative explanation is that similarity is different at different levels of scale: higher than expected at small scales and lower than expected at large scales. The positive effect of environmental conditions under AES may cause species diversity to increase over time, and hence seems to contribute to species diversity changes among target species at the overall landscape scale.

Spatial variation in species composition

The patterns of species similarity between plots for all plant species are mainly influenced by variation in dispersal. The rate of distance decay in species composition was far greater for the target species than for all species together. This difference may be caused by the combined effects of environmental and dispersal variation. Plant species richness in terms of these target species is well known to be highly dependent on nutrient level, and thus showed significant correlations with this environmental factor. Moreover, a stronger effect of water dispersal was found for the target species as compared to all species, which might be attributable to the limited dispersal capacities of target species.

The effect of dispersal limitations on species similarity between plots differed for the various dispersal vectors. The negative relationship between agricultural activities and species similarity for each dispersal type indicated the limitation of dispersal by agricultural activities, regardless of species dispersal type. Limitation of dispersal by wind was only found for wind-dispersed species. We found no clear effect of limitation of dispersal by water on water-dispersed species, suggesting that water might be a good dispersal vector for ditch banks plants. This is also evidenced by the fact that the regression coefficient of the relationship between species similarity and geographic distance in water-dispersed species was only half of that for other dispersal types.

Part II Possible managements for plant diversity restoration

Site limitation or seed limitation?

Both the abundance of each individual species and the species richness decreased significantly with the distance from nature reserves. This emphasizes the importance of nature reserves for the presence of plant species on ditch banks in the agricultural landscape and shows that this presence is at least partly limited by seed availability.

Based on the data of ditch banks running transverse to nature reserves, the intercept of the relationship with distance was higher in AES-managed ditch banks, suggesting that site limitation is less important in AES ditch banks. No general pattern was found for the regression coefficients per species. Thus, AES do not change seed limitations for the species. Our results confirmed that, although seed limitation is an important factor in the species richness of ditch bank vegetation, Dutch AES for ditch banks only affect species richness through site limitation, if they affect species richness at all.

Nature reserves or agri-environment schemes?

A significant decline in species richness with increasing distance from a nature reserve was also found on ditch banks running transverse to nature reserves. Ditch banks under AES management showed higher species richness over the first 200 metres from the nature reserve than non-AES ones. A significant decline in species richness with increasing distance from a nature reserve was also found on non-AES ditch banks running parallel to nature reserves, confirming that the distance between such a bank and a species-rich site is an important determinant of species diversity on ditch banks. Upwind nature reserve location had a distinctly positive impact on plant species richness by increasing seed dispersal. Nitrogen supply on adjacent fields had a negative impact on plant species richness because of the greater site limitation on certain species. Compared with the transverse banks, less decline in species richness with distance from the nature reserve was observed on the parallel ditch banks, which was probable due to less human disturbance.

Of the parallel ditch banks, AES-managed banks showed a higher species richness than the non-AES ones if they were situated at distances of over 200 m from the nature reserve. In other words, the positive effects of AES appears to be present close to the nature reserves in transverse running ditch banks, while on banks running in the parallel direction it was more pronounced, but only at a considerable distance from the nature reserve. This stresses the importance of a landscape perspective in the restoration of plant diversity in agricultural landscapes.

Mowing earlier or later?

Among double mowing regimes, mowing on July 1st and Sept. 1st resulted in the highest total number of seed-setting species. This suggests that when mowing twice a year, mowing on July 1st and Sept. 1st, may enhance seed dispersal on ditch banks. Regarding seed transportation, six species showed no impact of the second mowing on the maximum seed set. The rest of species showed an impact of both first and second mowing, depending on the interval between two mowing dates. Some species which reached their maximum seed set percentage within a shorter time were among the commonest species considered in our study and had a longer interval time between the beginning and end of flowering.

The number of species setting seed is influenced by differences in nutrient availability between management regimes. The lower number of seed-setting species and earlier timing of the seed-set peak on conventionally managed agricultural plots compared with nature reserves suggest that the lower nutrient availability plays an important role in the seed set of ditch bank species.

Perspectives

Perspectives for conservation

The pattern of species diversity has been suggested to be determined by processes at multiple scales in space and time (Gering et al., 2003; Leibold et al., 2004). Understanding what mechanisms operate at a given scale to cause differences in species composition and diversity is thus important for an understanding of the functioning of ecosystems and is helpful for the conservation of biodiversity (Gering et al., 2003; Hendrickx et al., 2009). The theoretical framework of spatial population and community dynamics, known as metacommunity theory, may help to understand the ecological processes at multiple scales that are crucial for conservation. A metacommunity can be defined as a set of local communities which are linked by the dispersal of multiple interacting species (Wilson, 1992). Leibold et al. (2004) identified four theoretical models of metacommunities, providing insight into the way species diversity might be influenced by local and regional processes. These four models can be classified along four broad perspectives which are called the *species-sorting*, *patch-dynamic*, *mass-effect* and *neutral* perspectives.

The *species-sorting* perspective is based on theories of community change over environmental gradients (Whittaker, 1972) and considers the effect of local conditions and habitat heterogeneity on population vital rates and species interactions (Leibold, 1998). The *patch-dynamic* perspective is based on the equilibrium theory of island biogeography. The existence of local communities is subject to both stochastic and deterministic extinctions (Harrison and Taylor, 1997). Dispersal between communities is necessary for the maintenance of local and regional diversity. The *mass-effect* perspective is based on a multispecies version of source-sink dynamics (Holt, 1985; Pulliam, 1988) and rescue effects (Brown and Kodricbrown, 1977). The immigration and emigration between local communities can be influenced both by differences in population density at different locations and by dispersal. Finally, the *neutral* perspective concerns the temporal random change in species composition and assumes a time scale over which speciation counteracts the extinction process due to drift (Hubbell, 2001).

Importantly, these four models illuminate different aspects of spatial community dynamics, since the dominant factors explaining species richness differ between the models. According to Bengtsson (2009), studies of metacommunities should therefore investigate the mechanisms driving dynamics, but should not focus on deciding which model is more appropriate for a particular study system, since they are not mutually exclusive. At least four factors from these four models need to be taken into consideration when studying metacommunities: environmental gradients, connectivity, population densities and speciation. And although it may not be appropriate to try and assess which model fits the data, one could try to answer the question which factor dominates species richness in the system we studied, i.e. ditch banks.

Of the four main factors, it is obvious that speciation is not relevant at the time scale we studied, so this factor can be ignored. Since chapter 3 suggests that the plant species richness in terms of all plant species is probably not affected by environmental gradients, dispersal and population densities may be regarded as the potential dominant factors. By contrast, the species richness in terms of target species seems to be affected by environmental gradients (*Chapter 3*), as well as connectivity (*Chapter 4*). Furthermore, although population densities were not themselves taken into consideration in our research, the numbers of seeds produced may be limiting for target species (*Chapter 6*). In this respect, Blomqvist et al. (2003b) showed that the density of vegetation might also be an important limiting factor.

Bengtsson (2009) offered some general considerations for ecosystem management, based on the four perspectives. The *species-sorting* perspective emphasizes the importance of proper local management and conservation of regional diversity in order to maintain local diversity, and, on the other hand, preservation of some connections between patches to allow environmental tracking. The *patch-dynamics* perspective emphasizes dispersal between patches to maintain both local and regional diversity. Local diversity to maintain the regional species pool, combined with low dispersal rates, results in high variability among patches. The *mass-effect* perspective suggests identifying and managing source patches and maintaining dispersal. However, high regional dispersal may prevent local sorting of efficient species. The *neutral* perspective points out the long-term management implications for local and regional diversity. The relevant management recommendations based upon the results obtained at Krimpenerwaard are summarized in Table 1. This study mainly recommends protecting the nature reserves (source patches) and promoting seed dispersal among local communities, so it emphasizes the *patch-dynamic* and *mass-effect* perspectives. In addition, providing suitable environmental conditions for species remains necessary, especially for local communities of target species, which derives from the *species-sorting* perspective.

Table 1. Ecological processes and management recommendations at different scales

Scale	Ecological processes	Management recommendations
Local Communities	Lower nutrient levels leading to higher diversity (*Chapter 3*)	Continued reduction of nutrient inputs (*Chapters 3, 4*)
	Seed limitation (*Chapters 4,5*)	General: mow twice a year, early on July 1st and late after Sep 1st; early mowing regimes for certain rare species (*Chapter 6*)
Between local communities	Dispersal limitations may be important (*Chapters 2,3,4*)	Take location of nature reserves into consideration when choosing locations for AES (*Chapters 4,5*)
		Delivery systems like AES improve matrix quality (*Chapters 4,5*)
		AES should be preferentially implemented downwind of and parallel to nature reserves (*Chapter 5*)
		Mow on July 1st and Sept 1st to enhance seed dispersal (*Chapter 6*)
Regional communities	Dispersal from the source population (*Chapters 4, 5*)	Increase number of source populations (*Chapters 4,5*)
		Expand the size of the AES area (*Chapters 2, 5*)

Local community management

As regards local communities, previous research suggested that lowering nutrient levels improves plant diversity on ditch banks (Blomqvist et al., 2003a). Our research confirmed this finding. The spatial pattern of composition in terms of target species revealed the importance of environmental conditions, expressing itself in a higher sensitivity of these species to nutrient levels than that shown by other species.

Since the potential value of the seed bank for the restoration of ditch banks is marginal, the crucial question is how to increase seed availability at the relevant locations. One possible restoration measure is to apply optimized mowing times (Hansson and Fogelfors, 2000; Stammel et al., 2003). Our study showed that mowing twice a year with early mowing on July 1st and late mowing after Sep 1st may lead to higher seed availability at the relevant locations and could thus in principle be a useful strategy to increase plant species richness on ditch banks. On the other hand, the effect of mowing times differs between species. Some rare species like *Caltha* *palustris* and *Lythrum salicaria* in particular showed a favourable effect of early mowing on germination. From this point of view, early mowing might be good for certain species, and establishing tailored mowing regimes would therefore be useful to protect these rare and internationally relevant species.

Dispersal among local communities

The spatial variation in composition in terms of all species as well as target species has been explained primarily on the basis of dispersal processes. Differences in distance decay between species with different dispersal types further reveal the rarity of long-distance dispersal, for instance by wind and agricultural activities, on ditch banks. These results imply that conservation management should focus on facilitating dispersal between sites.

Previous research has indicated that natural or seminatural habitats in intensively farmed landscapes can act as source communities and promote plant diversity on agricultural fields under extensive management (Steffan-Dewenter and Tscharntke, 1999; Ockinger and Smith, 2007; Cousins and Lindborg, 2008). The creation and maintenance of nature reserves is often hampered by both ecological and economic factors, while the ecological effectiveness of AES is still being questioned. Suggestions to improve plant diversity include adopting a conservation strategy in which nature reserves are more fully integrated with farmland (through AES) (Blomqvist et al., 2003a; Kleijn and Sutherland, 2003). Our results support the idea of the importance of nature reserves in addition to AES for the protection of plant species on ditch banks (Blomqvist et al., 2003a; Soons et al., 2005; Kohler et al., 2008; Maes et al., 2008). Our studies on the ditch banks, both those running transverse to and those running parallel to the nature reserve, showed that the species diversity decreased with increasing distance from the nature reserves, and higher species diversity was found in AES-managed ditch banks compared to non-AES ones. Furthermore, we observed that AES-managed ditch banks running parallel to a nature reserve featured greater plant diversity at larger distances than ditch banks running transverse to a nature reserve. For spatial planning purposes, we therefore recommend that AES be preferentially implemented on ditch banks running parallel to nature reserves.

Species richness also appears to be affected by several other factors, such as the location relative to the prevailing wind direction and the nitrogen input on adjacent fields. This means that implementation of AES on ditch banks downwind of nature reserves and running parallel to the reserves, as well as reduced nitrogen fertilizer application on adjacent fields, may lead to conservation of a wider diversity of plant species (Middleton et al., 2006).

Our studies indicated that using delivery systems like AES to improve matrix quality would be of potential benefit to the approach involving increased landscape connectivity (Donald and Evans, 2006).

Traditional mowing regimes in farming sometimes lead to high plant species richness, partly by affecting the amount of seeds available for transportation by mowing equipment (Huhta and Rautio, 1998). Mowing has recently been discussed as a possible restoration measure, and its practicability has been tested in a range of ecosystem including fens, meadows, semi-natural grassland and field margins (Hansson and Fogelfors, 2000; Stammel et al., 2003; Middleton et al., 2006; Musters et al., 2009). On ditch banks, mowing on July 1st and Sept 1st would enhance seed dispersal. The higher number of seed-setting species found in nature reserves, combined with the later peak in seed set, further suggests it may be necessary to mow later in nature reserves and banks under long-term AES than on conventionally managed and short-term AES plots. Our studies also showed the highest number of seed-setting species on July 1st and Sept 1st, so other dispersal vectors, such as cattle, may also be arranged to transport the seeds at these times to achieve the highest level of seed transportation. For instance, farmers may let cattle out into the fields on July 1st and Sept 1st and move them among fields to promote seed transportation.

Regional community management

Since our studies suggest that nature reserves can act as a source of seeds for the surrounding areas, the presence of nature reserves should be given greater consideration in management policies.

In view of the large areas of agricultural land in the Netherlands, these areas can contribute considerably to the country's overall plant diversity. Agri-environment schemes should therefore consider large-scale contributions to diversity rather than focus entirely on the farm scale. Since several studies have demonstrated that fragmentation is a problem for nature reserves and our study found greater species diversity in larger AES-managed areas (Geertsema, 2005; Gabriel et al., 2006; Smits et al., 2008), expanding the size of AES areas adjacent to nature reserves would be helpful to enhance the plant species richness on ditch banks. We suggest that farmers implementing AES would be more successful if they selected ditch banks adjacent to those where a similar management regime is already in force.

Future research

Our research was a short-term study to describe species diversity patterns. Since dispersal processes on ditch banks are extremely limited and more time may be needed to make the dispersal from small-scale to large-scale measurable, it will still remain important to trace long-term species diversity patterns. This may eventually lead to a better understanding of the factors controlling the spatial and temporal distribution of biodiversity and help design effective strategies for conserving diversity on ditch banks (Loreau, 2000; Summerville and Crist, 2005).

Our understanding of the spatial variation in species composition on ditch banks will especially be increased by further studies addressing the effect of historic factors, as the environmental and dispersal factors we evaluated only explain a small portion of the spatial variation of the species composition. It has been suggested that historical factors may play an important role in the spatial variation in species composition (Hawkins and Porter, 2003; Nakamura et al., 2009) and therefore need to be investigated.

Our studies showed that AES-managed ditch banks running in parallel to nature reserves had much higher plant diversity at larger distances. The underlying ecological mechanism requires further study. It is worth investigating whether the effects of implementing AES adjacent to nature reserves would be enhanced by expanding the size of the AES-managed area, as several studies have demonstrated that fragmentation is a problem for nature reserves and our study found greater species diversity in larger AES areas (Geertsema, 2005; Gabriel et al., 2006; Smits et al., 2008). In addition, our study focused on species richness patterns at the level of individual landscape elements, whereas studying overall biodiversity on a regional or even larger scale would greatly improve our understanding of the ecological mechanisms behind the combination of nature reserves and AES. The effects of the size of nature reserves and of other landscape elements like wooded patched might also influence overall species diversity on ditch banks.

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Summary

The decrease in species diversity of European agricultural ecosystems has been widely documented in recent years. Most of the former agricultural biodiversity is now retained in non-productive landscape elements like nature reserves and ditch banks. Over the past 30 years, however, the species diversity of Dutch ditch banks has been in decline. Management practices aimed at conserving remnants of species-rich sites (i.e. nature reserves) or at enhancing the botanical diversity of agricultural areas (i.e. agri-environment schemes (AES)) have attracted growing attention. However, these practices often produce poor results and the effectiveness of the techniques used is still being questioned. The studies reported on in this thesis focused on restoration of plant species diversity on ditch banks.

The pattern of variation in species composition represents one of the central issues in modern ecology and provides the scientific basis for conservation planning. Compared with the patterns of species richness, however, spatial ddifferences and temporal changes in species composition have received far less attention. One aim of our study was thus to investigate the spatial and temporal patterns of species composition and to use this ecological information to reveal the processes that create or maintain diversity, and are therefore critical for plant diversity restoration on ditch banks (Part I, *Chapter 2* and *Chapter 3*). Previous research into ditch bank systems found that enhancing colonization, for instance by improving dispersal, rather than reducing extinction, might be more effective to increase species richness. Our studies examined the opportunities to improve the dispersal of plant species on ditch banks (Part II). One option is to focus restoration efforts on areas in the vicinity of species-rich locations (such as nature reserves). *Chapter 4* and *Chapter 5* tried to evaluate the possible spatial arrangements of nature reserves and AES-managed ditch banks for the most effective protection of biodiversity. Another aspect we studied is that of mowing regimes, which are likely to have major effects on plant species richness, in view of their impact on seed availability and dispersal. It was therefore important to test the effect of mowing date on seed-setting under different management regimes, to establish the most effective mowing regime for protecting and increasing plant diversity (*Chapter 6*).

Our study focused on the ditch banks located in the Krimpenerwaard area (in the western peat district of the Netherlands), which is among the most intensively exploited areas in Europe and is particularly rich in ditch banks. In this area, an extensive network of shallow ditches, canals, other water courses and dykes is part of the present-day “polder” landscape, which was created by reclamation and cultivation of the peat bogs formed after the last glacial period. Three main

management types are applied on ditch banks in this area: nature conservation, AES and conventional agricultural management. The nature conservation areas (nature reserves) are part of the same landscape as the surrounding areas. Their strategy aims for the conservation and restoration of the traditional farming landscapes with their associated extensive forms of agriculture and diversity of wildlife in a limited number of areas. The AES are characterized by a “no cure, no pay” system, whereby farmers are free to choose a particular management regime, but are recommended to apply the following treatments: first mowing at the end of June or beginning of July, zero fertilizer inputs, low stocking rate and deposition of material dredged from the ditches on the top of ditch banks. Conventional management is the regime implemented by farmers when given complete freedom. We mainly focused on 25 target species of nature conservation in our study. These species are valuable ditch bank plants as defined by the Dutch government and are used in rewarding farmers for AES implementation. They are not only easy to recognize, but are also supposed to be indicative of AES-based management of ditch banks.

Chapter 2 discusses hierarchical additive partitioning of plant species richness to analyze the spatial and temporal patterns of plant diversity on ditch banks. For all species, the beta diversity at different scales contributed more or less equally to the total species diversity, underlining the importance of differences in species composition between different spatial and temporal scales. The analysis of target species revealed that a larger proportion of the beta diversity was explained by spatial scales and much less by temporal scales, compared to that for all species. The rate of distance decay for target species decreased over time, probably due to improved environmental conditions rather than dispersal processes.

The proportions of diversity components differed between nature reserves and agricultural areas, with a higher within-site species diversity and lower between-site diversity in nature reserves. The different patterns of species diversity may be caused by characteristics of the management regimes, such as nutrient levels and grazing intensity. The dispersal of plant species in both nature reserves and agricultural areas is still limited and ecological restoration projects should therefore focus particularly on ways of increasing seed availability.

Chapter 3 presents a model to explain the spatial pattern of species composition in terms of the combined effects of dispersal and environmental factors on ditch banks. Dispersal factors such as geographic distance and spatial limitation of agricultural activities of individual farmers had significantly negative effects on the similarity of all species between plots, while other dispersal factors like the spatial limitation of water systems and environmental factors such as nutrient levels also had statistically significant effects on similarity of target species between plots.

The target species showed a higher rate of distance decay in species similarity compared with other species, and environmental determinants seem to be more important for these species.

Chapter 4 uses a conceptual model to determine whether the effects of restoration measures on ditch banks affect site-related limitations or seed availability limitations or both. We investigated whether nature reserves (seed sources) can improve species diversity in the surrounding areas and to what extent AES can enhance this effect, by studying the plant diversity of ditch bank vegetations at increasing distances from nature reserves. Plant diversity decreased significantly with the distance from the source communities in the reserves. There were considerable differences in species diversity between AES-managed and non-AES ditch banks, with the former showing greater plant diversity especially in the first 200 meters from nature reserves. The presence of all individual species decreased with the distance to a nature reserve, but the strength of this relationship and the effects of AES differed between species. AES-managed ditch banks had less severe site-related limitations for most plant species, but AES management did not affect the seed availability limitation. The study reported on in *Chapter 4* left unanswered the question of trends in plant diversity along banks running parallel to the edge of the reserves, which is necessary to get a clear picture of the impact of the entire network of nature reserves, AES and ditch banks.

The study reported on in *Chapter 5* therefore aimed to estimate the effects of synergy between nature reserves and AES on plant species within a network of ditch banks. Plant diversity was investigated on AES and non-AES ditch banks running parallel to the edge of a nature reserve, and compared with ditch banks running transverse to such reserves (*Chapter 4*). On non-AES ditch banks running parallel to nature reserves, there was a significant decline in species richness with increasing distance from the reserve, which demonstrated that synergy between nature reserves and AES can enhance plant diversity. Furthermore, this decline of diversity with distance appeared to be less pronounced than that occurring on ditch banks running in the transverse direction. Less human disturbance and more appropriate ditch water levels below the field surface would benefit the species diversity in relation to the distance. The effect of AES differed between ditch banks running in the transverse and parallel directions, with a significant effect beyond 200 m on the parallel banks and within 200 m on the transverse banks. Priority should therefore be given to implementing AES on the banks of parallel ditches at some distance from a nature reserve.

Chapter 6 reports on a comprehensive field study about the effect of mowing date on seed-setting on ditch banks. We applied biannual mowing regimes on plots under different management regimes (nature reserves, AES with short-time management, AES with long-time management and conventional management). The number of seed-setting species at the first mowing rose significantly as the time of mowing was delayed, whereas the number of seed-setting species at the second mowing was highest when the first mowing took place on May 15th and the second on Sept. 1st. Under biannual mowing regimes, considerably higher numbers of seed-setting species were observed when the first mowing was carried out on July 1st and the second on Sept. 1st. This suggests that mowing biannually, on July 1st and Sept. 1st may in principle be a optimal strategy to enhance seed dispersal on ditch banks. On plots under short-term AES and on conventionally managed plots, seed set peaked on Aug. 15th, while in nature reserves and on long-term AES plots this was on Sept. 1st. This suggests that nature reserves and long-term AES ditch banks should be mown at later dates than conventionally managed and short-term AES plots.

Chapter 7 presents a synthesis of the discussions in Chapters 2-6 and discusses options for conservation and further research. The results of the research support the idea of combining nature reserves and AES to increase plant diversity on ditch banks. The locations of AES should be chosen carefully, since their effect differs between banks running in different directions. Other factors which might enhance the effect of AES, such as location downwind of and parallel to nature reserves, and lower nitrogen inputs on adjacent fields, should also be taken into consideration in conservation strategies. Mowing was considered as a possible restoration measure, and the effect of the mowing regime on seed availability for transportation suggested a general mowing scheme to increase seed dispersal. Moreover, for the conservation of some rare and internationally valued species tailored mowing regimes may be needed.

Samenvatting

De achteruitgang van de soortenrijkdom in de Europese landbouw gedurende de afgelopen jaren is uitgebreid gedocumenteerd. Veel soorten van het vroegere agrarisch landschap komen alleen nog voor in natuurreservaten en in niet-productieve landschapselementen, zoals slootkanten. Toch gaat ook in de slootkanten in Nederland de plantensoortenrijkdom achteruit. Natuurbeheer richt zich enerzijds op het behoud van soortenrijke locaties, zoals in natuurreservaten en anderzijds op het verbeteren van de biodiversiteit in de agrarische gebieden zelf: agrarisch natuurbeheer. De bereikte resultaten van het agrarisch natuurbeheer zijn beperkt en de effectiviteit van de genomen maatregelen staat dan ook ter discussie. Dit proefschrift richt zich op het herstel van de plantendiversiteit in slootkanten.

In de moderne ecologie is het ruimtelijk patroon in de verscheidenheid van soortengemeenschappen een van de centrale thema’s. Dit levert een wetenschappelijke basis voor de ruimtelijke planning van het natuurbehoud. Vergeleken met de patronen in soortenrijkdom, krijgen de patronen in soortensamenstelling (ruimtelijke verschillen en temporele veranderingen) veel minder aandacht. Het eerste doel van deze studie is dan ook om de ruimtelijke en temporele patronen in soortensamenstelling te onderzoeken en om zichtbaar te maken welke processen de soortendiversiteit op landschapschaal bepalen. Inzicht in deze processen is van cruciaal belang voor het herstel van de plantendiversiteit in slootkanten (deel I, hoofdstuk 2 en hoofdstuk 3).

Eerder onderzoek aan slootkantvegetaties toont aan dat, om de soortenrijkdom te verhogen, vergroting van de kolonisatiemogelijkheden van soorten efficiënter kan zijn dan de vermindering van het lokaal uitsterven van soorten. Het tweede doel van deze studie (deel II) richt zich dan ook op de mogelijkheden om de verspreiding van plantensoorten in slootkanten te verbeteren. Een mogelijkheid is om het agrarische natuurbeheer uit te voeren in de nabijheid van gebieden die al soortenrijk zijn, zoals natuurreservaten. Hoofdstuk 4 en hoofdstuk 5 beschrijven het onderzoek naar de ruimtelijke schikking van slootkanten met agrarisch natuurbeheer ten opzichte van natuurreservaten. Een andere mogelijkheid om de verspreiding van plantensoorten te verbeteren is een optimale afstemming van de maaidatum op de beschikbaarheid van zaden voor transport met bijvoorbeeld maaimachines (hoofdstuk 6).

Het onderzoek is uitgevoerd in slootkanten van de Krimpenerwaard, een deel van het westelijk veenweidegebied van Nederland dat behoort tot de meest intensief gebruikte gebieden van Europa. In dit gebied komt een uitgebreid netwerk voor van sloten en andere waterlopen die vanaf de middeleeuwen zijn ontstaan bij de ontginning van de venen. Drie belangrijke vormen van slootkantenbeheer worden hier momenteel toegepast: natuurbeheer in reservaten, agrarisch natuurbeheer en gangbaar agrarisch beheer. Het beheer in natuurgebieden is gericht op het in stand houden en herstellen van de diversiteit aan planten en dieren behorende bij het traditionele agrarische landschap. Het agrarisch natuurbeheer wordt gekenmerkt door een "no cure, no pay"-systeem, waarbij de boeren vrij zijn hun beheer te kiezen. De boeren wordt evenwel aanbevolen om: niet maaien vóór eind juni of begin juli; geen meststoffen toe te dienen; een lage veebezetting te realiseren; en het materiaal van het schonen en baggeren van de sloten niet op de slootkanten achter te laten. Gangbaar beheer passen de landbouwers toe op slootkanten die niet vallen onder het agrarisch natuurbeheer. Het slootkantbeheer in het agrarisch gebied is voornamelijk gericht op 25 doelsoorten. Deze soorten worden door de Nederlandse overheid beschouwd als waardevolle slootkantplanten en worden gebruikt bij de beloning van boeren voor hun agrarisch natuurbeheer. Ze zijn niet alleen gemakkelijk te herkennen, maar worden ook geacht indicatief te zijn voor succesvol agrarisch natuurbeheer van slootkanten.

Hoofdstuk 2 bespreekt de opdeling van regionale plantensoortenrijkdom (gamma-diversiteit) in lokale soortenrijkdom (alfa-diversiteit), ruimtelijke verschillen in soortenrijkdom (ruimtelijke beta-diversiteit) en verandering in soortenrijkdom (temporele beta-diversiteit). Het blijkt dat voor alle soorten samen, de twee vormen van beta-diversiteit min of meer in gelijke mate bijdragen aan de totale soortenrijkdom. Bij de analyse van de doelsoorten blijkt dat een groter deel van de beta-diversiteit wordt verklaard door de ruimtelijke verschillen en een veel kleiner deel door veranderingen in de tijd. Voor de doelsoorten geldt tevens dat de afname van de similariteit in soortensamenstelling tussen plots met de geografische afstand tussen plots in de loop der jaren is verminderd, waarschijnlijk als gevolg van verbeterde milieuomstandigheden.

De verhouding tussen de diversiteitcomponenten (alfa- vs. beta-diversiteit) verschilt tussen natuurgebieden en agrarische gebieden. Er is een hogere alfa-diversiteit en een lagere ruimtelijke beta-diversiteit in natuurgebieden. Dit verschil in de verhouding tussen de diversiteitcomponenten kan veroorzaakt worden door verschillen in voedselrijkdom en beweidingintensiteit, ten gevolge van verschillen in beheer. De verspreiding van plantensoorten tussen zowel natuurgebieden als agrarische gebieden is beperkt en bij projecten gericht op herstel van soortenrijkdom dient dan ook aandacht te worden geschonken aan manieren om zaad beter te verspreiden.

Hoofdstuk 3 presenteert een model om het ruimtelijk patroon van de plantensoortensamenstelling in slootkanten te verklaren op grond van verspreidings- en omgevingsfactoren. Als alle soorten in de analyse worden betrokken, dan hebben verspreidingsfactoren zoals de geografische afstand en de ruimtelijke beperking van de activiteiten van individuele boeren een significant negatief effect op de similariteit tussen plots. Bij de doelsoorten hebben andere factoren, zoals de ruimtelijke beperking van de watersystemen en nutriëntenniveaus ook een significant effect op de similariteit tussen plots. De doelsoorten vertonen een sterkere afname van similariteit met de geografische afstand dan alle soorten samen, en milieufactoren lijken belangrijker te zijn voor de doelsoorten.

Hoofdstuk 4 maakt gebruik van een conceptueel model om te bepalen of de effecten van agrarisch natuurbeheer op slootkantenplanten een gevolg zijn van het opheffen van beperkingen van de standplaats, van de zaadverspreiding of van beide factoren. Onderzocht is of de nabijheid van een natuurgebied (als zaadbron) de plantensoortenrijkdom in de slootkanten in de omliggende gebieden kan verbeteren en in welke mate agrarisch natuurbeheer dit effect kan versterken. De plantensoortenrijkdom neemt in slootkanten die van een natuurgebied af lopen aanzienlijk af met toenemende afstand tot het natuurgebied. Er waren grote verschillen in soortenrijkdom tussen slootkanten met agrarisch natuurbeheer en gangbaar beheerde slootkanten, waarbij het eerste type slootkanten een grotere soortenrijkdom vertoonde in de eerste 200 meter van het natuurgebied. Alle individuele soorten namen in abundantie af met toename van de afstand tot het natuurgebied, maar de mate waarin en het effect van agrarisch natuurbeheer verschilde tussen soorten. Voor de meeste plantensoorten zijn de standplaatsbeperkingen in slootkanten met agrarisch natuurbeheer kleiner, maar agrarisch natuurbeheer had geen invloed op de beperking van zaadverspreiding.

De studie beschreven in hoofdstuk 4 laat de vraag onbeantwoord of dit ook geldt voor slootkanten die evenwijdig lopen aan de rand van de natuurreservaten. Beantwoording van deze vraag is nodig om een duidelijk beeld te krijgen van het gehele netwerk van natuurgebieden en de ligging van agrarisch natuurbeheerde slootkanten daarbinnen. In hoofdstuk 5 zijn dan ook de effecten van de synergie tussen natuurgebieden en de ligging van de slootkanten met agrarisch natuurbeheer onderzocht. De plantensoortenrijkdom is onderzocht in slootkanten met agrarisch natuurbeheer en conventioneel beheerde slootkanten die parallel lopen aan de rand van een natuurgebied, en vergeleken met slootkanten die van de natuurgebieden af lopen (hoofdstuk 4). In conventioneel beheerde slootkanten die evenwijdig lopen aan natuurgebieden, wordt een significante daling van de soortenrijkdom met toenemende afstand tot het natuurgebied gevonden. Deze daling van de diversiteit is echter minder sterk dan die in de slootkanten die van het natuurgebied af lopen. Minder menselijke verstoring en een ander slootpeil lijkt dit verschil te verklaren. Het effect van agrarisch natuurbeheer verschilde tussen de aan het natuurgebied parallellopende slootkanten en de van het natuurgebied af lopende slootkanten, met een significant positief effect op afstanden groter dan 200 m in parallelle slootkanten en juist een positief effect op minder dan 200 m in af lopende slootkanten. Voor de parallel georiënteerde slootkanten geldt dus dat agrarisch natuurbeheer vooral zou moeten plaatsvinden in slootkanten op enige afstand van een natuurgebied.

Hoofdstuk 6 beschrijft een uitgebreide veldstudie naar het effect van de maaidatum op de beschikbaarheid van zaad voor zaadverspreiding in slootkanten. Een tweejaarlijks maairegime is toegepast op slootkanten onder verschillend beheer (natuurbeheer in natuurgebieden, langjarig agrarisch natuurbeheer (langer dan 16 jaar), kortstondig agrarisch natuurbeheer (korter dan 6 jaar) en gangbaar beheer). Het aantal zaaddragende soorten op de eerste maaidatum neemt sterk toe als de maaidatum wordt opgeschoven in het seizoen. Het aantal zaaddragende soorten op het tweede maaitijdstip is het hoogst wanneer de eerste maaidatum 15 mei en de tweede maaidatum 1 september is. Het totaal aantal zaaddragende soorten onder een tweejaarlijks maairegime is het hoogst wanneer de eerste maaidatum 1 juli en de tweede maaidatum 1 september is. Dit suggereert dat de kans op verspreiding van zaden optimaal is als er eerst rond 1 juli wordt gemaaid en daarna rond 1 september. In slootkanten met een kortstondig agrarisch natuurbeheer en met gangbaar agrarisch beheer, is het aantal zaaddragende soorten het hoogst rond 15 augustus, terwijl in slootkanten met natuurbeheer en met langjarig agrarisch natuurbeheer dit rond 1 september is. Dit suggereert dat slootkanten in natuurgebieden of met langjarig agrarisch natuurbeheer gemaaid moeten worden op een later tijdstip dan slootkanten met gangbaar agrarisch beheer of met kortstondig agrarisch natuurbeheer.

Hoofdstuk 7 presenteert een synthese van de discussies in de hoofdstukken 2-6 en bespreekt mogelijkheden voor natuurbeheer en verder onderzoek. De resultaten ondersteunen het idee van het afstemmen van natuurbeheer in natuurgebieden en agrarisch natuurbeheer in het omringende agrarisch gebied ter verhoging van de soortenrijkdom in slootkanten. De locaties voor het agrarisch natuurbeheer moeten zorgvuldig worden gekozen, omdat het effect ervan afhangt van richting waarin de slootkanten lopen ten opzichte van het natuurgebied. Ook is de positie van de slootkanten ten opzichte van de natuurgebieden in relatie met de windrichting, en een lagere nutriëntengift op aangrenzende percelen van belang. Een algemeen geldend maairegime kan gebruikt worden om de vergroting van de soortenrijkdom door optimale verspreiding van zaden te bevorderen. Maar voor de bescherming en het herstel van bepaalde mindere algemene soorten kan een maairegime op maat nodig zijn.

Curriculum Vitae

Xin Leng was born on Nov. 11th, 1981 in Danyang, Jiangsu, China. In 1999, she started her university education at the Department of Biology, Nanjing University, China. During this period, she carried out a six-month research project for her undergraduate dissertation in the group of Prof. Shuqing An. The project focused on genetic diversity of insular endangered species *Ilex integra*. After she achieved her Bachelor's degree in June 2003, she became a graduate student at the Department of Ecology of the same university, exempted from the entrance examination. Her master project is a follow up study of her bachelor's dissertation, focusing on genetic diversity of insular endemic species and rare and endangered species. In the year 2005, she obtained her Master's degree at the Nanjing University, China. The same year, she was awarded a scholarship by the Chinese Scholarship Council (CSC) to pursue her PhD at the Institute of Environmental Sciences, Leiden University, The Netherlands. From 2005 to 2006, she followed successfully a one-year professional research training programme at the Graduate School of Science of Leiden University and started with her PhD research. From 2006 to 2010 she did her study on the subject *Restoration of ditch bank plant diversity: the interaction between spatiotemporal patterns and agri-environmental management*, under the supervision of Prof. Dr. Geert R. de Snoo and Dr. C.J.M. Musters. Since Jan 1st, 2010, she is appointed as lecturer in Nanjing University, China.

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Restoration of plant species diversity of ditch banks
ecological constraints and opportunities