



Adaptation

Biodiversity in a changing environment: predicting spatio-temporal dynamics of vegetations

Dr. Ir. P.M. van Bodegom

Prof. Dr. R. Aerts

Prof. Dr. Ir. J.P.M. Witte



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Authors

Dr. Ir. P.M. van Bodegom ¹

Prof. Dr. R. Aerts ¹

Prof. Dr. Ir. J.P.M. Witte ²

¹ VU University Amsterdam

² KWR Watercycle Research Institute



VU University *Amsterdam*

KWR

Watercycle Research Institute

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Summary



Summary in Dutch

Om geschikte adaptatiemaatregelen te kunnen ontwerpen, is het noodzakelijk over betrouwbare schattingen van de vegetatiesamenstelling en de functionele biodiversiteit onder verschillende klimaatveranderingsscenario's te beschikken. Huidige benaderingen zijn daarvoor ongeschikt. Daarom presenteren we een nieuw concept om klimaat via planteigenschappen aan vegetatie te koppelen. We kwantificeren klimaatrobuuste op processen gebaseerde relaties tussen milieu en vegetatie. Milieuv variabelen zoals stikstofmineralisatie, droogtestress en zuurstofstress worden medebepaald door klimaat. Door het toepassen van 'assembly theory' concepten wordt vervolgens de reactie van planteigenschappen op die variabelen gekwantificeerd. De voorspelde planteigenschappen zijn gebruikt om de kans van voorkomen van verschillende vegetatietypen te voorspellen. De benadering is gevalideerd door een groot aantal vegetatiemetingen uit heel Nederland te analyseren.

Daarnaast hebben we aangetoond dat met name een combinatie van droogtestress en zuurstofstress het aantal bedreigde soorten nadelig beïnvloedt. Dit geeft het belang van extreme gebeurtenissen voor de kwaliteit van een habitat aan. De analyse van klimaatscenario's gaf aan dat een dergelijke combinatie in een toekomstig klimaat waarschijnlijk toeneemt, waardoor een aantal bedreigde soorten zou kunnen uitsterven als geen passende adaptatiemaatregelen worden getroffen. Via nationale simulaties hebben we bepaald welke regio's waarschijnlijk het meest getroffen zouden kunnen worden. We presenteren verschillende hydrologische adaptatiemaatregelen om de kwaliteit van natuurgebieden te behouden.

Summary

A critical condition towards developing appropriate adaptation measures to deal with climate change is to have reliable estimates of vegetation composition and its functional diversity under various climate change scenarios. Current approaches suffer from several drawbacks that hamper such predictions. Therefore we developed a new conceptual framework to link climate to vegetation through plant traits. We used process-based climate-versatile approaches to quantify environmental drivers as affecting vegetation responses. Climate, as prescribed by climate scenarios, was allowed to affect these drivers, like nitrogen mineralization, oxygen stress and drought stress. Applying assembly theory concepts, we quantified trait responses to these environmental drivers. Subsequently, plant trait combinations were used to predict the probability of occurrence of different vegetation types. The approach was validated using a large number of vegetation recordings throughout the Netherlands.

It was also shown that particularly a combination of drought stress and oxygen stress affects the number of rare species, highlighting the importance of extreme events in determining the quality of a habitat. Climate scenario analyses indicated that events of drought stress and oxygen stress are expected to increasingly coincide, which will decrease the number of rare species if no adaptation measures are taken. Through national simulations, we also determined which regions are likely to be affected most severely. We present several hydrological adaptation measures to enhance the robustness of nature areas.



1. Context

In a world that is influenced by climate change and by frequent human interference, knowledge of the response of living organisms and ecosystems is critical for a complete assessment of these effects. The current empirical relationships between vegetation and environment that were derived from equilibrium conditions in the current climate lose their validity upon climate change. Existing models have several drawbacks. First of all, these models contain some rather indirect empirical relationships that have been deduced from field data under current climate conditions. Application of such relationships to a future climate scenario is therefore questionable. Secondly, none of the current models take account of the response time of different species within the vegetation. Thirdly, we question if the existing mechanistic models will ever become generally applicable, because it is not feasible to model the interspecific responses and interactions between all species of the Dutch flora. A fourth shortcoming is that most models do not account for feedback mechanisms during succession or couple these feedbacks to process-based parameters that are intrinsically more dynamic than allowed for by the time step of the model. Finally, none of the existing models give an estimation of the uncertainty of the output. Given these shortcomings, there is clearly a need for a set of models that do not suffer from these problems and that can be used to model vegetation dynamics under various climate change scenarios.



2. Aims

2.1 Project objective

Our project objective was to predict the effects of climate change, i.e. changes in temperature, precipitation and potential evapotranspiration, on the spatial distribution of vegetation and its functional diversity within ecosystems in the Netherlands.

2.2 Research aims

We aimed to use the knowledge generated by our research to:

- (1) run scenario analysis for various scenarios of climate change to predict changes in the spatial distribution in vegetation and its functional biodiversity in order to allow optimal spatial planning to conserve or even enhance biodiversity;
- (2) identify areas that are or may become hotspots of plant biodiversity in the Netherlands under various scenarios of climate change and water management; and
- (3) find 'Early Warning Systems' for climate change.

To this end, we developed a set of models based on a novel conceptual idea to make vegetation model applicable to changing environments and that accounted for the drawbacks mentioned in the context section.

The outcomes of this analysis are of prime importance for spatial planning and to design management strategies to ameliorate or use climate impacts to sustain ecological quality under climate change.




2.3 Specific research questions

In order to achieve the three aims indicated in section 2.2, we formulated the following research questions:

- 1) How can we classify vegetation on the basis of (proxies for) abiotic factors and plant traits? This is the core question of the project and tests the feasibility of a trait-based functional vegetation model.
- 2) How do climate variables and climate change interact with plant available oxygen and moisture in the root zone? This aims to unravel the ecological relation between various abiotic factors determining moisture regime in order to improve empirical relationships between moisture regime and vegetation and replace these by process-based relationships between moisture regime and plant traits.
- 3) How fast and to which extent does vegetation respond to abiotic factors? Hardly anything is known about the response time of the vegetation and it has not been incorporated in present ecosystems models, yet this factor might be decisive for species composition and ecosystem succession.
- 4) How do climate variables in interaction with moisture regime and climate change affect the soil nutrient regime? The interactions between nutrient availability and plant species composition is a research topic with a long history. Still, a good measure that compromises between nationwide data availability, general applicability and mechanistic soundness has not yet been developed.
- 5) How does vegetation in the course of (climate change induced) succession feed back to abiotic factors? It is generally known that plants actively modify their environment, but none of these feedbacks between plant traits and abiotic factors are accounted for in currently available spatial nationwide species based models.
- 6) How can we assess the uncertainty in the outcome of model scenarios? Each model contains relationships and parameters that have been obtained with a certain degree of uncertainty. In order to judge the output of climate and water management scenarios, it is necessary to know the accumulated effect of these uncertainties on the predicted biodiversity.
- 7) How do dispersal limitations affect the dynamics of vegetation composition? Dispersal and seed bank limitations are frequently identified in vegetation models as a main reason for improper predictions. However, none of the present nationwide spatial models incorporates these limitations.

3. Approach and methods

Within this project, we developed a new conceptual framework to link climate to vegetation biodiversity. Up to now, all vegetation models, both nationally and internationally (the so-called Dynamic Global Vegetation Models), are based on predicting plant species directly. As outlined in the introduction, the use of empirical relations with plant species (without varying plant attributes) hampers the application of fully mechanistic models. In international global models, this is solved by the use of so-called plant functional types, groups of plant species with presumably the same characteristics and thus responsiveness to climate change. This reduces the complexity of the models, but creates a new set of assumptions, that are hard to maintain in a changing climate. Particularly the assumption that species within a functional group are functionally similar is not



very appropriate. There is a large range of functional characteristics within plant functional types, sometimes even larger than between plant functional types [Kattge et al., 2011; van Bodegom et al., 2011a]. One might relax this assumption by allowing functional characteristics to vary within a functional type, but then one has to assume that species composition within a plant functional type remains the same in a changing climate, which is doubtful given the differences in dispersal rates among species.

Within this project, we developed an entirely different and novel approach, based on plant traits. Plant traits are morphological, anatomical, physiological or phenological features measurable for individual plants [Violle et al., 2007]. Plant species respond to their environment through their traits. In other words, plant traits are selected or filtered by their environment. The use of plant traits links to new developments within ecology over the past two decades (i.e. within functional ecology and community ecology), but more importantly, it describes how vegetation is functionally affected by global change and how the vegetation will respond to climate change [van Bodegom et al., 2011a]. The set of traits allowed for in a given environment, as affected by climate change, is a direct measure of the functional diversity allowed for by the environment.

In our approach, we thus predicted sets of plant traits as a function of soil, hydrology and climate. These traits were linked to novel statistical tools to compute vegetation responses in terms of species composition. Given that this second step was not part of the estimation of vegetation responses, we created full flexibility of using any vegetation classification (thus increasing the flexibility for stakeholders). Moreover, our tools allowed quantifying the uncertainty in the outcome. Partly, such uncertainties are true uncertainties, because plant species do functionally overlap. Therefore, it is by definition not always possible to predict the occurrence of one species if that has the same set of functional characteristics of another species. Partly, this procedure allows identifying model imperfections that may be solved in a later project.

The use of these process-based links between vegetation and climate through traits allowed for the development of universal predictors/indicators of climate change, more robust and with better general applicability than indicators based on individual species. Our methods have been implemented in national ecosystem models of PBL Netherlands Environmental Assessment Agency that enabled us to assess the impact on biodiversity of scenarios for water management and climate change by applying climate change scenarios developed by KNMI-06. This allowed for full scale implementation of our results into simulations that are used in national policies. Together, these models will help to select and design adaptation strategies to ameliorate or use climate impacts for preserving biodiversity.

Given that land use change effects, apart from nature and water management measures as affecting soil and hydrology, were not accounted for, we predicted vegetation responses only for areas known to be assigned to nature. This approach thus omits land use change impacts on areal distribution of nature areas in the Netherlands (which was the scope of another BSIK-project, i.e. the LANDS project).

Our general theoretical framework has been developed and tested by a team of three PhD students and members of the research consortium. Also PBL was involved as a public organisation and has contributed to the implementation of the framework into simulations. Synergistically (Figure 3.1), this allowed achieving our overall aim of predicting the effects of climate change on vegetation dynamics and biodiversity. The first two PhD students, Jenny Ordonez and Ruud Bartholomeus, both handed in their thesis within a month after the end of the contract and both theses have been praised by the evaluation committee for their quality. Ruud Bartholomeus even received the prestigious three-yearly hydrology price of the Nederlandse Hydrologische Vereniging (Dutch Hydrological Society) for “the best scientific paper within the field of hydrology”, that he published as part of his PhD-thesis. The contract of the third PhD student, Bob Douma, was extended by four



months to financially compensate for the consequences of a car accident earlier in the project, after which also he handed in his thesis. The project has already yielded various scientific papers in leading scientific journals and it is anticipated that more will follow during the coming one or two years.

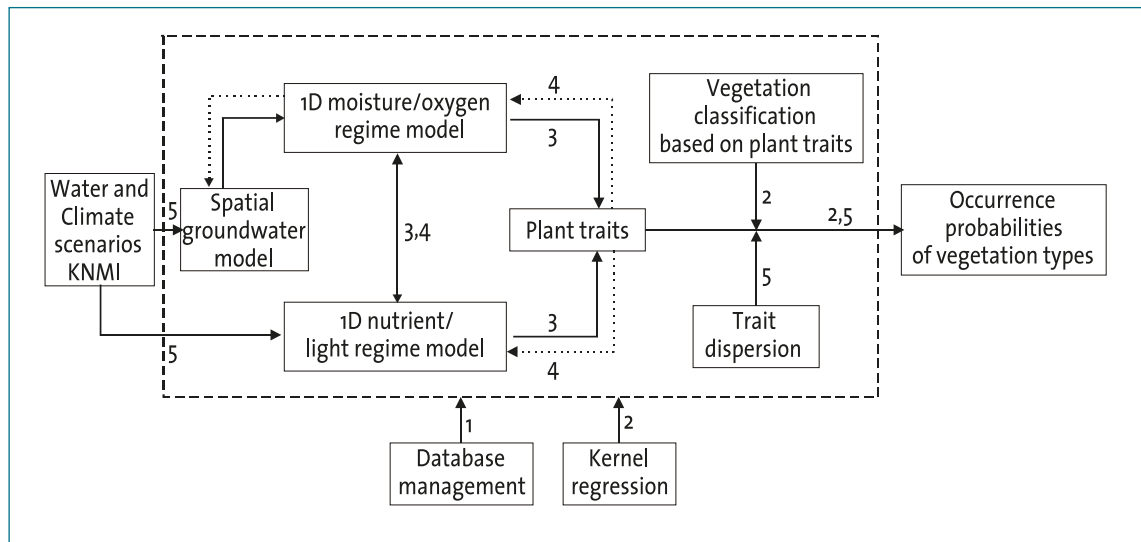


Figure 3.1.

General set-up of our project. Numbers refer to various sub-projects involved.

4. Synthesis

4.1 Quantification of assembly processes

The selection of plant species and vegetation characteristics by the environment is one of the leading paradigms within ecology and is very relevant in the context of the current program. At the same time, this paradigm has been challenged many times, e.g. by the neutral theory – indicating that although species are different, this does not affect their abundance [Hubbell, 2001] – or by theories stressing the importance of biotic interactions, like competition and facilitation. Quantitative tests of the importance of those selection processes were lacking until now.

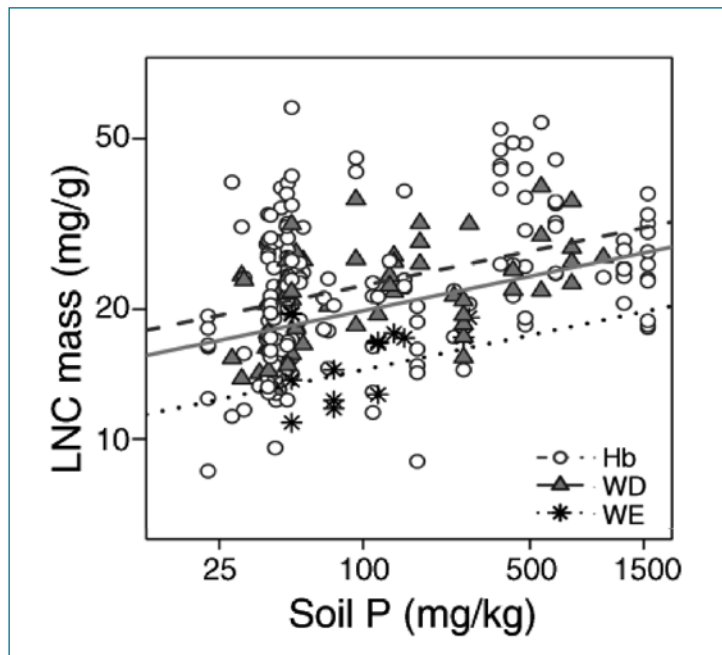


Figure 4.1.

The relationship between leaf nitrogen content (LNC) and soil phosphorus (P) for 200 species sampled across a wide range of habitats in the Netherlands. Results show a strong effect of habitat filtering, in this case soil P on traits. Simultaneously, different growth forms (herbaceous species (Hb), woody deciduous species (WD) and woody evergreen species (WE)) have specific responses. Adapted from: Ordonez et al., 2010b.

All vegetation models implicitly assume that the selection by the environment is strong and in our functional vegetation model this link is made explicit. Therefore, within the project much effort has been spent to quantify the role of the so-called environmental filters, such as hydrology, soil fertility and pH. Within our research, we derived climate-versatile links between hydrology and vegetation traits [Bartholomeus et al., 2008a; 2008b; 2011b]. In addition, soil pH was linked to indicator values of pH [Cirkel et al., 2011]. We also quantified the importance of soil fertility to select so-called leaf economics traits [Ordonez et al., 2009]. Leaf economics traits are traits that define the photosynthesis (and respiration) rates of plants [Wright et al., 2004]. As a consequence, they play an important – if not dominant – role in Dynamic Global Vegetation Models. Its proper quantitative prediction is therefore of prime importance. Our global analysis of leaf economics traits [Ordonez et al., 2009] showed that the selection of these traits by the environment was not as strong as presumed by the scientific community. Given that those results had been obtained by a meta-analysis of data compiled from literature, it might have contained large data uncertainties. However, a re-analysis of this relationship in a database that was gathered by ourselves through measurements of soil conditions, hydrology and plant traits showed exactly the same relationship with the same strength [Ordonez et al., 2010b] (Figure 4.1). Finally, we quantified the relationship between seed mass and disturbance, another important driver of ecosystems [Douma et al., 2011b].

Although each of these relationships provide an important quantification of the selection of vegetation functional characteristics by the environment, the ultimate proof can only be given by combining various traits into one analysis. For this purpose, we compiled a large national database consisting of twelve traits for the large majority of the Dutch flora. We linked this trait database to a database of 35,000 relevés classified into different vegetation types. Subsequently, we tested which combination of traits could best distinguish the different vegetation types. For this purpose, we used a statistical method developed by our team [Witte et al. 2007] in which the trait space occupied by a vegetation type is described by Gaussian mixture density kernels (Figure 4.2).



Subsequently, trait combinations are translated into a probability occurrence for each vegetation type (given the kernels). The probability of occurrence is subsequently compared to the observed vegetation type to test the performance of a trait combination. Interestingly, this analyses proved that trait combinations different to those predicted in internationally accepted plant strategy schemes ultimately allow to distinguish among vegetation types [Douma et al. 2011a].

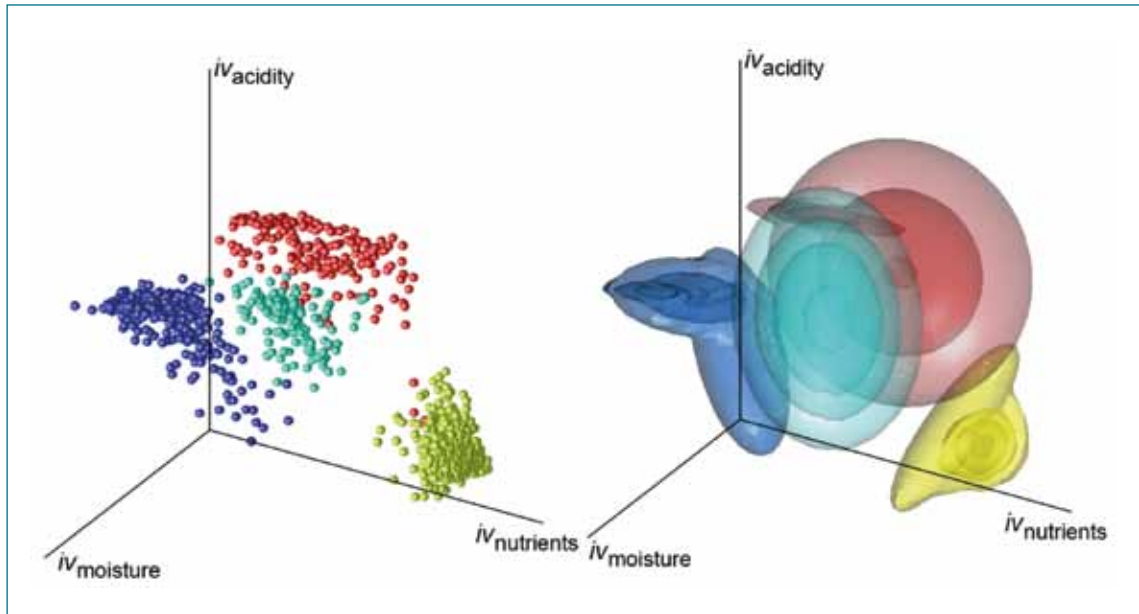


Figure 4.2.

Three-dimensional plots of observed relevés (balls in left figure) and fitted Gaussian mixture density per vegetation type (right figure) plotted in relation to their indicator values for different environmental conditions (as integrative traits) From: Witte et al., 2007.

The insights obtained by this research were integrated into a trait-based national model to predict vegetation occurrences as a function of climate-versatile environmental drivers [Douma et al., 2011c]. A total of 52% of the relevés were assigned to the correct vegetation type, based on environmental data only. If corrected for chance, this coincides with a degree of agreement (kappa index) of 0.43. The overall Kappa index was 0.74, showing that the observed frequencies of the vegetation types matches well with the predicted frequencies by our model. These kappa values compare favourably to those of other vegetation models, while our approach is more ‘climate proof’ than current vegetation models by its better inclusion of functionality. This shows that our approach has an important potential for future model applications to predict vegetation change both in a national and in an international context, showing that a functional trait-based approach is at least as good. Indeed, within the European Terrabites programme, and in collaboration with the Max Planck Institute for Meteorology, this concept will be implemented and tested in Dynamic Global Vegetation Models.

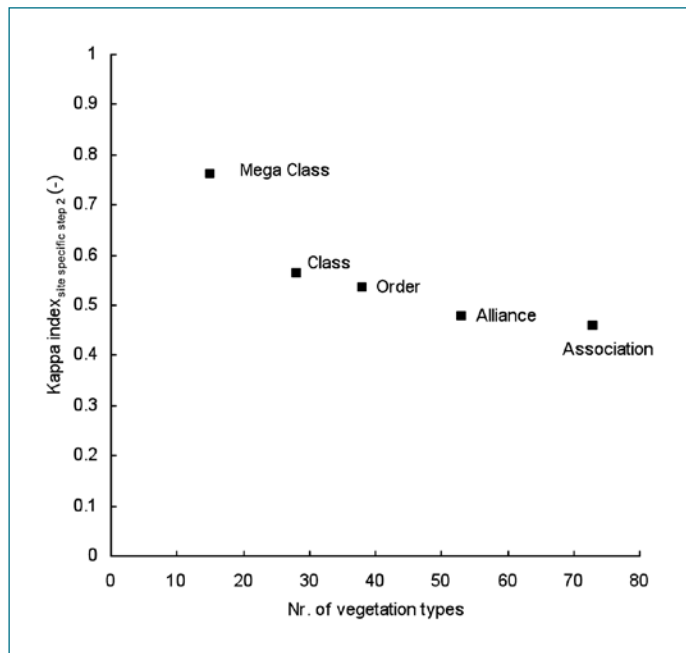


Figure 4.3.

The relationship between the number of vegetation types and the ability to predict the correct right vegetation type, for five different vegetation type classifications (finer vegetation type classifications nested in coarser ones). From: Douma et al., 2011c.

The kappa index, as a measure of goodness of fit, partly depended on the aggregation level of the applied vegetation classification (Figure 4.3). With a higher number of vegetation types distinguished, the kappa index decreased. This shows that the functional redundancy of vegetation types increases with a higher number of vegetation types: Accuracy (as indicated by the kappa index) is thus sacrificed for precision (i.e. number of vegetation types). This has important implications for policy as it implies that it will be impossible to predict for all individual plant species simultaneously how they will respond exactly to climate change (as this will imply an even large number of classes, unless a very strict a priori selection is made on the species involved). Our approach shows the environmental drivers (i.e. the fundamental niche of each plant species), but the realised niche will equally depend on historical influences, random processes and biotic interactions, which cannot be predicted by our model (nor by any other vegetation model). This is an important message to be passed on to policy makers, to avoid unrealistic expectations.

4.2 Hot spots of vegetation

We have created sketch maps of predicted vegetation changes under influence of climate change. The research to create these maps consisted of two parts. In the first part, a map of current vegetation types was compared to the outcomes of different hydrological models for the KNMI scenarios W and W+, available for the whole of the Netherlands at a spatial resolution at 25x25 m. In this way, each vegetation type could be coupled to hydrological variables like groundwater level, moisture shortage and the percentage of water derived from other sources. Subsequently, it was investigated to which extent these hydrological parameters are likely to change for each vegetation type identified. In the second part, the outcome of the first part were combined to literature data and expert knowledge on the processes involved to sketch the consequences of climate change for nature. The sketch consists of a map (Figure 4.4) and an accompanying text. The aim of this map was to not only to show the predicted change for nature in the Netherlands, but also to start on discussion on these



consequences of climate change to enlarge the knowledge on the ecohydrological effects of climate change. This sketch map thus provides policy makers with first critical insights.

The map (Figure 4.4) shows that particularly vegetation types that depend on the atmosphere as their major source of water are vulnerable. Groundwater independent vegetation types on sandy soils, like glacial ridges, dunes and the higher parts of stream valleys, will suffer from a larger groundwater shortage within the growing season. This shortage is particularly expected to increase for scenario W+. Also wet and rainwater-fed ecosystems are expected to be prone to large hydrological changes. Characteristic vegetation types of bogs, fens and wet heathlands are likely to suffer in the near future. The development of living bogs is extremely unlikely for the conditions created upon scenario W+. Seepage to lower regions of the Netherlands, like the lower parts of stream valleys and the edges of large infiltration areas will increase for the scenario W (and potentially for scenario W+ too, although that is highly uncertain). This effect may positively affect the biodiversity for these vegetation types.

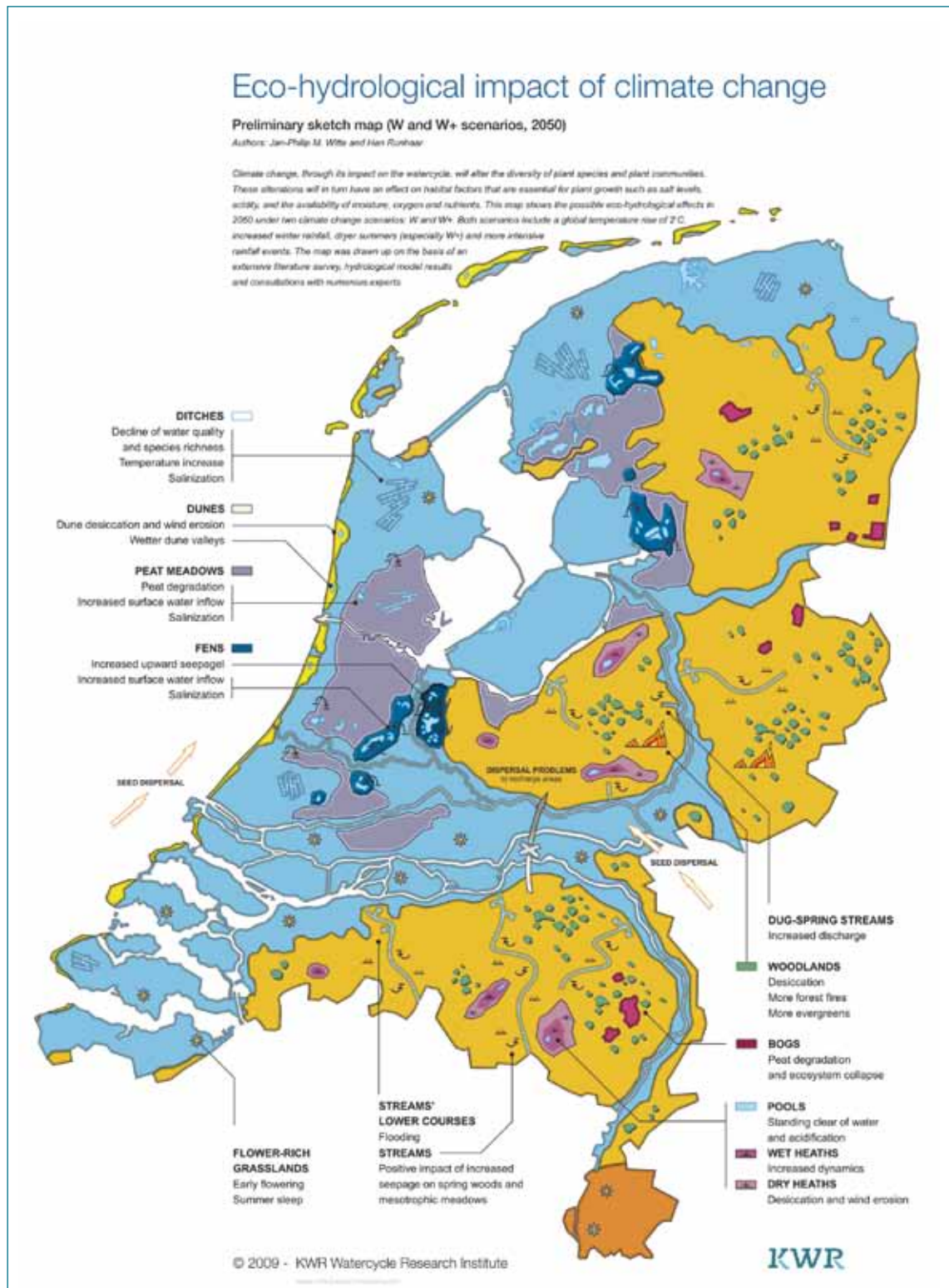


Figure 4.4.

Sketch map of vulnerable vegetation in the Netherlands as affected by climate change. Translated into English based on Witte et al. [2009a].



In addition, the research described here identified gaps in our current knowledge needed to better predict the effects of climate change on nature in the Netherlands. Particularly, the spatial resolution of current hydrological models, knowledge on the effects of weather extremes, feedbacks of the vegetation on the water balance and on the physiological adaptation and acclimation of plant species need to be improved and will be part of our future research for the Knowledge for Climate programme.

The sketch maps have been disseminated through a report of KWR, a information brochure of IPO ('interprovincial consultation'), a policy analysis of PBL [Vonk et al., 2010], the 'Bosatlas water', and two publications for a wider public in the Dutch journals H_2O and de Levende Natuur, respectively [Witte et al., 2009a; 2009b].

Interestingly, using a completely independent approach, another KVR project also found that particularly moist to wet nutrient-poor vegetation types (like bogs, fens and wet heathlands) are likely to suffer from climate change. We have just submitted a joint manuscript to an applied-science Dutch journal to describe these results [van Bodegom et al., 2011b].

4.3 Scenario analyses

As explained in the section 1, current vegetation models apply indirect empirical relations between environmental conditions and vegetation characteristics. It is unlikely that these relations will hold in a changing climate. Therefore, developing climate-versatile measures of environmental conditions was central to our project. We used nitrogen mineralization, as driven by temperature and hydrology, to quantify soil fertility conditions.

Likewise, we replaced spring groundwater levels (measured on the 1st of April) by potential oxygen stress and potential drought stress as experienced by a hypothetical reference vegetation [Bartholomeus et al., 2008b]. Potential oxygen stress reflects the potential reduction in respiration due to limited oxygen availability (as affected by soil texture, temperature, rainfall dynamics and groundwater levels). Similarly, potential drought stress reflects the potential reduction in transpiration due to limited moisture availability (as affected by CO_2 , temperature, soil texture and groundwater levels). Inputs for the calculations of oxygen and drought stress were simulated daily soil moisture and soil temperature, as calculated using the hydrological model SWAP [van Dam et al., 2008] based on daily groundwater levels as interpolated from biweekly measurements by *Menyanthes* [von Asmuth et al., 2002].

Subsequently, our trait-based national model was coupled to a series of climate and biogeochemical models in order to run scenario analysis to predict changes in the spatial distribution of vegetation and functional biodiversity in a future climate. Specifically, the transformation series were used to create series of temperatures and rainfall for the different KNMI-06 climate predictions [Bakker and Bessembinder, 2007]. These series of temperature and rainfall have been coupled to the National Hydrology Instrument (NHI) to predict daily groundwater levels for each 250x250 m² pixel within the Netherlands. The predicted groundwater levels were coupled to (1) SMART-SUMO to calculate daily soil temperatures and daily nitrogen mineralization rates; and (2) our oxygen and drought stress routines [Bartholomeus et al., 2011b] to calculate potential oxygen and drought stress, corrected for reduced transpiration upon higher CO_2 concentrations [Kruijt et al., 2008]. These predicted rates of biogeochemical processes, in combination with information on nature management (to predict the time since disturbance), have been coupled to our trait-based national model PROBE to predict trait distributions for each 250x250 m² for each of the climate scenarios in the year 2040. Finally, based on the predicted trait values, probabilities of all fifteen vegetation types have been calculated.

As a first control analysis, we coupled predicted soil pH and soil nitrogen mineralization rates to indicator values for acidity and nutrients, respectively. Based on measurements, we know that these parameters are tightly coupled [Douma et al., 2011c]. The relations for the simulated current soil

pH and soil nitrogen mineralization rates were much weaker, indicating that these processes were not appropriately predicted by SMART-SUMO. Therefore, the results were not suitable to predict vegetation types occurrences and shifts therein. Instead, we will focus our future research to developing better soil chemistry routines within theme 3 of the Knowledge for Climate programme.

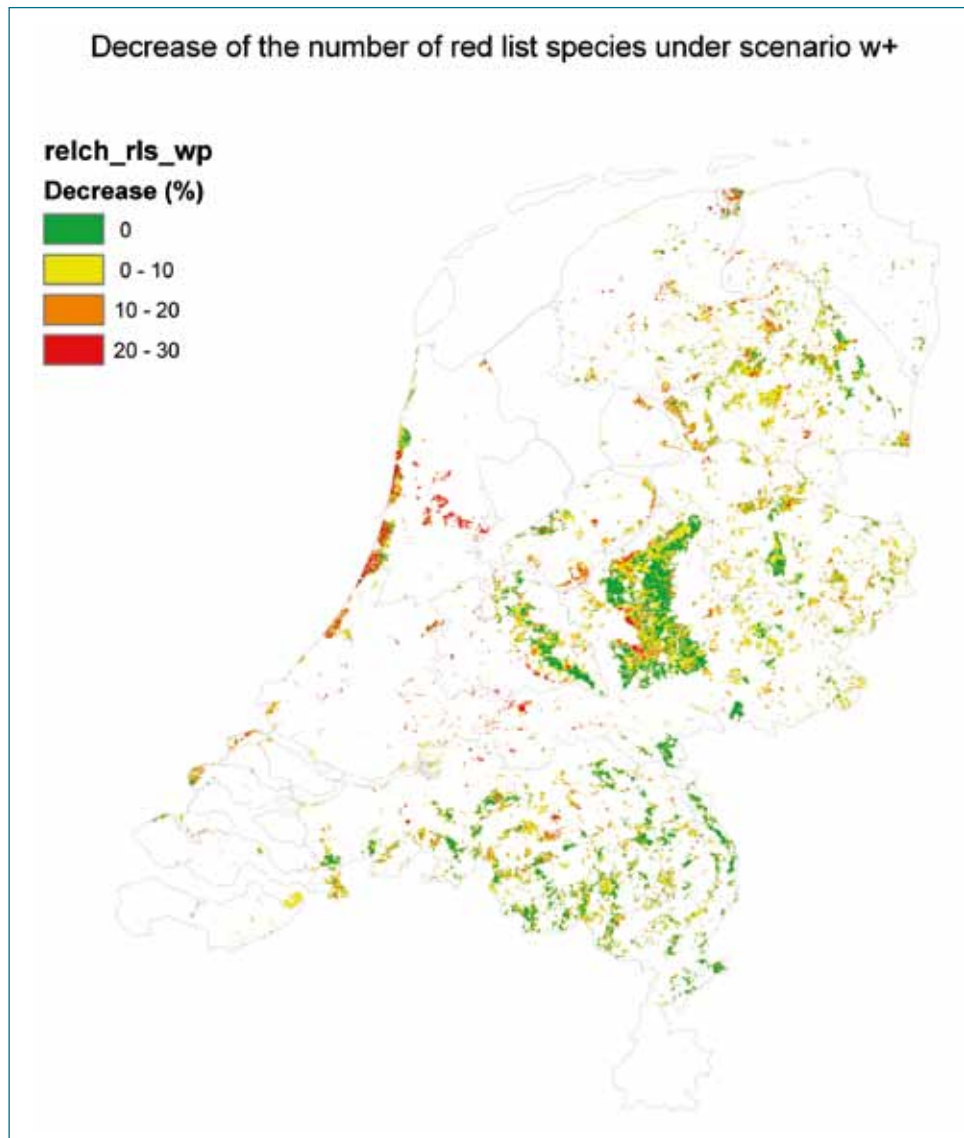


Figure 4.5.

Predicted change in the number of endangered species in a vegetation plot for the Netherlands in a future climate under the W+ scenario. Only grids with natural vegetation were used in the calculations.

The hydrological predictions were much better and calculated oxygen and drought stress related well to indicator values for moisture, as found in observations too [Bartholomeus et al., 2008b]. Given that the coincidence of oxygen and drought stress is coupled to a significantly lower potential number of endangered plant species within a vegetation plot, we used the hydrological predictions to spatially explicitly predict changes in the number of endangered species (Figure 4.5). The results (Figure 4.5) converge with those presented in section 4.2, indicating the susceptibility of regions with fluctuating groundwater levels. The strongest decrease are expected to occur in peatlands with fluctuating groundwater levels (province of North-Holland and parts of South-Holland), at the verges of the glacial ridges (province of Gelderland) and in the dunes (along the complete coast). Interestingly, and refining the sketch map (Figure 4.4), the effects in bogs seem to be less severe



than in some of the other ecosystems. However, it should be noted that the hydrological simulations assume that all substrates (i.e. the bog itself) remains intact, whereas the sketch map predicts that this will disappear.

4.4 Early warning systems of climate change

At the start of our project, we hypothesized that a threshold in environmental drivers may be surpassed upon climate change, causing a rapid change in vegetation properties or composition. The scenario analyses (section 4.3) nor our analysis of historical changes in vegetation composition in the Netherlands [Douma et al. 2011d] show indications for such threshold. In addition to thresholds and rapid shifts, conceptual theory on early warning systems [Scheffers et al., 2009] shows that increased variance in system properties may be used as early warning system. In contrast, our results do not show any sign of increased variance in system properties, i.e. trait distribution, either. This might indicate that vegetation responses in the Netherlands will be moderate.

However, this does not seem to be the complete story. When calculating oxygen and drought stress for the current climate and for the W and W+ scenarios, as outlined in [Bartholomeus et al., 2011a], we found that both oxygen stress and drought stress will increase in a future climate. Moreover, they will increasingly coincide, i.e. both stresses will occur more often within the same vegetation (Figure 4.6).

We also linked oxygen and drought stress to approximately 200 vegetation plots from a variety of natural habitats, ranging from dry to wet within the Netherlands for the current climate. To this end, we determined the current number of endangered species according to the Red List [van der Meijden et al., 2000] for each vegetation plot and described the relation between oxygen and drought stress and this number by the 95% regression quantile [Koenker and Basset, 1978]. There was a highly significant interaction for the combination of oxygen and drought stress for the 95% regression quantile that described the potential number of endangered species as function of oxygen and drought stress. This indicates that, under the current climate, the coincidence of oxygen and drought stress is coupled to a significantly lower potential number of endangered plant species within a vegetation plot. In contrast, common species were not affected by coinciding oxygen and drought stress.

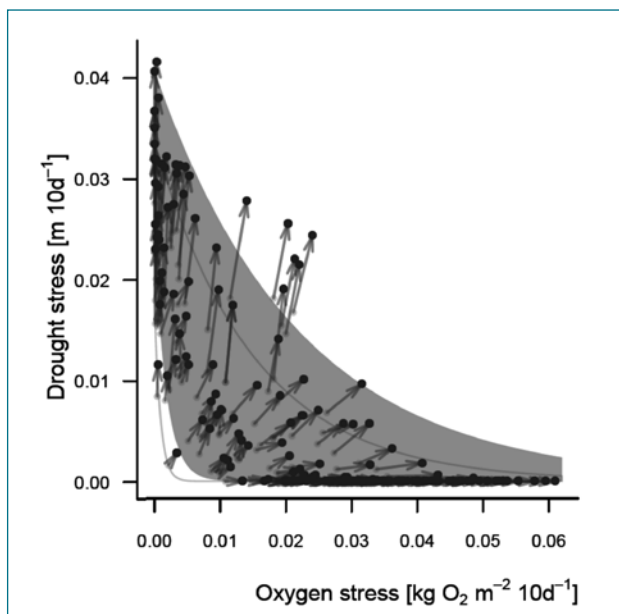


Figure 4.6. Predicted changes in oxygen and drought stress in a future climate under the W+ scenario. The shaded area indicates the 95% confidence interval of drought stress and oxygen stress in the current climate. From: Bartholomeus et al., 2011a.

In combination, these results suggest that increased oxygen and drought stress will particularly affect endangered species (independent of particular habitats), while endangered species tend to be the target of nature management. This pleads for a general consideration of endangered species and habitats within the Netherlands that still contain large number of endangered species. Combined with the results of section 4.2, it even more strongly suggests that particularly wet, nutrient-poor environments of the Netherlands that (1) generally contain many endangered species and (2) are likely to be prone to more co-occurring drought stress and oxygen stress, deserve special protection.

This result also suggests that increasing co-occurrence of environmental stresses might be considered to use as Early warning system, given that this may predict impacts on endangered species before the actual decline in the number of endangered species occurs.

5. Conclusions and recommendations

5.1 Reflection on the study aims

As discussed in section 4, we achieved all three aims that we had formulated in our original project proposal. This achievement is not only important for our own project, but also for the theme of adaptation and the programme as a whole. First of all, our analyses showed which vegetation types are likely to be negatively affected by climate change if no additional measures are taken. Given that most of these vegetation types of wet and nutrient-poor environments are typical for the Netherlands (and North-Western Europe in general), the Netherlands have special responsibility for these vegetation types (e.g. within the EU- Habitat Directive). This is important information when organizing the spatial planning and should ideally be accounted for. Therefore, we made our results public for use in other BSIK projects, like the LANDS project. As an additional step in that direction, we applied our PROBE model to an Environmental Impact Report for one of the Dutch dune nature reserves [PWN, 2010].

Our results show that endangered species are particularly sensitive to combinations of drought stress and oxygen stress, which might be used to create appropriate adaptation measures, e.g. by particular hydrological measures. Finally, by developing climate-versatile measures of environmental drivers that have been linked to functional traits of vegetation, climate impact predictions may be improved. Insights gained by our approach may be incorporated in current dynamic vegetation models and indeed will be within theme 6 of the Knowledge for Climate programme.

In the process of achieving our aims, we answered most of our research questions. Apart from the results already discussed in previous sections, our analysis of vegetation records did show that the response time of the vegetation was not important. Instead, analysis of time series of plant species composition showed that species responded almost immediately to a perturbation. Our analysis further showed that only a limited number of vegetation types can be distinguished functionally (with appropriate precision). These vegetation types merge various vegetation associations and (may) occur throughout the Netherlands and surrounding countries. Consequently, at a national scale, dispersal limitations are not expected to be important and were not explicitly accounted for. For local patterns with locally defined vegetation types, this situation may be different.

Finally, we showed [Douma et al., 2011d] that during succession, the main change in functional characteristics is related to height (and related traits). The effects of these changes were dealt with



by accounting for the time since disturbance. In addition, Douma et al. [2011d] showed that locally nitrogen dynamics may deviate due to local feedbacks. Unfortunately, the current-state-of-art in science did not allow to quantitatively incorporate feedbacks into our approach in the current project. At which conditions these local feedbacks are important and the quantification thereof will therefore receive more attention in our future research within theme 3 of the Knowledge for Climate programme.

5.2 Feasible adaptation measures

Given the uncertainties of this study, no conclusions can be drawn that may have far-reaching consequences, such as giving up certain nature targets because they would no longer be feasible in the future climate. However, one could at least anticipate on the possible negative effects of climate change by taking a number of mitigating measures that enhance the robustness of nature reserves. Desiccation of wet heathlands and rain-fed grasslands can be combated by converting highly evaporating dark coniferous woods in less water consuming deciduous forests, grasslands or heaths. Also damming of gullies, insofar as they are still present from e.g. the former buckwheat fire cultivation, is a way to prevent water loss and stimulate groundwater recharge. External measures are the creation of hydrological buffer zones, setting up surface water levels in agricultural areas, a ban on sprinkling in dry times and re-allocation or closing of groundwater abstraction wells. Although these measures are appropriate for nature, they may lead to spatial conflicts with agriculture. Such conflicts are not straightforward to solve. Therefore, developing adaptation measures to optimize conditions for both nature and agriculture will be a focus of our future research within theme 3 of the Knowledge for Climate programme.

Increasing the surface area of contiguous nature areas makes it easier to maintain high groundwater and surface water levels in relation to the surroundings and increases the supply of upwelling alkaline groundwater into the root zone of plants. In addition, this measure helps species to migrate to locations that in the future offer favourable habitats. In nature areas with a controlled water level, such as fens, a more flexible water regime can significantly help to reduce the inlet of surface water of a poor quality. The inlet-need of fens may also be reduced by minimizing downward seepage through a number of external measures: submerging adjacent deep polders, closing nearby groundwater abstraction wells and promoting the groundwater recharge in infiltration areas, such as in the ice-pushed ridge 'Utrechtse Heuvelrug'.

All these measures are aimed at combating desiccation and increasing the area of contiguous nature reserves. They are of great importance if scenario W+ becomes reality, and potentially of interest under scenario W, that, although wetter on an annual basis than the current climate, has a slightly drier summer. All in all, climate change should be a stimulus to combat with greater diligence the desiccation of nature and to stimulate the enlargement of the Natura-2000 network.

5.3 Recommendations for future studies

In addition to better understand feedbacks and their local importance, we recommend that research is devoted to understand the impacts of extreme (climatic) events on functional vegetation characteristics. So far, our approach has been devoted to average functional traits and average environmental conditions. However, it has been hypothesized that extreme events might be more than proportional impacts, but those effects are yet to be quantified. At the same time, the insights obtained on environmental stress measures, in particular those related to drought and oxygen stress, may aid to improve the current HELP-tables used to calculate yield losses in agriculture. Another aspect, that is likely to be important, is to improve our understanding on trait coordination

(which was started in [Ordonez et al., 2010a]) as it affects which vegetation types are likely to be abundant. In this same context, it will be important to understand adaptation and acclimation strategies of plant species and the extent to which this differs among plant species (although our approach is likely to be relatively insensitive to this aspect, because in traits-based approaches it does not matter whether a trait shift occurs due to acclimation or due to species turnover -unlike current vegetation models).

Finally, a better quantitative prediction of local gradients in hydrological and soil nutrient conditions is needed to better predict local differences in vegetation. Several of these aspects will receive attention in our research projects for themes 3 and 6 of the Knowledge for Climate programme.

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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 optimise 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.

Programme Office Climate changes Spatial Planning

c/o VU University Amsterdam, FALW
De Boelelaan 1085
1081 HV Amsterdam
The Netherlands
T +31 20 598 7318
office@klimaatvoorruijnte.nl

c/o Alterra, Wageningen UR
P.O. Box 47
6700 AA Wageningen
The Netherlands
T +31 317 48 6540
info@klimaatvoorruijnte.nl



www.climatechangesspatialplanning.nl