


climate changes spatial planning

Adaptation

Climate change and habitat fragmentation; impacts and adaptation strategies

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Contents

Summary

Summary in Dutch

In het onderzoeksproject zijn de effecten van klimaatverandering op de natuur onderzocht, met speciale aandacht voor de interactie met versnippering. Uit de resultaten blijkt dat soort eigenschappen een goede indicator zijn om de gevoeligheid van soorten voor klimaatverandering te voorspellen. Vier groepen van eigenschappen zijn daarbij bepalend: dispersiecapaciteit, mate van habitatspecialisatie, groeicapaciteit en de omvang en ligging van het huidige verspreidingsgebied. Er is aangetoond dat versnippering van leefgebied de negatieve effecten van klimaatverandering versterkt. Door klimaatverandering verschuiven de geschikte klimaatzones van soorten.
Versnippering vertraagt of blokkeert het kolonisatieproces dat nodig is voor het volgen van deze verschuivende klimaatzones. Modelsimulaties tonen aan dat de verwachte toename van weersextremen als gevolg van klimaatverandering in versnipperd leefgebied vaker tot extincties zal leiden. Een nuancering van deze algemene conclusie geldt voor dagvlinders. Uit het onderzoek blijkt dat dagvlinders bij hogere temperaturen mobieler worden wat de kolonisatie juist bevordert. Diverse adaptatiestrategieën zijn ontwikkeld om het adaptief vermogen van de Ecologische Hoofdstructuur (EHS), te versterken en daarmee de natuur klimaatbestendiger te maken. Het is aan te bevelen deze maatregelen te concentreren in zogenaamde klimaatcorridors of clusters. Uit bijeenkomsten met regionale stakeholders blijkt dat groenblauwe dooradering als adaptatiemaatregel in het multifunctionele landschap de meeste steun krijgt.

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Summary

In the project the impacts of climate change on biodiversity, was studied, especially focusing on the interaction with habitat fragmentation. Based on the results it was concluded that species traits are useful indicators to predict species sensitivity to climate change. Four groups of traits stand out as important regarding the sensitivity for climate change: dispersal capacity, degree of habitat specialization, demographic traits related to population growth rate, and the present size and position of the species' range.
It was shown that habitat fragmentation increases the negative effects of climate change. Climate change causes a shift of suitable climate zones for species. Fragmentation slows down or even blocks the colonization process that is necessary to track the shifting climate zones. Model simulations predicted that increased weather variability would lead to higher extinction probability, especially in fragmented landscapes. A refinement on this general conclusion should be made for butterflies, which were found to become more active and more successful colonizers under warmer conditions. Several adaptation measures were developed to enhance the adaptive capacity of the national ecological network to cope with climate change and it was recommended to concentrate these measures in 'climate adaptation zones'. The implementation of 'green blue veining' as an adaptation measure in multifunctional landscapes was best accepted by regional stakeholders.

Extended summary

Species traits are good predictors for sensitivity to climate change

One of the main research questions of the research project was whether it would be possible to predict species' sensitivity to climate change. It was concluded that several species traits and range characteristics are useful indicators to predict which species are most vulnerable for the impacts of climate change. One of the impacts of climate change is the shift of suitable climate zones. As a response species need to expand their range to be able to track the shifting suitable habitat zone. Therefore traits that are related to colonizing capacity are especially important to identify species sensitivity: a large dispersal capacity, a large number of dispersers (related to small area requirements and/or a broad habitat choice) and a large population growth capacity are all traits that enhance the colonization and population establishment capacity. Also the current size of the species range is an important indicator to identify vulnerable species, especially when species are not able to keep track with the rate of climate change. A large range provides more time until the climate will stabilize again.

Sensitivity to weather extremes partly relates to habitat choice and type of extremes. Weather extremes in the Netherlands, for instance, will lead to more frequent and longer periods of drought or extreme downpours. Especially species that are sensitive to environmental stochasticity may show more population fluctuations with increasing weather variability: e.g. small short lived species are more sensitive than large long-lived species.

Interaction between climate change and habitat fragmentation

An important focus of the project was on the interactions between climate change and habitat fragmentation and their impacts on species survival and genetic adaptive capacity. Model simulations and analysis of empirical data showed that habitat fragmentation increases the negative effects of climate change. It slows down or even blocks the colonization process that is necessary for range expansion. A refinement on this general conclusion should be made for butterflies, where a field experiment revealed that butterflies become more active and hence more successful colonizers under warmer conditions. Thus the warming of the climate might to some extent reduce the effects of habitat fragmentation for butterflies and perhaps also for other ectothermic species.

Metapopulation models predicted that increased weather variability, which is expected to become more pronounced under climate change, lead to higher extinction probability of populations, especially in fragmented landscapes. This negative effect of climate extremes could be compensated by enlarging patch size, thus increasing the amount of habitat in the landscape.

Remarkably, model simulations predicted that species will lose genetic diversity during range shifts, even when the population size remains stable and the species seems to be able to track the shifting suitable climate zone. More habitat in the landscape has some positive impact on genetic diversity, but is not able to completely compensate the loss. As loosing genetic diversity will diminish the capacity within species to cope with present and future disturbances, it is important to protect areas where species have existed for a long time or where the future climate is predicted to remain suitable, as modern refugia of genetic diversity.

We developed a general indicator that predicts which species are most vulnerable to climate change-induced range shifts. Survival time depends on species' range size (the larger the better), the observed northward species' expansion (the faster the better), which is an interplay of species traits (large dispersal and growth capacity) and landscape characteristics (good spatial cohesion), and the rate of climate change (the slower the better). This general indicator is a potentially powerful tool for identifying those species most at risk and those areas where the landscape cohesion is insufficient. An important future research step should be to test its usefulness using field observations.

Adaptation strategies for the national ecological network (EHS)

Two impacts of climate change emerged that might reduce the effectiveness of the EHS to protect biodiversity: 1) temperature rise may necessitate species' range shifts that might be blocked by habitat fragmentation; 2) increased weather variability may cause additional population fluctuations that will increase extinction risks. It was recommended to increase the robustness of the EHS to cope with these additional effects of climate change.

The following adaptation measures were defined:

- Improving (international) connectivity over large distances by resolving dispersal bottlenecks and thus facilitating range shifts. Linking habitat networks will enable species to colonize habitats that will become suitable, and this will compensate for the loss of habitat at the contracting side of its range.
- Increasing the carrying capacity of protected areas by either enlarging the size of protected areas or improving habitat quality, or both. Increasing the carrying capacity gives room to larger populations, and thereby compensates for increased extinction probabilities caused by increased weather variability.
- Increasing spatial heterogeneity within a nature area and better accommodating natural landscape-forming processes e.g. sedimentation, marshland development, meandering of rivers and freshwater-salt water gradients. This is a strategy to cope with increased weather variability, as large scale correlated population fluctuations can be avoided. For instance, in heterogeneous habitat some parts may allow a positive growth rate in very dry years, whereas other parts may be optimal during wet years.

It was recommended to combine and spatially concentrate these adaptation measures in so called 'climate adaptation zones'.

Two regional case studies were performed in order to explore which adaptation strategies, to increase the adaptive capacity of the EHS in the multifunctional landscape, are best accepted by regional stakeholders. Several adaptation measures outside nature areas were developed that contribute to the adaptive capacity of the EHS. By implementing these adaptation measures on farmland adjacent to nature areas the amount of area to be acquired for nature at the expense of farmland can be minimized. It is expected that multifunctional adaptation will contribute to the regional support for these measures, especially when also other benefits are achieved as well, such as climate adaptation of water management and improvement of recreational and aesthetical landscape values.
The adaptation measure to increase the amount of green-blue veining was rated most positive in all focus group discussions. According to farmers these linear measures along field margins fit best with modern farming practices. According to nature managers and policy makers green-blue veining is the most effective adaptation measure to improve the quality of nature areas.

PART I

1. Introduction

Climate change has large impacts on biodiversity and the functioning of ecosystems. It is expected to become the greatest driver of global biodiversity loss together with land-use change (Thomas et al. 2004; Millennium Ecosystem Assessment 2005). Climate change is likely to continue, leading to a global temperature increase of 2–4 °C in 2100 (IPCC 2007). In the Netherlands the changes in climate are already apparent and relatively strong (KNMI 2008). Since 1900 the mean temperature has increased with 1.7 oC, compared to a worldwide mean increase of 0.8 °C. Also the precipitation in this period has increased with 18%, with more frequent extreme downpours. Future climate change scenarios for the Netherlands, derived from the IPCC scenarios (KNMI 2006), predict an additional rise in temperature, compared to 1990, ranging from 1.8 to 5.2 °C by 2100.

For ecosystems it is recognized that they are on the one hand threatened by climate change but on the other hand part of the adaptation solution as they perform important services for society such as climate regulation, carbon sequestration, protection against flooding and prevention of soil erosion. To safeguard these services for society resilient ecosystems are needed that are able to cope with impacts of climate change, such as the increased dynamics caused by weather extremes and the shifting of suitable climate zones (Commission of the European Community 2009).

One of the major concerns for nature conservation is that nature cannot adapt adequately, because the rate of climate change is unprecedented and the effects of climate change are expected to be aggravated by habitat deterioration and fragmentation (Opdam & Wascher 2004).

Ecological networks are a well known strategy for sustainable biodiversity protection in highly fragmented landscapes (Jongman & Pungetti 2004). In the Netherlands the National Ecological Network (EHS) was developed in the beginning of the 1990's, in order to improve conditions, extend natural areas and enhance functional connectivity. This habitat network concept also plays an important role in building the Natura 2000 network, the European Union system of protected areas. Recently the question has surfaced whether the EHS, including the Natura 2000 areas that are embedded in the EHS, is sufficient to cope with climate change or that additional measures are necessary to make ecosystems more resilient to the effects of climate change.

The research project 'Strategies for optimizing the nature conservation potential of the Dutch Ecological Network (EHS) and the surrounding multifunctional farm landscape under predicted climate change scenarios' focused on the following main research questions:
Section I Research on the impacts of climate change on biodiversity:

- Is it possible to predict species responses to climate change based on species traits and to identify which species and ecosystems are sensitive to the negative effects of climate change and which might benefit from climate change?
- What are possible interactions between climate change and habitat fragmentation and their impacts on species survival and genetic adaptive capacity?

Section II Application of our results in case studies:

- What are possible adaptation measures for increasing the adaptive capacity of the EHS, including the Natura 2000 areas, to cope with the effects of climate change?
- What are possible measures to increase the adaptive capacity of the EHS and the Natura 2000 areas in the multifunctional landscape? In regional case studies it is being explored which measures are best accepted by regional stakeholders.

2. Species traits and responses to climate change

2.1 Introduction

One of the main research goals of the project was to identify species traits that are sensitive to the negative effects of climate change or might benefit from climate change. To answer this question empirical field data were analyzed and experimental research was performed in order to link species traits and responses to weather conditions for different taxonomic groups: birds, plants and butterflies. Two aspects of climate change were distinguished: gradual changes such as the increase in temperature and increases in weather variability (or weather extremes); the latter resulting for the Netherlands in more frequent and longer periods of drought and heavy precipitation (KNMI 2006). A database was generated that gives the response to climate change for about 3000 species in the Netherlands. This enabled us to generalize our results from single species to habitat types.

2.2 Analysis of empirical data and experimental research

2.2.1 Plants

One of the best documented effects of climate change on biodiversity of different taxa is the observed shift of species' distributions towards the poles and to higher elevations (e.g. Juliard *et al*. 2004; Hickling *et al*. 2006). In our project we analysed to what extent vascular plant species distributions have changed as a consequence of climate change in the coastal dunes, using data from FLORBASE (Pierik *et al.* in prep). We selected km-cells along a south – north gradient along the Dutch coast (c. 240 km). This database offers the opportunity to compare the plant species composition and distribution in the period before climate change became apparent (1975-1991) with that after climate change became clear (1992-2006). Our results showed a strong increase of thermophilic species in the period 1992-2006 compared to the period 1975-1991, which was also found in a nation-wide analysis (Tamis *et al*. 2005). This increase of thermophilic (warmth prefering) species especially occurred in the relatively urbanized areas in the dunes. Overall, the mean northern border of the species distributions shifted 3.3 km northwards. The marginal, thermophilic species, which are mainly colonizing the Netherlands from the south, also shifted northwards. However the average southern border of all species distributions did not significantly change between the periods, which means that we did not observe an overall range contraction. An asynchrony between range contraction and expansion has been reported in literature (e.g. Walther et al. 2002) and this might be caused by a time lag to extinction (extinction debt). However it might also be due to local adaptation, if species are (to some extent) able to survive the new climatic conditions. No evidence was found that the dispersal ability of species influenced changes in the distribution significantly (but see chapter 3). This might be related to the fact that the coastal dunes form a relatively well connected ecosystem.

The extent to which vascular plant species are sensitive to increased climate variability is, for temperate regions, probably linked to resistance to heat waves and consequently resistance to summer droughts, which is positively correlated with nutrient stress tolerance (Tamis & Pierik submitted). There are indications that effects of climate extremes are already visible in the Dutch flora, as plants of dry sites showed a stronger increase compared to plants of moist or wet conditions (Tamis & Pierik submitted).

2.2.2 Butterflies

For butterflies response to climate change has been reported to depend on species mobility and degree of habitat specialism. Warren *et al.* (2001) showed that only those species capable of dispersing over large distances or using widespread habitats were able to respond to climate change by expanding northwards. This was supported by a Finnish study where mobile butterfly species living in forest edges and using woody plants as their larval hosts, exhibited the largest range shifts towards the north (Pöyry et al. 2009). As the research project especially focussed on the interaction between climate change and habitat fragmentation an experiment was carried out to study the impacts of weather conditions on butterfly mobility, in order to investigate the potential impact of future weather conditions on colonization in fragmented landscapes.

The experiment showed that climate change actually may reduce effects of fragmentation by enhancing flight behaviour and dispersal of butterflies, in which the body temperature is controlled by weather conditions. Behavioural components of dispersal of butterflies were enhanced, and colonization frequencies increased under weather conditions associated with anticipated climate change (Cormont *et al.* submitted a). In a field experiment, flight behaviour and mobility of four butterfly species under different weather conditions were recorded: two habitat generalists, small heath (*Coenonympha pamphilus* L) and meadow brown (*Maniola jurtina* L.), and two specialists, heath fritillary (*Melitaea athalia* Rott.) and silver studded blue (*Plebejus argus* L.). As expected activity generally increased with temperature and decreased with cloudiness. Net displacement generally increased with temperature. When butterflies fly longer, start flying more readily, and span longer distances, we expect dispersal propensity to increase. Data on colonization over the period 1990-2008 (Dutch Butterfly Monitoring Scheme, Van Swaay *et al.* 2008), showed a significant increase in colonization frequencies with temperature and radiation and decreased with cloudiness. Increased dispersal propensity at local scale might therefore increase functional connectivity in fragmented habitat at a regional scale. Thus future temperature increase might to some extent reduce the effects of habitat fragmentation for butterflies, which might also hold for other ectothermic species.

Another analysis (WallisDeVries et al. submitted) showed that while increasing temperatures indeed benefit a good number of butterfly species, weather extremes such as summer drought, are especially detrimental to habitat specialists.

2.2.3 Birds

Population dynamics of bird species are changing in response to increased occurrence of weather extremes, presumably through increased variation in adult survival and reproduction success, and this was shown to be dependent on species traits (e.g. Jiquet et al. 2006). In our project, we investigated whether forest and marshland bird species could be divided in groups based on various life-history traits and whether these groups correlate with differential trends in abundances and responses to weather conditions (Cormont *et al.* submitted, b). Several strategies or traits that jointly appear in bird species stood out. Waterfowl that often breed at ground or water level, feed on plant material, and in which the young are relatively mobile from the moment of hatching, and are residential in general, were negatively impacted by severe winters, probably due to increased adult mortality. These species are expected to benefit from the milder winters predicted by the climate change scenarios.

Furthermore, we found a decline in population sizes of insectivorous long-distance migrants

correlated with mild winters and warm springs. This could possibly be explained by a reduced reproduction success due to mismatches in food supply because of different phenological responses in the food chain (Van Turnhout *et al.* 2010).
The demographic traits clutch size, number of clutches, and age at first reproduction were correlated with enhanced recovery after a drop in population size following severe winters. If we extrapolate these correlations to future climate predictions we are able to point out species that are expected to show most significant responses to weather circumstances under climate change.

2.3 Generalizing to impacts on communities

A CD-ROM was produced with data on potentially shifting suitable climate zones for more than 3000 European species (Van der Veen et al. 2010). Bio-climate envelope models predict additional large future range expansions of several hundred kilometers during the 21st century. The extend of the range shift will depend on the climate change scenario (Harrison et al. 2006; Huntley et al. 2007), while ranges are predicted to contract where the climate is no longer suitable. These potential range shifts were interpreted for their impacts on the occurrence of species in the Netherlands, identifying species for which the suitable climate zone is either expected to contract, to expand or to remain central in the Netherlands in the next century (Geertsema et al. 2010). These different responses may lead to reorganization of existing communities. In Figure 2.1 the percentages of expanding or contracting target species for the main ecosystem types of the EHS are presented. Out of eleven important ecosystem types for nature conservation six have larger percentages of contracting than of expanding species, for four types these percentages are approximately similar, while one ecosystem type (dry oligotrophic grasslands) showed a higher percentage of increasing than decreasing species. The most sensitive ecosystem type is the oligotrophic bogs and moist heathlands. The predicted range shifts indicate that for about half of the target species in this ecosystem type the Netherlands will become unsuitable with the future climate.

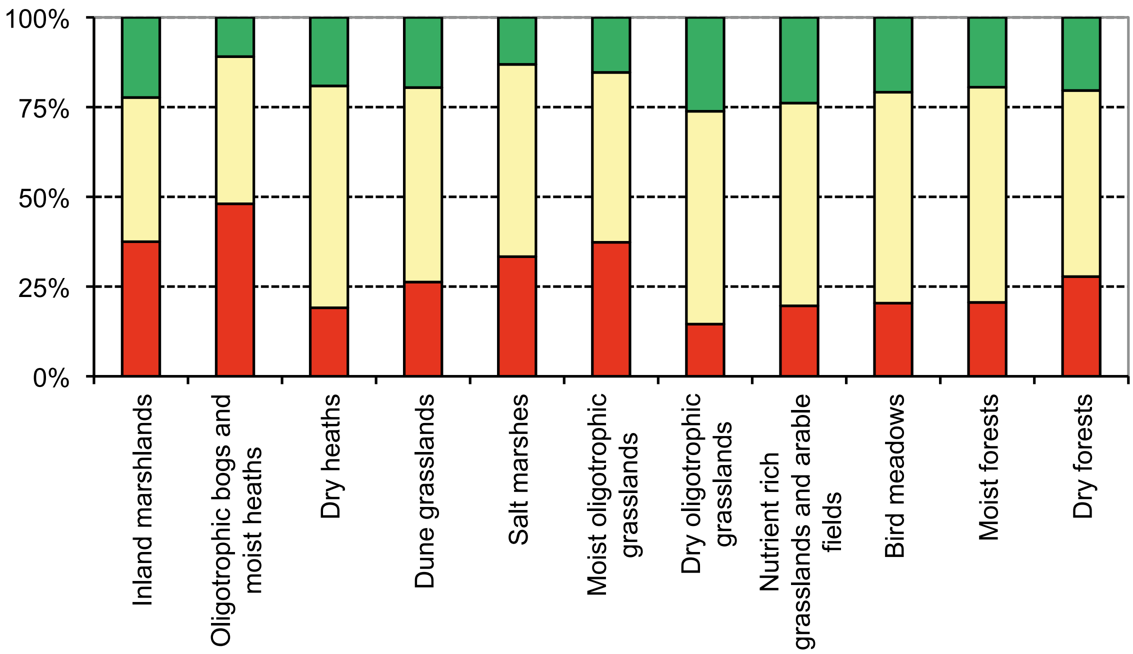

Figure 2.1. Percentage of contracting (red), neutral (yellow) or expanding (green) target species of important ecosystem types for nature conservation in the Netherlands.

3. Interaction between climate change and habitat fragmentation

3.1 Introduction

A special focus was put on the interaction between climate change and habitat fragmentation. For instance species with limited dispersal capacity or scarce suitable habitat might not be able to follow their shifting suitable climate space (Warren *et al.* 2001). This possible interaction was illustrated by analyzing the colonization process by plants species of a recently developed polder in the Netherlands (section 3.2.1). Also we developed a method to identify bottlenecks in the spatial cohesion of ecosystem networks, where species might not be able to disperse (section 3.2.2).
To keep track with climate change, species not only need to be able to colonize new climate space, but they also need to do this fast enough. Devictor *et al.* (2008) analyzed population trends in French bird communities. Although bird communities have shifted 90 km northwards in the last 20 years, the temperature shifted 270 km in the same period. Thus even relatively mobile species like birds are not keeping track, which might partly be caused by lack of suitable habitat. To better understand the underlying processes, we modeled metapopulation dynamics in shifting suitable climate zones (section 3.2.3).
Subsequently the impacts of range shifts on the genetic diversity of species were studied. Loss of genetic diversity might reduce species' adaptive capacity to future climate change and other disturbances (section 3.2.4). Empirical studies into the effects of species' range expansions after the ice ages have shown that populations in newly colonized regions contain only part of the total genetic diversity present in the ice age refugia (Hewitt 1996).

Another interaction between climate change and habitat fragmentation concerns the impact of weather extremes. It is expected that large scale synchronized disturbances, such as flooding or periods of extreme drought, will increase population fluctuations and extinctions. In section 3.3 the impact of additional weather variability on spatial standards for viable populations in habitat networks was explored.

3.2 Range expansion and habitat fragmentation

3.2.1 Colonization capacity of plants

The ability of plant species to colonize new habitats in the Dutch IJsselmeerpolders, the youngest of which were reclaimed from the sea 70 years ago was analyzed (Pierik et al. 2010). In these polders, forest lots have been planted throughout the agricultural landscape, which has created habitat islands for specialist forest species in an inhospitable matrix of intensively used agricultural land (cf. Holt et al. 1995). We related the distribution of forest specialist species in the understory of 55 forests in these polders to the following forest characteristics: age, area, connectivity, distance to the mainland (as a proxy for distance to the seed source) and path density.
The importance of the forest parameters differed between dispersal groups and also between individual species. After 60 years, 75% of the potential pool of wind-dispersed species had reached the polders, whereas this was only 50% for the species which lack specific adaptations to long distance dispersal. The colonization success of common species that lack clear adaptations to long-distance dispersal is affected by the spatial configuration of the forests and the majority of the rare species that could potentially occur in these forests is still absent.

These findings imply that especially rare species which lack specific adaptations to long distance seed dispersal and which are underrepresented in the regional species pool will have difficulties with colonization of new areas, when, due to climate change, they have to migrate to remain in their suitable range.

3.2.2 Identifying bottlenecks for range expansion in NW-Europe

Ranges are predicted to shift over hundreds of kilometers (Huntley *et al.* 2007). For European nature policy makers this raises the question whether the current conservation strategy allows species to track the moving suitable conditions. For example, it is unknown to what extent and where the spatial cohesion within the Natura 2000 network is sufficient and where isolation of protected sites may prevent the expansion of species ranges into new climate space. By combining bioclimate envelope models (SPECIES model; Pearson *et al.* 2002) with dispersal models (GRIDWALK model Schippers *et al.* 1996), areas were identified where the spatial cohesion of the ecosystem pattern was expected to be insufficient (Vos *et al.* 2008). For each of three ecosystem types, three species were selected that showed a shift in suitable climate space and that differed in habitat fragmentation sensitivity. For 2020 and 2050 (climate change scenario HadCM3, A2 scenario IPCC 2001), the amount of climatically suitable habitat in northwest Europe diminished for all studied species. Figure 3.1 shows that a significant amount of new suitable habitat for the Agile frog (*Rana damatina*) could not be colonized because of isolation. Together, this will result in a decline in the amount of suitable and occupied habitat protected in Natura 2000 sites. These model results can be applied to identify areas where an increase of the spatial cohesion of the Natura 2000 network would be most effective to facilitate range expansions.

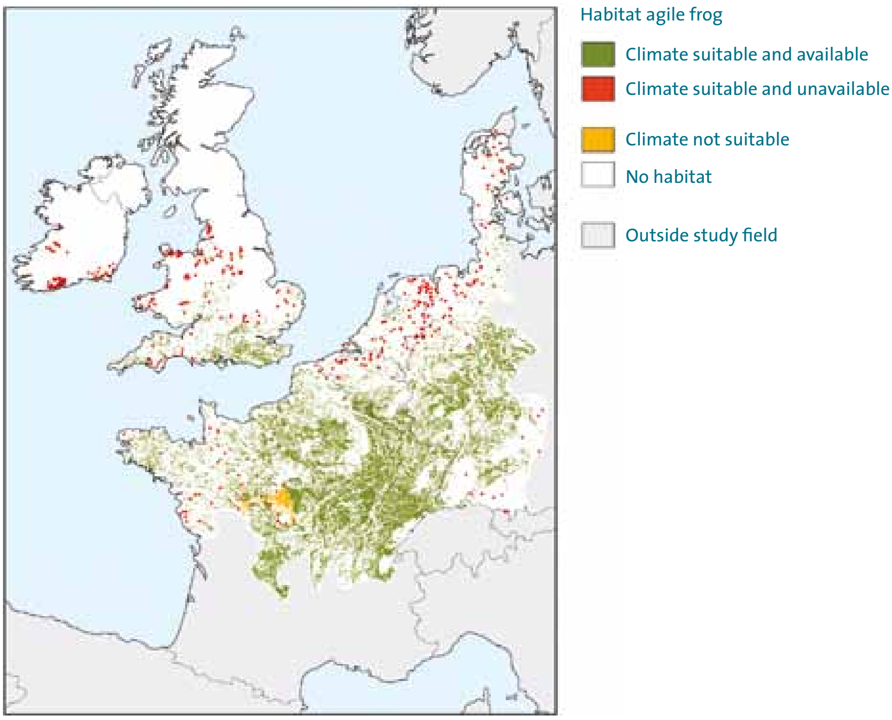

Figure 3.1. The green areas are climate proof for the agile frog: the climate is suitable and the habitat is well connected. In the red areas the climate will become suitable but cannot be colonized because of isolation. In the orange areas the climate will no longer be suitable (prediction for 2050 climate change scenario HadCM3, A2 scenario, IPCC 2001).

3.2.3 Keeping track of climate change

To gain insight into the processes that determine whether a species is able to track climate change, the population dynamics of expanding species was modelled, while varying the rate of climate change, the amount of habitat in the landscape and species traits (Schippers *et al.* in press).

The simulated northward expansion was typically only up to 3 km per year, which was much slower than the maximum dispersal capacity of the bird species. This could be explained by the additional time required for population establishment and population growth in new habitat, only after which the population is able to produce new dispersers for the next step in the colonization process. The modeled expansion rate is too slow to track the climate change-driven range contraction of 4 or 8 km per year in the south – corresponding with 2 and 4°C temperature increase per century – and this eventually results in metapopulation extinctions.

These results suggest that many species will not be able to keep track, even if the maximum dispersal distance for an individual is much larger than the velocity of climate change. For the bird species modelled, climate change scenarios based on low temperature increase are markedly less catastrophic. This illustrates that CO_2 reduction (mitigation) is an important measure for conservation of biodiversity in fragmented landscapes.

Increasing the amount of habitat in the landscape helps to enhance species survival. Enlarging patch size was more effective than increasing patch density. Scenarios with large patches yield higher front velocities and longer survival times than the same amount of habitat divided over many smaller patches.

Species traits matter as well. In our study especially the large bird species with large area requirements and slow population growth was found to be vulnerable, in spite of its large dispersal distance.

Based on these model results a general standard formula was derived that predicts which species will be most vulnerable to climate-induced range shifts:

The mean time to extinction T_e depends on: species' range size (Y), the observed northward expansion (V_a), which is an interplay of species traits and landscape characteristics and the speed of climate change (V_c). Obviously the usefulness of this general formula should be demonstrated using field observations, it is however a potentially powerful indicator to identify species most at risk and to quantify the occurring effects of climate change.

3.2.3 Will species be able to preserve their genetic diversity?

We explored how range shifts induced by climate change may affect the level and distribution of genetic diversity in a species range using a modeling approach (Cobben et al. in press). For this the model, used in section 3.2.2, was extended to provide each bird species with a genome of 10 unlinked loci with genetic variation. Results showed loss of genetic diversity in the species range under all investigated range shifts (temperature increase 1, 2 and 4 °C per century). This was the consequence of three processes (Figure 3.2): (1) genetic diversity in newly colonized areas was on average lower due to iterated founder effects from the range margin; (2) the loss of alleles at the trailing edge of the metapopulation where populations went extinct; and (3) the loss of alleles as a result of decreasing metapopulation sizes?.

The most important factors that influenced the loss of genetic diversity were the initial metapopulation size and the rate of temperature rise. Loss was stronger when the initial metapopulation size was smaller (e.g., when the species occupied less habitat) and with increased weather variability.

Even when the population size remained stable and the species seemed to be able to track the shifting suitable climate zone, genetic diversity declined. These results indicate the importance of conserving areas where species have existed for a long time or where the future climate is predicted to remain suitable as modern refugia of genetic diversity.

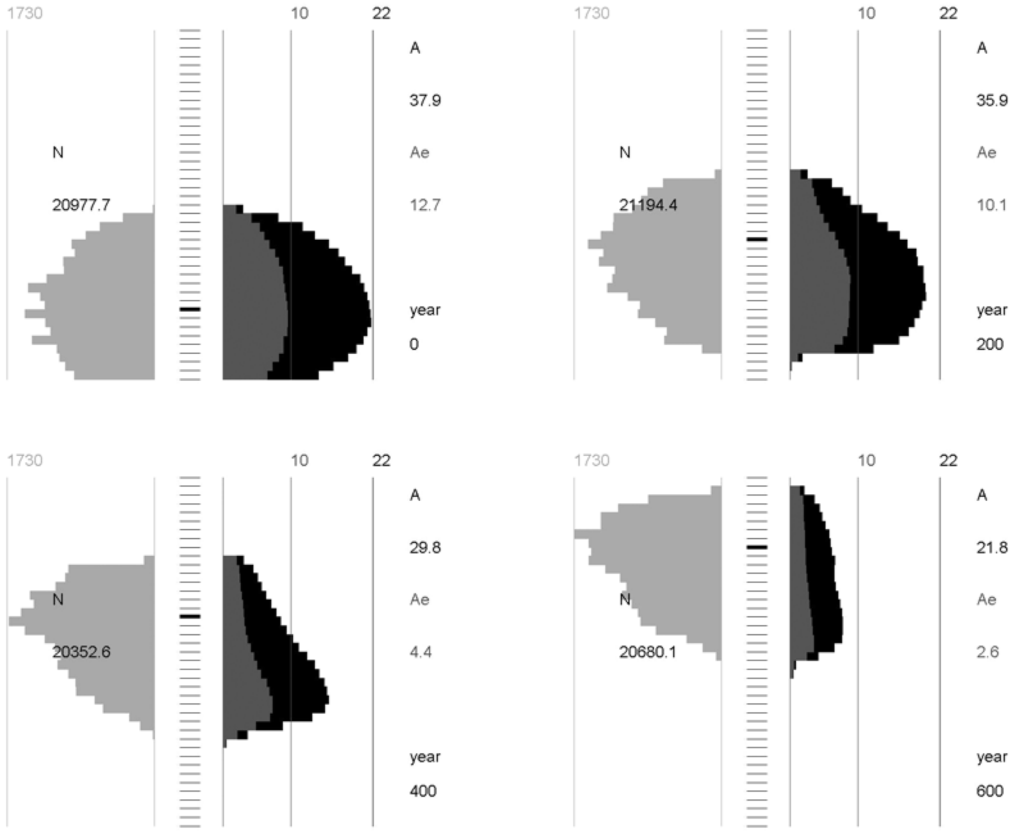

Figure 3.2. The spatial distribution of individuals per 50 km range (N, light gray), alleles (A, black) and effective number of alleles (Ae, dark grey) during the movement of the habitat optimum northwards at 2 km per year, in 4 time steps: year 0, 200, 400 and 600 (temperature rise 1°C per century).

3.3 Weather extremes and species survival

The increase in weather variability caused by climate change is illustrated in figure 3.3, causing a significant increase in variation in conditions for plant and animal populations. Effects of extreme drought, heavy rain and heat waves on species composition of vegetations have been documented (Jentsch & Beierkuhnlein 2008). A negative interaction with habitat fragmentation is to be expected, as spatially correlated disturbances will shorten metapopulation time to extinction (Akcakaya & Baur 1996). Especially small populations are at risk as was illustrated for the little blue butterfly (*Cupido minimus*) where local extinctions after the extreme summer heat wave of 2003 were correlated with small population size (Piessens *et al.* 2008).

The impact of additional environmental variation on species survival, was modeled by raising the variation in vital demographic rates e.g. survival and reproduction (Verboom *et al.* 2010). We simulated population dynamics for a key patch, a large habitat patch with a relatively stable population within a metapopulation (see Verboom *et al.* 2001), under different levels of environmental variation. More variation in vital demographic rates led to higher population extinction rates, but this could be compensated for by increasing patch size. A small, short-lived bird species like a warbler that is highly sensitive to environmental fluctuations needed more area for compensation than a large, long-lived bird species like a bittern. Although the extent of future weather variability is still unknown it is to be expected that spatial standards for sustainable ecological networks need to be adjusted.

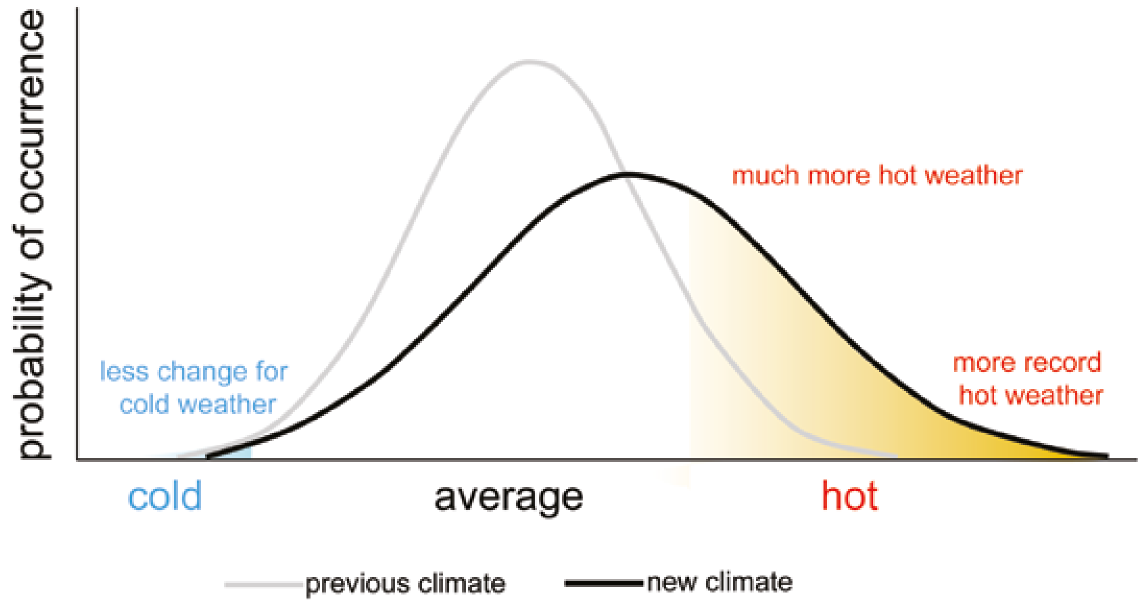

Figure 3.3. Schematic diagram showing the effects on extreme temperatures when the mean increases, leading to more record hot weather, and also the variance increases(drawn after IPCC 2001). For precipitation an increase in the occurrence of both extremes (droughts and severe precipitation events) is expected.

4. Synthesis

4.1 Species traits and responses to climate change

Based on the project results it was concluded that species traits and range characteristics are useful indicators for predicting species sensitivity to climate change. Table 4.1 provides an overview of all traits that were identified to be of significant importance in the empirical, experimental and modeling studies of the project. Four groups of traits stand out as important regarding the sensitivity for climate change: dispersal capacity, habitat specialism, demographic traits related to population growth rate and characteristics of the species range.

One of the impacts of climate change is the shift of suitable climate zones. As a response species need to expand their range to be able to track the shifting suitable habitat zone. Therefore traits that are related to colonizing capacity are especially important to identify species sensitivity: a large dispersal capacity, a large number of dispersers (related to small area requirements and/or a broad habitat choice) and a large population growth capacity are all traits that enhance the colonization and population establishment capacity. Also the current size of the species range is an important indicator to identify vulnerable species, especially when species are not able to keep track with the rate of climate change. A large range provides more time until the climate will stabilize again.

Sensitivity to weather extremes partly relates to habitat choice and type of extremes. Weather extremes in our country will for instance lead to more frequent and longer periods of drought or extreme downpours. In addition species that are sensitive to environmental stochasticity show more population fluctuations when increasing weather variability: e.g. small short lived species are more sensitive than large long-lived species.

4.2 Interaction between climate change and habitat fragmentation

The research project showed that habitat fragmentation increases the negative effects of climate change. It slows down or even blocks the colonization process that is an essential component of range expansion. A refinement on this general conclusion should be made for butterflies, which were found to become more active and hence more successful colonizers under warm conditions. Thus the warming of the climate might to some extent reduce the effects of habitat fragmentation for butterflies and perhaps also other ectothermic species.

Increased weather variability was shown to lead to higher extinction probability of populations, especially in fragmented landscapes. This negative effect of climate extremes could be compensated for by enlarging patch size, thus increasing the amount of habitat in the landscape.

Remarkably, in the models used, species lose genetic diversity during range shifts, even when the population size remains stable and the species seems to be able to track the shifting suitable climate zone. More habitat in the landscape has some positive impact on genetic diversity, but is not able to compensate the total loss. As losing genetic diversity will diminish the capacity within species to cope with present and future disturbances, it is important to protect areas where species have existed for a long time or where the future climate is predicted to remain suitable as modern refugia of genetic diversity.

We developed a general formula that predicts which species are most vulnerable to climate-induced range shifts. Survival time depends on:

- species' range size (the larger the better),
- the observed northward species' expansion (the faster the better), which is an interplay of species traits (large dispersal and growth capacity) and landscape characteristics (good spatial cohesion),
- the speed of climate change (the slower the better).

This general formula is potentially a powerful indicator to identify those species that are most at risk and identify those areas where the landscape cohesion is insufficient.

Some research priorities and recommendations that came forward from this study:

- Analyse species distribution data to test the usefulness of the general indicator that predicts which species are most at risk to become extinct because of climate-induced range shifts.
- Prioritise regions in European Natura 2000 network where improvement of connectivity to facilitate range shifts is most urgent or in the potential gain is highest.

Table 4.1. Overview of all traits that showed a response to climate change that came forward during the research project. Negative impacts of climate change are indicated in red and positive impacts in green. The type of study is given between brackets: empirical, experimental or modelling research.

Dispersal capacity		Habitat specialism		Population growth capacity		Range characteristics	
Species with large dispersal capcity are better capable of following range shifts (modelling research)	birds	Marshland species that are also residential, herbivore and precocial benefit from less severe winters (empirical research)	birds	Species with small area requirements and large population growth capacity are better able to track the rate of climate change induced range shifts (modelling research)	birds	Species have expanded their range along the coastal dunes with 3.3 km northwards (empirical research)	plants
Warmer conditions improve mobility and colonizing capacity (experimental research)	butterflies	Thermophilic species benefit from warmer conditions (empirical research)	plants	Species with large clutch size, large number of clutches, and low age at first reproductuin have a larger capacity to recover after extreme weather events (empirical research)	birds	Species at the northern part of their range benefit from range expansion (modelling research)	all species
		Species of dry conditions benefit from increase of warm and dry weather (empirical research)	plants				
Species that lack adaptations to long distance seed dispersal are less succesfull colonizers (empircal research)	plants	Long distance migrants such as insectivorous forestspecies suffer from foodchain mismatches (empirical research)	birds	Small, short living species are more sensitive to increased weather variability (modelling research)	birds	Shifting ranges leads to loss of genetic diversity (modelling research)	birds
		Habitat specialists that are underrepresented in the regional species pool are less succesfull colonizers (empirical research)	plants			Species with a small range size have a higher extinction risk during range shifts (modelling research)	birds
		Species that prefer wet conditions have declined during warm and dry periods (empirical research)	plants			Species at the southern part of their range suffer from range contraction (modelling research)	all species

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PART II

6. Development of adaptation strategies

6.1 Introduction

Adaptation to climate change is fundamentally linked to the concept of vulnerability, the degree to which systems are likely to experience harm due to exposure to perturbations or stresses (Kasperson et al. 2005). Adaptive capacity refers to the ability of society to cope with climate change including increased climate variability (weather extremes) in order to (a) moderate potential damages, (b) take advantage of emerging opportunities, and/or (c) cope with its consequences (Smit & Wandel 2006). The research project focused on adaptation strategies for the national ecological network (EHS), the Dutch conservation strategy for the sustainable protection of biodiversity. For the adaptation of natural systems the definition of Wilson and Piper (2008) was followed, who define that biodiversity adaptation requires a double focus. The first focus is on adaptation measures that reduce vulnerability on the spot by increasing ecosystem resilience to disturbances and by accommodating change. The second focus is on adaptation measures that facilitate species and habitats to move elsewhere into newly suitable areas. In the project several adaptation strategies to increase the adaptive capacity of the EHS to cope with the effects of climate change were developed (section 6.2).

As a next step towards implementation, the adaptation measures need to be translated into regional multifunctional adaptation plans that are adopted by regional stakeholders. Therefore two regional case studies were performed to explore which adaptation strategies to increase the adaptive capacity of the EHS in the multifunctional landscape, are best accepted by regional stakeholders (section 6.3).

6.2 Defining an adaptation strategy for the EHS

In part I two impacts of climate change emerged that might reduce the effectiveness of the EHS to protect biodiversity: (1) temperature rise causes species' range shifts that might be impeded or slowed down by habitat fragmentation; and (2) increased weather variability may cause additional and/or much more severe population fluctuations that will increase local extinction risk. Facilitating range shifts would require linking ecosystem networks on a much larger scale, not only between present habitat but also into areas located in the future suitable climate zones (section 3.2, Vos *et al.* 2008). Second, larger and more heterogeneous habitat networks are necessary as this may counterweigh the increased weather variability and reduce the extent of population fluctuations (section 3.3, Verboom *et al.* 2010). Facilitating range shifts and avoiding weather extreme-driven extinctions is not only beneficial for the protection of individual species. It is also important to maintain a high level of functional biodiversity in ecosystems, thus compensating for unavoidable species losses at the contracting sides of species' ranges, where the climate will become unsuitable. There are indications that a high level of biodiversity is an important prerequisite for the adaptive capacity of ecosystems (e.g. Hooper *et al.* 2005; Johnson et al. 1996).

Ecological networks find broad international support as the most suitable strategy to cope with climate change especially in areas where high land use pressure (Heller & Zavaleta 2009). Nevertheless, it is to be expected that the national ecological network of the Netherlands (EHS) needs to become more robust to be able to cope with the above mentioned additional effects of climate change.

Several adaptation measures to enhance the adaptive capacity of the EHS to cope with climate change were developed. Adaptation measures can be implemented either within nature areas or outside nature areas in the surrounding multifunctional landscape. The adaptation measures are:

- Improving (international) connectivity over large distances by resolving dispersal bottlenecks and thus facilitating range shifts. Linking habitat networks will enable species to colonize habitats that will become suitable, and this will compensate for the loss of habitat at the contracting side of its range.
- Increasing the carrying capacity of protected areas by either enlarging the size of protected areas or improving habitat quality, or both. Increasing the carrying capacity gives room to larger populations, and thereby compensates for increased extinction probabilities caused by increased weather variability.
- Increasing spatial heterogeneity within a nature area and better accommodating natural landscape-forming processes e.g. sedimentation, marshland development, meandering of rivers and freshwater-salt water gradients. This is a strategy to cope with increased weather variability, as large scale correlated population fluctuations can be avoided (Bengtsson et al. 2003; Hodgson et al. 2009). For instance, in heterogeneous habitat some parts may allow a positive growth rate in very dry years, whereas other parts may be optimal during wet years.

It was recommended to combine and spatially concentrate these adaptation measures in so called 'climate adaptation zones' (Vonk et al. 2010; Vos et al. 2010). A 'climate adaptation zone' is defined as: a focus zone for adaptation measures to enhance the adaptive capacity of the EHS to cope with climate change and which provides spatial planning protection so that the potential negative impact of activities on the spatial cohesion and on the abiotic conditions of the EHS can either be avoided or mitigated. The climate adaptation zone should function as a zone where no irreversible actions are to be taken that would block future adaptation of the EHS, e.g. large scale urbanization or new infrastructure. Within the zone it remains possible to adjust measures in future, when the effects of the changing climate on ecosystems become more apparent. By this approach future adaptive capacity will be safeguarded.
Within the climate adaptation zone adaptation measures can be implemented either within nature areas or outside nature areas in the surrounding multifunctional landscape.

Figure 6.1 gives an overview of the climate adaptation zone for wetlands, one of the important ecosystem types of the Netherlands. The optimal location for the climate adaptation zone was determined by the large existing wetlands (strongholds), a high spatial cohesion of the wetland network, a low number of dispersal bottlenecks, high suitable conditions for wetland restoration and potential international connectivity (see Vonk et al. 2010; Vos et al. 2010 for details).

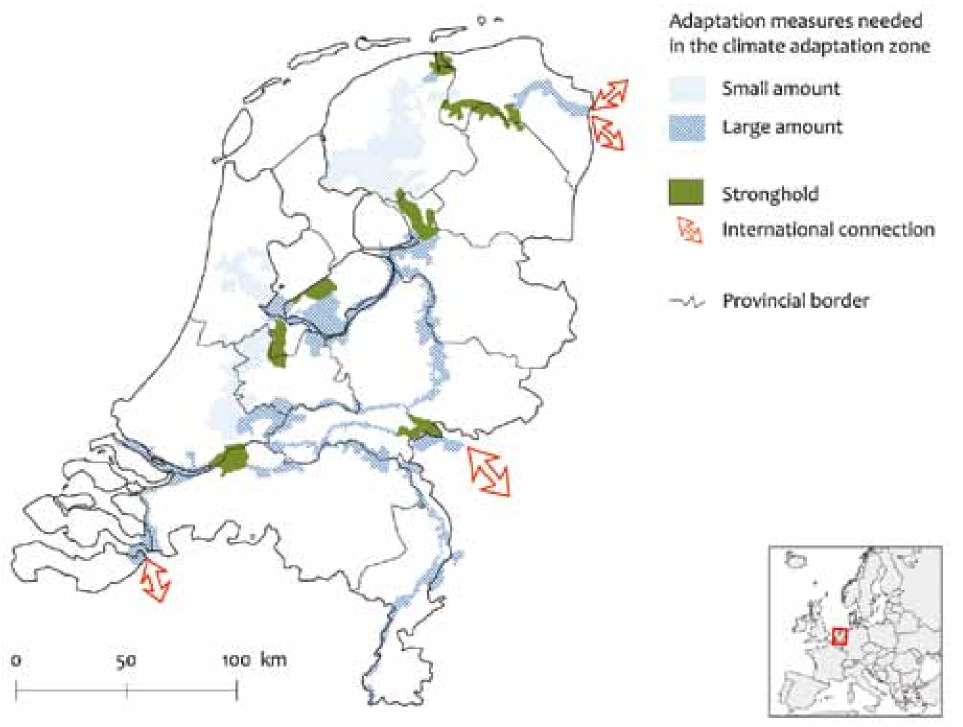

Figure 6.1.The proposed climate adaptation zone for wetland ecosystems is indicated in blue and green. The climate adaptation zone is a search area for adaptation measures (Vonk et al. 2010; Vos et al. 2010).

6.3 Adaptation in multifunctional landscapes

Two regional case studies were performed in order to explore which adaptation strategies, to increase the adaptive capacity of the EHS in the multifunctional landscape, are best accepted by regional stakeholders. Several adaptation measures outside nature areas were developed that contribute to the adaptive capacity of the EHS. By implementing these adaptation measures on farmland adjacent to nature areas the amount of area to be acquired for nature at the expense of farmland can be minimized. It is expected that multifunctional adaptation will contribute to the regional support for these measures, especially when also other benefits are achieved as well, such as climate adaptation of water management and improvement of recreational and aesthetical landscape values (Agricola et al. 2010).

The multifunctional adaptation measures are (Figure 6.2):

- Creating green-blue veining. Increasing the density and quality of green blue veining (Grashof-Bokdam & Van Langevelde 2004) between fields (e.g. ditches, hedgerows, wooded banks, field margins and verges along roads, railways and canals) increases the connectivity between nature areas. It also promotes the ecological heterogeneity (gradient function) of the landscape, thus stimulating species diversity (Smith et al. 2010). Green-blue veining is situated along field margins, which are the relative low productive parts of the farm. Therefore these measures fit relative easily into common farm practices and claim a relatively small area of productive farmland.
- Adapting management at field level. Measures to improve habitat quality by adapting grassland management or by growing different crops. For example, the first cut of grass can be delayed until mid summer to allow the vegetation to flower and produce mature seeds, or long grass can be kept standing during winter time to offer insects and birds suitable winter habitat. These adapted fields may act as stepping stones for several species and fit well into agri-environmental schemes (Korevaar & Geerts 2007; Peel 2010).

- Creating buffer zones surrounding nature reserves. The farmland contributes to regional water retention and water quality in these buffer zones by maintaining higher water levels in ditches and ground water and increasing water quality by minimizing nutrient and pesticide losses from agriculture to ground and surface waters. These measures serve multiple adaptation purposes: they avoid regional dehydration during warm and dry periods in summer (a benefit for nature and farmers) and improve water quality (a benefit for nature and water management).

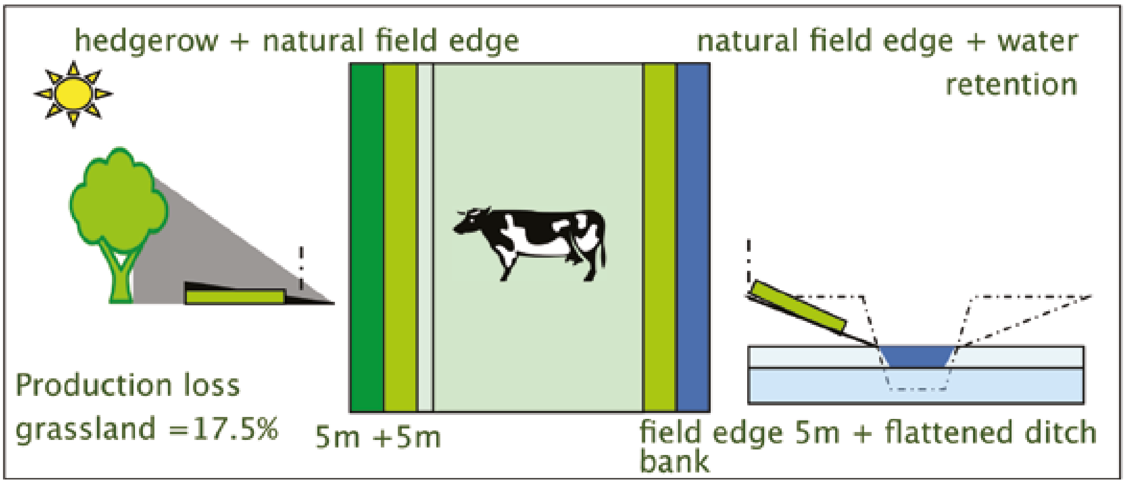

Figure 6.2. To the left an example of green veining is shown: a hedgerow and a field margin are combined to mitigate the negative effects of the hedgerow on production. To the right an example of blue veining is shown: a widened ditch bank is combined with a field margin. The remaining area of the field is used for production. The production loss is estimated to be 17.5% if the production area is used as water retention area. The total production loss on the grassland is estimated to be 50%.

In focus group discussions stakeholders emphasized that cooperation between stakeholders is a prior condition to effectively implement adaptation measures in agricultural landscapes. The adaptation measure to increase the amount of green-blue veining was rated most positive in all focus group discussions. According to farmers these measures along field margins fit best with modern farming practices. According to nature managers and policy makers green-blue veining is the most effective adaptation measure to improve the quality of nature areas (see example 'De Venen'). However, according to the stakeholders, the current agri-environmental schemes do not sufficiently stimulate a coordinated increase of green-blue veining, which is necessary to sufficiently increase connectivity on the landscape level between nature areas.

Example De Venen

The Venen forms part of the climate adaptation zone for wetlands (section 6.2, figure 6.1). Increasing the connectivity between the Nieuwkoopse Plassen and the Loosdrechtse and Vinkeveense Plassen (figure 6.3a) is one of the proposed adaptation measures within the climate adaptation zone. Figure 6.3.b shows how a dense network of green-blue veining could contribute to connectivity, by adapting the management of the low productive field margins along ditches and small canals especially at the end of the fields, so called 'weteringen'.

Figure 6.3a. The landscape between Nieuwkoopse, Loosdrechtse and Vinkeveense Plassen consists of intensively managed grassland areas.

Figure 6.3b. A possible coherent network of green-blue veining in De Venen. Green lines are field margins along ditches and small canals and the red blocks are already designated nature reserves.

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Climate changes Spatial Planning

Climate change is one of the major environmental issues of this century. The Netherlands are expected to face climate change impacts on all land- and water related sectors. Therefore water management and spatial planning have to take climate change into account. The research programme 'Climate changes Spatial Planning', that ran from 2004 to 2011, aimed to create applied knowledge to support society to take the right decisions and measures to reduce the adverse impacts of climate change. It focused on enhancing joint learning between scientists and practitioners in the fields of spatial planning, nature, agriculture, and water- and flood risk management. Under the programme five themes were developed: climate scenarios; mitigation; adaptation; integration and communication. Of all scientific research projects synthesis reports were produced. This report is part of the Adaptation series.

Adaptation

Dutch climate research uses a 'climate proofing' approach for adaptation. Climate proofing does not mean reducing climate based risks to zero; that would be an unrealistic goal for any country. The idea is to use a combination of infrastructural, institutional, social and financial adaptation strategies to reduce risk and optimalise opportunities for large scale innovations. Climate changes Spatial Planning realised projects in a multidisciplinary network that jointly assessed impacts and developed adaptation strategies and measures. The following themes were central to the programme: water safety, extreme precipitation, nature and biodiversity, agriculture, urban areas, transport (inland and road transport) and the North Sea ecosystem. In special projects, the so called hotspots, location-specific measures were developed that focused on combining 'blue', 'green' and 'red' functions.

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