Programme

Biodiversity works

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Earth and Life Sciences
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Linking floral preference to reproductive performance in solitary wild bees

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Introduction

The pollinator decline experienced across European intensive agricultural landscapes is probably related to the scarcity of available floral resources for pollinators (Scheper et al. 2014; Potts et al. 2010). Increasing land-use intensity reduces the amounts of extensively managed landscape elements and those elements also contain most flowering plant species. Increasing land-use intensification is also accompanied by higher fertiliser inputs, which generally correlate with a declining species richness of flowering forbs (Kleijn et al. 2011). In turn, recent studies have shown that a decline of wild bees may not be only related to the abundance of available floral resources in agroecosystems, but also to the diversity of floral resources. A recent analysis suggested that a mismatch in floral preferences of and flower availability for solitary wild bees might explain their declines (Scheper et al. 2014).

An important question that remains unanswered is how foraging decisions influence reproductive success and population dynamic responses of wild bees, under conditions when the species composition of floral resources is changing (Roulston & Goodell 2011). Few mechanistic studies exist that focus on correlating floral preferences with reproductive performance of wild bees on different flower species. Our aim in this study was to understand how floral preferences in solitary bees affect reproductive success and offspring performance and how the observed trends differ between solitary bee species.

Conservation efforts aimed to mitigate the negative impact of landscape intensification on wild pollinators, emphasise that floral resources need to be temporally available for wild bees at times when reproductive investment is highest (Scheper et al. 2013). For species that overwinter as adults and begin foraging early in the season, such as the mason bees Osmia bicornis and O. cornuta, floral resources need to be present early in the season, in order for the bees to survive and reproduce (Holzschuh et al. 2013). Recent studies have suggested that mass-flowering crops such as oil seed rape (OSR) may represent valuable floral resources for bee species that begin their activities early in the year, when few forbs are present in landscapes (Jauker et al. 2012; Holzschuh et al. 2013; Riedinger et al. 2014). However, several aspects about the value of such mass-flowering crops for wild bees remain unclear. For example: how readily will species use OSR when other flowers are also available, how profitable it is for bees to visit different flowers that are all accessible, and how valuable are different flower species in terms of reproductive performance?

Several details of their foraging biology mean that the flower preferences of solitary bees strongly impact their reproductive performance. Solitary bees are central-place foragers with limited dispersal ability (Gathmann & Tscharntke 2002). As a result of their restricted foraging ranges, and because mothers provision their offspring with a finite amount of pollen, natural selection is expected to act strongly on foraging decisions and reproductive output. Therefore a capacity to maintain high reproductive rates when the quantity and quality of floral resources are limiting, may enable species to better cope with the varying environments that agroecosystems represent. However, studies that have considered the role of floral resources in offspring performance have often ignored the possible role of foraging behaviour.

Studying the relationships between foraging preferences and reproductive performance of solitary bees may provide interesting insights into the possible role of dietary breadth in dealing with floral resources of variable quality (Haider et al. 2013). Solitary bees show large variation in their dietary breadth (Williams 2003; Müller et al. 2006). Floral preferences of wild bees may be driven by a number of factors, such as limitation in processing perceptive information, profitability and accessibility of floral resources (Müller et al. 2006). Pollen from different
flower species may also have different nutrient content or contain varying concentrations of allelochemicals. Recent studies underlined the importance of nutritional constraints in explaining pollen use by oligolectic bees (Praz et al. 2008; Sedivy et al. 2011). Also polylectic bee species may exhibit floral preferences, which may be related to abundance of different available floral resources (Williams 2003; Müller et al. 2006). Alternatively, polylectic bees might also make foraging choices on the basis of nutritional quality of available pollen. The mechanisms underlying dietary choices should translate into differences in the mother’s floral preferences, her reproductive output and in the quality of her offspring (Bosch & Vicens 2006). For example, when no alternative choices are present, foraging on pollen of inferior quality should translate into lower quality offspring, such as smaller weight and more male-biased sex ratios, even when pollen is provided ad libitum (Haider et al. 2013). As adult bees also require nectar and pollen for maintenance, the longevity and thus the lifetime fecundity of the mother bee may be lower on poorer quality floral resources. In contrast, foraging on highly profitable and good quality pollen should result in more brood cells produced per unit of time invested in foraging, which should also result in more female-biased sex ratios and possibly larger offspring.

Under field conditions however, polylectic bees are almost always presented with more than a single flower species to forage on, even when floral resources are very limiting. As substantial amounts of pollen from flowers are needed for offspring provisioning, solitary bees likely face a limitation of available pollen in the field (Müller et al. 2006), and thus mixing different pollen species may allow bees to meet the quantitative demands of pollen requirements. On the other hand, foraging on several different floral resources may allow bees to circumvent the deleterious effects of inferior resources by mixing them with resources of higher quality. Despite its possible importance, the role of foraging preferences in determining foraging efficiency and reproductive performance in solitary bees has remained largely unexplored.

Using controlled experiments we examined the floral preference, reproductive output and offspring quality of two solitary mason bees, *Osmia bicornis* and *O. cornuta*. We placed preferred and less preferred flower species in mixed stands (patches) in large walk-in flight cages and offered flowers to bees. The ranking of plant species was established based on bee preference behaviour. Our main hypothesis was that bee species perform best when using their most preferred plant species. Furthermore, we expected that the offspring’s performance would not only depend on the mother’s efficiency to gather provisions (quantity pollen available) but also on the nutritional quality of the pollen. To test this, we also analysed foraging behaviour of bees in scenarios where flower resources were offered either as single-species stands or mixtures, and the reproductive output was compared as well as offspring quality. Finally, we expected that low quality pollen alone would result in low offspring quality, but mixing pollen of different qualities may still make the production of high-quality offspring possible. What follows is an overview of our approach and the first preliminary results.

**Materials and Methods**

Experiments were carried out in 2013 and 2014. Three plant species, representing highly preferred (frequently collected) to little preferred (occasionally collected) flower species (*Centaurea cyanus*, *Brassica napus* and *Borago officinale*) were selected. Within large flight-cages, groups of potted plants were offered to individual (mated) parent bees, so that bees were forced to collect pollen from the plant species provided. Within a tent either a monospecific stand of one of the four plant species, or a mixture of all four plant species was established. Monospecific stands contained the same number of pots per tent as species mixtures, and the number of flowers, and the amounts of pollen and nectar in each tent were quantified. Each tent contained one custom-made trap-nest that allowed periodic counting of the brood cells constructed during the experiments (Figure 1). The number of brood cells produced by bees was recorded. All tents were periodically visited by two observers and bee behaviour was continuously recorded for 15 minutes, with observations repeated several times during the lifespan of each bee. We used the event recording software The Observer (Noldus Information Technology) installed on handheld PCs that enabled us to blind-score behaviour. The effects of foraging efficiency (handling time) and resource quality on offspring production were disentangled by scoring the duration and location of different behavioural elements in the foraging arena and relating behaviour to reproductive output. For analysis, foraging times and handling times will extracted from the dataset. The behavioural variables of interest are the time spent foraging per foraging bout (between visits to trap nest), and handling time per flower. In order to test our main hypothesis that bee foraging preference is positively related to reproductive output, we will correlate the average time spent on foraging to the number of brood-cells made. This relationship will then compared between flower and bee species combinations using GLM type analysis of variance models with categorical and continuous
explanatory variables. Finally, the mother's foraging choices will be linked to offspring performance in each flower treatment by comparing reproductive output with offspring quality (i.e. sex ratio, body size).

![Part of the experimental set-up showing the walk-in tents with flower patches and trapnests inside.](image)

**Figure 1** | Part of the experimental set-up showing the walk-in tents with flower patches and trapnests inside.

**Status update**

The experiments were successfully finalised and we have collected data both from *Osmia cornuta* as well as *Osmia bicornis*. Approximately ten days after emergence, *O. bicornis* began laying eggs into to artificial nest tubes provided in the experimental set-up (Figure 2.). The total number of brood cells made per *O. bicornis* was on average between 7.5 and 15.5, and the production of brood cells peaked around 25 days after emergence. There were differences in longevity of adult bees among the treatments ($\chi^2 = 11.145, P=0.011$), with *O. bicornis* in monotypic *Brassica* and mixed stands having the shortest lifespan (Figure 3.). We are currently in the process of determining whether possible differences existed between the flower treatments in the efficiency of bees to provision their offspring with pollen and nectar, and if yes, to what extent such differences were reflected in the sex ratio, and quality of the offspring.

![The lifetime reproductive output of *O. bicornis* bees released in the experimental cages. Graph shows data across all treatment groups.](image)

**Figure 2** | The lifetime reproductive output of *O. bicornis* bees released in the experimental cages. Graph shows data across all treatment groups.
Figure 3 | Longevity of Osmia bicornis in the experimental cages containing different flower species. Experiment was prematurely terminated by two days of heavy rainfall (at 45 days) that killed all bees that survived until that timepoint. These observations were censored and marked with ‘+’.

Acknowledgement

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References


Development of dynamic resource maps for ecosystem service providing arthropods in agro-landscapes

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Introduction

Beneficial arthropods like pollinators and natural pest enemies are important ecosystem service providers in agricultural landscapes. Increasing the levels of pollination and natural pest control supports the ecological intensification of agricultural production.

Several studies have shown the influence of both local and landscape scale factors on the abundance and diversity of pollinators and natural enemies. In many cases diversity of plant species at the local scale and diversity of land use and area of non-crop habitats at the landscape scale correlated positively with ecosystem service levels. This is explained by the presence of resources for beneficial arthropods in non-crop habitats. Nectar and pollen, shelter and alternative food are essential for pollinators and natural enemies in non-crop habitats.

Effective management makes sufficient resources available for the targeted ecosystem service providers at the right time and place in a landscape. An important step in the development of such management options is an analysis of the available resources in a landscape for different ecosystem service providers.

We evaluated the seasonal dynamics of floral resources available and accessible for different functional groups of beneficial arthropods in an agricultural landscape. Here we provide preliminary results and discuss the application of the results in the following steps of the project.

Methods

We related plant trait data with data on vegetation composition in two agricultural areas in the Netherlands: the Hoeksche Waard and the Flevopolder. In this contribution we present the results for the Hoeksche Waard.

Plant functional traits related to the availability and accessibility of nectar and pollen were derived from different data sources with the plant trait database BiolFlor (Klotz et al 2002), the Database of British Insects and their Foodplants (CEH, Biological Records Centre) and Holman (2009) as important sources of information. We integrated data in a new plant traits database, with the acronym PAMES (plants for arthropod mediated ecosystem services). For the plant species in the two case study areas we recorded traits like flowering time, nectar amount, flower type, pollination type, important pollinators and important herbivore pest species.

Vegetation composition data come from the Dutch National Vegetation Database (‘NVD’, Landelijke Vegetatie-databank) and from a report on the composition of sown flower strips along arable fields in the Hoeksche Waard (Van Rijn). These flower strips are sown to support natural enemies and to increase the attractiveness of the landscape for tourists.

The vegetation data record the abundance (% cover) of individual plant species in surveys in the Hoeksche Waard. Linking this to the plant traits we could calculate for each survey location the summed cover of plant species potentially providing floral resources for different insect groups in different months. In the NVD, surveys (relevés) are classified in vegetation types (i.e. vegetations with comparable species composition, related to similar biotic, abiotic conditions and management). We compared vegetation types with respect to the expected availability of resources for different insect groups. Here we give the results for syrphids. Their larvae are carnivorous and predate large numbers of aphids in crops. The adults contribute to pollination, as they need pollen and nectar from flowering plants.
Results and discussion

There were remarkable differences between different semi-natural vegetation types, but also between semi-natural vegetation types and sown flower strips (Figure 1). On average we saw a much higher cover of plant species with floral resources for syrphids in sown flower strips. The largest cover of flowering plants is expected in the summer months. In spring the amount of floral resources in these flower strips is low.

Within the semi-natural vegetations, the willow shrubs and forests had a relatively high cover of plants with floral resources, especially in spring. The abundant willow trees in this vegetation type produce large amounts of pollen and nectar. The willow shrubs and forests are potentially important sources of nectar and pollen in the whole landscape, as they are the only vegetation type that flowers abundantly in spring. Other vegetation types, such as ruderal communities and wet brushes provide moderate amounts of floral resources for syrphids, but compared to the willow shrubs, they are more important in late summer. Reed vegetations provide very little floral resources for syrphids.

The results show that not only the amount of floral resources differs considerably between vegetation types, but also between the seasons. For the continuous supply of floral resources for syrphids a mosaic of different vegetation types is needed. Other insect groups (data not shown here) also need different vegetation types for the continuous supply of floral resources during the year.

These results show the potential amount of floral resources per vegetation type. Actual amounts will also depend on the management of the vegetation (e.g. mowing regime) or drift of insecticides from adjacent fields. The contribution to stimulation of natural pest control will also depend on the spatial distribution of these vegetation types.

Figure 1 | Floral resources for syrphids, expressed as % cover of plant species with nectar and pollen accessible for syrphids in seven vegetation types and two types of sown flower strips. The % cover is calculated separately for each month (different colours), based on the plant species that are flowering at that time of the year.
Left | Floral resources for syrphids in different vegetation types in the Hoeksche Waard.
Right | Floral resources for syrphids in annual and perennial sown flower strips in the Hoeksche Waard.

Application

This study is part of the project ‘Exploiting knowledge on habitats used by arthropods to predict value of ecosystem services in agricultural landscapes’ that studies how to design agricultural landscapes in a participative approach with increased value creation for different stakeholders.

The result of this part of the study, the development of dynamic resource profiles, is being used for the development of spatially explicit models of the distribution of natural pest enemies and pollinators. A next step is to integrate these models in a spatially explicit modelling tool for the design and evaluation of landscapes for
multiple ecosystem services (LandscapeIMAGES). Changes in spatial pattern and management of arable fields, semi-natural habitats and flower strips will be used in optimisation procedures in LandscapeIMAGES to maximise the service level of different ecosystem services and minimise ecosystem disservices (e.g. based on the abundance of aphid host plants in semi-natural vegetations). Different landscape alternatives reflecting synergies and trade-offs between different aims of stakeholders will be the output of the optimisation model. These will be discussed with stakeholders in the case study areas.

Two contrasting vegetations in the Hoeksche Waard: a sown flower strip and reed vegetation along a creek.

References


Links

BiolFlor: http://www2.ufz.de/biolflor/index.jsp

Database of British Insects and their Foodplants: http://www.brc.ac.uk/dbif/

Ecosystem functions of invasive aquatic plants

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Goal

Globalisation and climate change increase the rate of biological invasions. The exotic invaders are often blamed for the loss of biodiversity and ecosystem functions. By definition, such species are called invasive exotic species and their management costs billions of euros each year. It seems that exotic species, especially invasive ones, cannot be beneficial for biodiversity and ecosystems as they are not within their natural range. However, the functions provided by native species are rarely compared to those provided by exotic species in a structured way. We are making such a comparison for exotic aquatic species, as their economic and ecological impact is rivalled only by terrestrial vertebrates in Europe. More specifically, we are comparing the functions provided by native and exotic submerged plants in aquatic ecosystems (see Figure 1). These ecosystems have been heavily altered by eutrophication, fragmentation and other human disturbances. Can exotic aquatic plants rival the suite of functions provided by native aquatic plants in this manmade landscape? This question is particularly important with regard to established exotic plants (Figure 2). Other species might already depend upon them for food, refuge or water quality and so removing such exotic species could damage the local habitat. On the other hand, if exotic plants provide none or just a few of the functions provided by native species, water and nature managers need to be encouraged to take action on the basis of solid evidence.

Figure 1 | Overview of our research goal, as well as the aquatic plant functions that we aim to compare for native and exotic plant species.
Preliminary results

So far we have obtained data on a variety of functions including refuge and habitat provisioning to macroinvertebrates, food quality and inhibition of algae (Table 1). Macroinvertebrate diversity correlates to habitat complexity and plants can be a major supplier of such complexity. Aquatic fauna use plants for cover, food and sites to deposit their eggs. They are also reliant on the oxygen produced by plants. However, will exotic plants provide the same benefits? We found that native and exotic submerged plants offered similar amounts of refuge to macrofauna predated upon by fish or dragonfly nymphs. Plant structural complexity is often assumed to be crucial for the strength of refuge provisioning, but our data suggests that this relies on the plants being sufficiently rigid. However, these results are based on short-term exposure to exotic plants. Therefore we also conducted longer experiments where we assessed the macrofauna biodiversity and community composition in planted monocultures of native and exotic plants. The results of these experiments have yet to be analysed but will be available soon. We did, however, analyse data on the food quality of native and exotic plants.

Aquatic snails depend on vascular plants and algae for food, as do many herbivore species living in aquatic ecosystems. It turns out that native and exotic plants are consumed in roughly similar ways, but there is a crucial piece of information confounding this result. The origin of exotic species varies considerably, from the USA to Brazil and South Africa to Australia. If the latitudinal origin of plants, in accordance with biogeography theory, is taken into account then a different result is obtained: temperate species are more edible than tropical species. Furthermore, this pattern is underpinned by plant traits. We therefore found that if plant origin is included then tropical plant invaders may pose more problems than temperate ones, at least in terms of food quality.

Figure 2 | Photograph of the Tienhovense Plassen, which has high plant diversity, clear water and contains a variety of macrofauna and waterfowl. However, the submerged plant visible in the foreground is *Cabomba caroliniana*, an exotic species. This links to the question posed in our project: does this exotic plant species provide the same ecosystem functions as native submerged plants? *Photo credit: Mandy Velthuis.*
Yet aquatic plant functions are not solely confined to interactions with fauna. Submerged plants ply a key role in keeping our water bodies clear. One of the major mechanisms involved in this is vascular plants outcompeting algae. If plants fail, however, and the water becomes turbid then phytoplankton take over and undesirable cyanobacterial blooms frequently occur. Plants excrete allelopathic substances to constrain algal growth, but not all may do so with similar efficiency (Figure 3). In laboratory trials we found no difference between the allelopathic potential of native and exotic plants to constrain the growth of a common cyanobacteria. In the near future we plan to further analyse experimental data on more facets of competition between aquatic plants and algae.

So far the comparison between native and exotic plant functions is progressing successfully. However further analysis and synthesis of the existing data is needed before any firm conclusions can be drawn. Interestingly, the data allow not just a comparison between native and exotic species but can also help build a better understanding of how plant traits affect plant function.

![Figure 3](image.jpg) Photograph showcasing a bioassay result where aquatic plant extracts were tested on a blue-green algae: *Anabaena flos-aquae*. Visible are three petri dishes where the blue-green algae are growing on agar. We spotted drops of plant extract onto these petri dishes. The effects give a crude but highly standardised indication of whether plant species excrete allelochemicals that kill or reduce the growth of cyanobacteria. Clearing spots indicate that cyanobacteria are inhibited or killed. *Photo credit: Benedetta Saccomanno.*

**Future work**

In addition to the field and lab work performed so far, we plan to investigate long-term biodiversity trends in native and exotic aquatic plants. Hopefully this will allow us to assess whether exotic plants are drivers in the decline of freshwater plant diversity. As functional plant traits and life history are potentially interesting, this work will be performed together with Dr Wim Ozinga and professor Joop Schaminee, the project leaders of another *Biodiversity works* project.

Together with the aforementioned preliminary results and new experimental data that will soon be analysed, we hope to be able to address our research goals.

In the end we plan to present and discuss our results with stakeholders in a symposium. This will hopefully allow water and nature managers to spend their limited budgets wisely, especially when exotic invaders are involved (Figure 2).
Social network effects and green consumerism

By Dominic Hauck, Erik Ansink, Jetske Bouma and Daan van Soest

According to reports from the European Union, consumer interest in sustainably produced food has increased in recent decades. Consumers want to spend more on food produced in an environmentally friendly and ecological manner where the negative impact of production on biodiversity is minimal. This phenomenon is often called “green consumerism”.

The feeling of a “warm glow” when consuming eco-friendly produced food seems to be one of the key drivers of green consumerism. However, there is empirical evidence that consuming “eco food” is increasingly becoming “hip”, i.e. some consumers purchase “eco food” because their friends do.

In our study, we are analysing the consequences of the existence of a “fashion” or “social network effect” in green consumerism on the total environmental impact of agricultural production. We are also evaluating if and how the social network effect influences aggregate societal welfare and then discussing the policy implications of this.

We are developing a model of a market in which three varieties of an agricultural product are sold – two varieties that are sustainably produced and a conventionally produced variety. Producers of the eco-products compete with respect to the price and greenness of the variety they produce. Those consumers who do not want to buy eco-products buy a conventionally produced product instead. Consumers differ in the amount of “warm glow” they receive from consuming a product with a specific environmental quality. Moreover, every consumer benefits from the positive impact of sustainable production on the overall environmental quality, independent of whether they purchased an eco-product or not. Those who purchase eco-products also benefit from “being fashionable” – the network effects associated with green consumerism.

Using this model, we have shown that the stronger the social network effects associated with green consumerism, the larger the market share of eco-friendly product varieties in the market. However, we also found that stronger network effects tend to reduce the overall environmental quality in the market, and may even decrease aggregate welfare. This is because producers of eco-products with a relatively low, positive environmental impact have an incentive to further reduce the quality of their product variety. Finally, we have shown that the stronger the network externalities, the more important it is for the regulator (or NGO) to set higher minimum quality standards or to impose stricter requirements on eco-labels.

In follow-up studies, we will validate these results using empirical/experimental methods. We will also study the impact of consumer coalitions, which may reduce the market power of large consumers, on the kind of market previously described.

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Linking microbial diversity to the functioning of soil food webs

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Introduction

Soil ecosystems contain a high trophic complexity and support huge amounts of biological diversity. The tremendous functional diversity that can be found among soil organisms is pivotal for a number of ecosystem services like the production of food, fibres and biofuels. Other ecosystem services like clean air, drinking water, nutrient cycling and carbon storage are also largely dependent on soil organisms. Due to increased intensive land use, it is expected that soil biodiversity will be affected with negative impacts on these soil ecosystem services. Land owners, policy makers and scientists are therefore making considerable efforts to optimise land management for maximum functionality.

The relationship between soil biodiversity and ecosystem functioning has been widely explored, but up until now it has mainly focussed on the effects of biodiversity change within a single trophic level. Since soil organisms are part of a complex network of trophic interactions, a multitrophic approach provides a more ecologically relevant perspective to study the relationship between biodiversity and ecosystem functioning in the soil. Soil food web models are great tools for studying this relationship at a multitrophic level. However, existing soil food web models have two major shortcomings. The first is the lack of chemical diversity of the soil organic matter and the second is the lack of a definition of biological diversity within the soil microbial community. Since litter type and microbial community structure and diversity are important drivers of multiple ecosystem processes, those aspects should be included in the existing food webs so that accurate models can be described.

The main aims of this project are to include microbial community structure and diversity, as well as diversity in litter type, into soil food web models. This is achieved by combining empirical studies with a theoretical approach, whereby the outcomes of experiments will be incorporated into existing food web models. This will provide a unique translation of how soil-borne microbial diversity influences food web structure and soil ecosystem functioning, leading to a better prediction of soil ecosystem functioning in terms of carbon sequestration and nutrient cycling. Those outcomes will provide important information regarding management strategies to optimise soil functionality under the threat of increased intensive land use.

The soil microbial community: a key player in nutrient management

During the first year of the project we studied the effects of different types of organic amendments on the soil microbial community structure in an agricultural system. This experiment was part of a bigger study, focussing on the impact of organic fertilisation on the nitrogen retention capacity and plant productivity of agricultural systems. In a big pot experiment, four different types of organic amendments were mixed with soil, after which Brussels sprouts were grown in the pots (Figure 1). The four different types of organic amendments differed in their quality (C:N ratio) and degradability (%lignin).

The development of the microbial community was followed during the experiment by analysing the abundance of 20 types of phospholipid fatty acids (PLFAs) in the soil. PLFAs are components of membranes and their abundance provides information regarding the soil microbial biomass and community structure. The results showed that there were no significant differences in microbial community structure after three months. However, after six months the microbial communities between the different treatments (types of organic amendment) were significantly different.
different (p<0.001). Those results show that different qualities of organic matter generate significantly different types of microbial communities in the longer term. Other results from the same experiment have also shown that those changes in microbial community structure are related to a number of important ecosystem services like carbon and nitrogen mineralisation but also crop growth.

Figure 1 | Pot experiment with Brussels sprouts growing on a mixture of soil and different types of organic fertiliser.

This study showed that changes in land use (from conventional to organic farming) can have significant effects on the structure of the microbial soil community. It also revealed that the quality of organic inputs plays a determining role in this and that important ecosystem services like plant productivity and carbon and nitrogen mineralisation are affected by this.

Successional soils: how the microbial community affects dynamic nature

The first part of the project revealed that various qualities of organic material may have different effects on the microbial soil community. In the second part of the project we want to collect more information regarding the exact routes of organic material through the microbial part of the soil food web. This information will then be used to improve the current soil food web models.

At the moment a first experiment is running in which the decomposition of organic material is followed through the soil microbial community in different soils originating from secondary successional fields on the Veluwe. A total of six ex-arable fields were visited in the autumn (three early stage successional fields and three late stage successional fields) and soil samples were collected in the field (Figure 2). These soil samples are currently being incubated in 180 microcosms together with 13C stable isotope labelled plant litter (Figure 3). The addition of labelled plant litter makes it possible to track the fate of carbon through the soil food web. At certain time points after the start of the incubation (1, 3, 7, 14, 28 and 56 days) a subset of those mesocosms will be harvested and stored in the freezer to stop all decomposition processes. At certain time points after the start of the incubation (1, 3, 7, 14, 28 and 56 days) a subset of those mesocosms will be harvested and stored in the freezer to stop all decomposition processes. In the near future PLFA and RNA will be extracted from those soil samples, and analysed for the presence of stable isotopes in specific groups of microbes and other soil organisms. In this way it can be determined when which organisms of the soil microbial community play a role in the decomposition of the labelled plant litter. This experiment will provide detailed information about the exact route of organic material through the microbial part of the soil food web. These results will partly be available in the spring of 2015, and hopefully be presented to you on the next NWO Biodiversity Works Symposium.
Figure 2 | Six ex-arable fields from which soil samples were taken. On the left you see three young successional fields: a) Oud Reemst as abandoned in 2005, b) Reijerskamp as abandoned in 2005 and c) Telefoonweg as abandoned in 2009. On the right you see three old successional fields: d) Boersbos as abandoned in 1982, e) Dennenkamp as abandoned in 1982 and f) Mosselse Veld as abandoned in 1985.
Figure 3 | Mesocosm experiment with soil from six different ex-arable fields on the Veluwe. Plants originating from these same fields were labelled with the stable isotope 13C (top left). The labelled plant material was ground (top right) and mixed the soil from different ex-arable fields before the mesocosm incubation experiment started.

References

Farmers as nature managers.
An analysis of people’s willingness to pay for farmers conserving nature

Mark Koetse, Barbara Agstner, Frank van Laerhoven and Jetske Bouma

Farming for Nature (FFN) is a cost-efficient approach to biodiversity conservation, where farmers in areas bordering protected, nutrient-poor wetlands, are encouraged to act as nature managers by adopting a different approach to production. In its broad form (FFN broad) the approach has the following characteristics:

- No use of pesticides, fertilisers or other environmentally harmful materials, and natural water levels are retained.
- Measures lead to a recovery of the natural balance and an increase in biodiversity, also on agricultural land and nature in the direct vicinity of the farm.
- Decrease in farmer revenues is around 50%, implying an average annual decrease in income of around 40,000 euros.

A slimmed down version of FFN (FFN small) has the following characteristics:

- No use of pesticides, fertilisers or other environmentally harmful materials, and natural water levels are not retained.
- Measures lead to a recovery of the natural balance and an increase in biodiversity, but only on the farm itself.
- Decrease in farmer revenues is around 25%, implying an average annual decrease in income of around 20,000 euros.

This research is explorative and is aimed at assessing the feasibility of a private-financing mechanism for FFN by means of a choice experiment. In a choice experiment respondents are presented a hypothetical market by asking them to choose between two or more alternatives described by attributes with varying levels. The choices are subsequently analysed by choice models, and produce as output the utility that an individual derives from the various attributes and attribute levels. Estimating economic value estimates for attribute levels is made possible by including a payment vehicle (e.g., price of a good or service).

In our experiment we asked respondents whether they were willing to donate to a fund from which farmers are compensated for their decrease in income. The public benefits people obtained in return are listed in the bullet points above. Respondents were presented with six different choice situations. Each choice situation consisted of three options: FFN small, FFN broad, and a ‘no contribution’ option. Each option had four characteristics. The first characteristic was the payment vehicle, in our case in the form of a six-year contract containing an annual donation to a fund, which takes on levels of 10, 20, 40 and 80 euros per year. We also included three characteristics with respect to institutional design. The second characteristic was related to an ongoing discussion about whether farmers should administer the fund themselves or whether a control and supervisory body needs to be established. We distinguished between three levels: Natuurmonumenten; Nationaal Groenfonds; Farmers themselves. The third characteristic was related to a potential refund. For FFN broad to be optimal, a large-scale implementation is needed. For this we defined a threshold of 10 farms for FFN broad to be optimally effective. The refund characteristic defined the consequences of not reaching the threshold. Three levels were distinguished: Money back; Use of money for FFN small; Use of money for FFN broad, but with a smaller increase in biodiversity. Finally, a characteristic was included which links biodiversity provision as a public good to a private good in the form of a small reward/benefit. Naturally such a private benefit needs to be adapted to the kind of public service offered, so in this study it took the form of an overnight stay at a B&B farmhouse, a tour of the farm and a selection of farm produce. We only varied between the inclusion and exclusion of a private benefit, so as to limit choice task complexity. Figure 1 provides an example of a choice card shown to respondents.
Due to resource constraints, drawing a sample representative of the entire Dutch population was unfeasible. Nevertheless, in an attempt to collect a sample that was as representative as possible, the questionnaires were distributed in five different cities: Amsterdam, Utrecht, Gouda, Doetinchem and Maastricht. The strategy of data collection was to intercept people in public spaces where a wide variety of respondents could be expected. In the end 63 interviews were conducted, which means that 378 choice cards were filled in. This is a satisfactory result for an explorative study of this type, but it is insufficient for a representative study. For example, our sample was biased towards young people with higher than average education and lower than average income, which affects results and compromises generalisability.

We estimated a multinomial logit choice model. The willingness to donate (WTD) estimates are shown in Table 1. For the two farming approaches a positive WTD for increased biodiversity provided by farmers was found. The average WTD for FFN small was around 26 euros per year, and as expected, the WTD for ‘FFN-broad’ was higher at 40 euros per year. This shows that respondents differentiated between varying scopes of biodiversity conservation.

Table 1 | Willingness to donate (WTD) estimates.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Attribute level</th>
<th>WTD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Farming practice</td>
<td>FFN small</td>
<td>€ 25.8</td>
</tr>
<tr>
<td></td>
<td>FFN broad</td>
<td>€ 40.3</td>
</tr>
<tr>
<td>Private benefit (reference category: No)</td>
<td>Private benefit</td>
<td>€ 1.2</td>
</tr>
<tr>
<td>Fund operator (reference category: Natuurmonumenten)</td>
<td>Farmers themselves</td>
<td>− € 4.6</td>
</tr>
<tr>
<td></td>
<td>Nationaal Groenfonds</td>
<td>− € 12.1</td>
</tr>
<tr>
<td>Threshold policy (reference category: Money back)</td>
<td>FFN small</td>
<td>− € 1.7</td>
</tr>
<tr>
<td></td>
<td>FFN broad</td>
<td>− € 20.6</td>
</tr>
</tbody>
</table>

The results also show that providing a private benefit hardly affects choices made by respondents. Fund operator appears to matter to a more substantial extent. Willingness to donate decreases somewhat when the fund is operated by farmers themselves compared to Natuurmonumenten, and decreases quite substantially when Nationaal Groenfonds is the operator. Finally, we found people care about not reaching the threshold for FFN broad. Where people are almost indifferent between getting their money back or using the money for FFN small, using the money for FFN broad but with smaller biodiversity benefits decreases the WTD for FFN broad substantially. Specifically, when the threshold has not been reached, people's WTD for FFN small (26 euros) and FFN broad (20 euros) are quite similar.

In conclusion, we found that that there is potential for the implementation of a private-financing mechanism for FFN. We also found that providing private benefits to induce people to donate has almost no effect and will ultimately cost time and money, and that the institutional setting (fund operator) may matter for the amount of money people are willing to donate. Finally, ensuring that the FFN broad programme is optimally implemented, i.e. that a certain threshold in terms of number of converted farms is reached, may increase donations substantially.
References


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Linking community traits to ecosystem processes: Soil community assembly explained by variation in species functional traits

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Community assembly follows some strict rules

Predicting the effect of climate change on biodiversity and the consequences of community compositional shifts for ecosystem functioning is a major challenge in community ecology (Woodward and Diament (1991), Keddy (1992), Chapin (2003)). One important constraint that reduces our ability to predict how communities respond to stress and how changes in community composition impact ecosystems is the often high context dependency of local ecosystems. Soil biodiversity responses to environmental changes are dependent on the taxonomy of the local species pool in combination with location specific environmental factors. Moreover, species differ in their effect on soil ecosystem functions but this effect is not necessarily coupled to their taxonomy. A trait-based approach\(^1\), instead of the classical taxonomical approach, with a focus on functional traits of species might enable us to understand how communities are shaped and function. For instance, environmental factors, such as soil moisture levels, act as filters that select soil fauna species with the right trait values from a regional species pool. Extreme climatic events, for example drought or high precipitation events are expected to cause shifts in this soil moisture filter, which affects the local species community based on the trait values of the species. Species that differ in taxonomy but have the same functional trait values (i.e. in this example drought resistance or inundation resistance) will respond similarly to environmental stress. With a focus on functional traits we hope to provide the necessary generality in community responses and functioning.

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**Figure 1** Environmental factors, such as soil moisture levels, act as filters that select soil fauna species with the right trait values from a regional species pool.

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\(^1\) Traits are physiological, phenological, morphological or behavioural features that can be measured on an individual.
Understanding how traits related to species responses to environmental factors (response traits) and traits related to species effects on ecosystem functions within communities (effect traits) are linked, makes it possible to predict how environmental changes affect ecosystems. If response and effect traits are coupled, either because response and effect traits are the same (i.e. body size) or via correlation of traits or trait trade-offs, we should be able to predict how changes in the environment, either natural or via management, act on ecosystem processes and services. We test this response-to-effect trait approach by analysing the response of soil macro-detritivore community composition to extreme soil moisture changes and the effect of community shifts on soil nutrient cycling and primary production. As a first step in this analysis, we measured the variation in response traits underlying drought resistance of 55 Dutch key macro-detritivore species (woodlice, millipedes and earthworms).

**Hypotheses**

- a. There is variation in water loss rate (WLR) between soil macro-detritivore species and between taxonomical groups of macro-detritivores.
- b. Interspecific variation in WLR predict shifts in soil community composition across soil moisture gradients.

**Measurements of response traits underlying drought resistance**

In total 55 macro-detritivore species (20 millipede, 21 isopod and 14 earthworm species) were collected throughout the Netherlands. The animals were kept for one week in a climate room at 15°C and fed with leaf litter from the sampling sites. Prior to the analysis, the animals were starved for three days in pots with moist plaster of paris. After this acclimation period, the animals were placed individually in pots placed in a larger pot in a climate room (15°C, 16:8 L:D cycle, Figure 2). These pots contained a glycerol/water solution to maintain an air humidity of 85%. Mass (=water) loss over time (mg H₂O h⁻¹) and animal dry weight (mg) were measured.

![Figure 2 | Experimental set-up.](image)

Species and taxonomical groups differ significantly in water loss rate ....

WLR is measured as the loss of water (mg) per hour as a proportion of the initial water content of the animal. Soil macro-detritivore species differ significantly in WLR and WLR is correlated with body dry mass (mg) (Figure 3). This pattern is strongest for woodlice and earthworms. Body size may therefore serve as a proxy for WLR. WLR differs also between the taxonomical groups, and is significantly lower for millipedes than for earthworms and woodlice.
Dias et al. (2013) showed that differences in WLR explain the composition of isopod communities over a soil moisture gradient in Hungary (Figure 4). Using our WLR measured under standardised laboratory conditions, the mean WLR was calculated for real communities in dry, moist and wet environments. The mean water loss rate of the community was calculated by weighting the WLR values of the species by the relative frequency of the species occurring. This means that the trait value of the most frequent species (i.e. the best adapted species, and hence the most informative trait value) contributed most to the community mean. In dry environments, species with a relative low WLR rate are dominant and in wet environments species with high WLR are dominant. From dry to wet soils there is a significant increase in the mean WLR of the community. This example shows that soil moisture condition (environmental filter) determines species distribution based on the functional trait values of the species in the regional species pool.

Future prospects: Testing community assembly in a natural grassland

The next step is to analyse community shifts under stress in a natural set up. For this we will create assemblages with realistic combinations of macro-detritivores, plants and litter and expose these to periodic drought and/or inundation events in a semi-natural grassland. Functional traits will be used to predict shifts in community composition under drought and inundation stress. Also the consequences of community shifts for nutrient cycling and primary production will be analysed by using effect traits (e.g. body size, litter consumption rate etc.). This experiment is planned to start in 2015.
References


Predicting changes in ecosystem functioning from shifts in plant traits

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Stakeholders: Netherlands Environmental Assessment Agency (PBL), State Forestry Service (SBB), National Authority for Data concerning Nature (GAN)

Background and aim

From a perspective of ecosystem functioning, not only species diversity is important but also the functional diversity within plant communities based on functional traits of the component species. A better understanding of how functional diversity is influenced by environmental change is a prerequisite for predicting changes in ecosystem functioning and for cost-efficient management strategies. In order to link environmental changes to ecosystem functions and associated ecosystem services, we will distinguish between two aspects: on the one hand traits determine the response of the plants to environmental change and on the other hand traits are instrumental for the effect that plants impose on ecosystem functions and ecosystem services (response-to-effect framework).

By using traits of known importance to ecosystem functions, shifts in trait composition within communities can be used as indicators (proxies) for changes in ecosystem functions and associated ecosystem services.

The objectives of this project are:
1. To develop a set of trait-based indicators of ecosystem functions and associated ecosystem services;
2. To link changes in habitat quality and connectivity to shifts in indicators of ecosystem functions and services.

By combining recent trait databases with the Dutch National Vegetation Database, containing over 550,000 georeferenced site descriptions of species composition and habitat characteristics (see Schaminée et al. 2012; Bongers et al. 2013), this can be done in a way that was not previously possible. For the analysis of trait-environment relationships we have developed a new generalised linear mixed model approach (see Jamil et al. 2013). We have established collaborations with several other research groups.

Some first results

In the first phase of the project we focused on the response-side of the story. At the species level we compared the performance of specialists and generalists on both ecological and evolutionary scales (Ozinga et al. 2013, see newsletter 1). Here we report on another subproject where we analysed the effect of nitrogen deposition on the local aboveground persistence of plant species in permanent plots (Hendriks et al. 2014).

Many empirical studies have shown that there is a continuous small-scale turnover of plant species, with the net result that plant species show temporal variation in their spatial distribution patterns as ‘shifting clouds in the sky’. While the direction of vegetation changes has received much attention, this is less the case for the rate of vegetation change. Local vegetation dynamics are determined by a dynamic balance between colonisation and local extinction. At the scale of small plots, the rate of local aboveground extinction can be expressed as the reciprocal of the mean or median time that a species persists in a plot. We used survival statistics (Kaplan-Meier analysis and Cox’ regression) to analyse the effect of life-history traits and local abiotic conditions on local aboveground persistence.

At the species level there may be intrinsic differences in the likelihood of local aboveground persistence (survival time), due to trade-offs between investments in attributes that enhance aboveground persistence and investments in other life-history traits. Adult lifespan is hypothesised to be negatively related to dispersal ability and to seed longevity. If there is a trade-off between aboveground persistence and dispersal ability, we may also expect a relationship between aboveground survival patterns and local environmental conditions, since environmental
constraints may impose restrictions on the viable trait combinations in a given habitat. The net effect of traits on the local persistence might depend on ecosystem properties such as disturbance regime and availability of resources. Comparative data on the local aboveground persistence of plant species across habitats are, however, sparse and generally from studies based on few populations of a limited number of species. Here we focus on the effect of nitrogen deposition, which is considered to be one of the strongest drivers of changes in species composition.

We combined information on local aboveground persistence of vascular plants in 245 permanent plots in the Netherlands with estimated levels of nitrogen deposition at the time of recording. We found a positive relation between local aboveground persistence of plants and high levels of nitrogen deposition (especially ammonia deposition). This was not only the case for species with high nitrogen requirements, but also for species with low nutrient requirements. The results are a preliminary indication of the importance of lower colonisation access due to nitrogen deposition. The ‘fixation’ of vegetation dynamics due to the lower accessibility to newcomers poses an extra threat to species diversity, since it may lead to further additional extinction of species due to population dynamic and population genetic effects. Follow-up research is required to see to what extent this influences traits that are instrumental for the effect that plants impose on ecosystem functions and ecosystem services (i.e. the response-to-effect framework).

Figure Long-term permanent with vegetation data are an important information source for the analysis of vegetation dynamics.

Publications


Understanding the role of plant traits and their plasticity in N:P stoichiometry and competition

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Supervisors: Prof. Martin Wassen, Dr Jerry van Dijk, and Dr Maarten Eppinga

Trait plasticity and the outcome of plant competition

We are investigating the effects of trait plasticity on plant competition and how this influences the plant biodiversity in Dutch grasslands. We are specifically focussing on the effect of the nitrogen: phosphorus ratio on these plant traits (Figure 1). To gain a better mechanistic understanding of this interaction, we carried out a greenhouse experiment in the Botanical Gardens of Utrecht University for two-years. This summer the second year harvest of the experiment was finished.

We chose six grasses and herbs that frequently occur in Dutch nature reserves: Alopecurus pratensis (Meadow Foxtail) and Rumex acetosa (Common Sorrel) as potential N-limited specialists, Briza media (Quaking Grass) and Centaurea jacea (Brown Knapweed) as potential P-limited specialists and Knautia arvensis (Field Scabious) and Prunella vulgaris (Selfheal) as potential opportunists. The species selection was based on the outcomes of exploratory fieldwork and the analysis of a large field database (database from Fujita et al., 2014).

Every pot contained four individuals, either four individuals of the same species (monoculture) or two opportunists and two specialists together (mixture). This allowed us to see what the effect of trait plasticity is - as measured in monoculture – on plant interspecific competition. The experiment had a full-factorial set-up, with an N:P ratio ranging from 1.67 (severe N-limitation) to 135 (severe P-limitation). To account for possible interaction effects between the N:P ratio and the total amount of nutrients, we also used three nutrient levels: low, intermediate and high. This resulted in 15 different nutrient treatments. The two-year experiment started with 2100 pots with 4 individuals each. Half of the pots were harvested in 2013, the other half in 2014. We measured many different plant traits and for both years it took a team of people to measure them all. The two harvests resulted in over 17,000 bags with dried plant roots, shoots, flowers etc. We are currently weighing these roots and shoots and analysing them in the lab for N, P and K content. We have already given a sneak preview of some of the outcomes at the Vegetation – Soil Interactions Symposium in Wageningen (held on 30 October 2014). As we are still gathering data, we hope to show you verified results at the next Biodiversity Works meeting.
Figure 1 | Research outline.

Figure 2 | Alopecurus pratensis (Meadow Foxtail) vs. Knautia arvensis (Field Scabious). All three pots have received the same nutrient solution: a low N:P ratio (1.67; indicating severe N-limitation). The Alopecurus leaves are clearly taller in the monoculture (left pot) when compared to the competition pot (middle). On the other hand, Knautia growth in monoculture (right pot) is not visibly different from interspecific competition. Photographs: Ineke Roeling (2013)
Figure 3 | Top-left: Annick van der Laan is weighing and scanning the roots to determine the specific root length. Top-right: Ineke is measuring the root phosphatase production. Below: Inge Schrijver (right) is washing the plant roots for the second harvest cycle of the day after which the plants are prepared for leaf area measurements and root scans at the central table (Annick and Hans van Someren Grêve). In the background Martin Tegelaar is measuring the phosphatase production of the first harvest cycle of the day. Photographs: Ineke Roeling (2013, 2014)
How reliable are European ecosystem service maps?

Dr C.J.E. Schulp

Several EU and global-scale policy initiatives depend on accurate and reliable maps of ecosystem service provision for successful implementation. Many methods for mapping ecosystem services have been developed over the past years. Few of these mapping studies are able to provide insight in the accuracy and reliability of the output maps. In a joint project by researchers from the EU project CONNECT, OPERAs, OPENNES and VOLANTE, a systematic comparison of ecosystem service maps was performed at the EU scale. Such a systematic map comparison provides insight in the uncertainty on ecosystem service provision, but does not tell if the maps are accurate. All maps included in this study originate from well-established methods based on solid process or empirical understanding. Nevertheless, only maps of climate regulation were reasonably similar. For erosion protection, there were no regions where all maps analysed agreed on the existence of a hotspot of provision of the service. For the other ecosystem services assessed (pollination, recreation, flood regulation) there was some agreement among the maps analysed. Differences among the maps were caused by differences in indicator definition, level of process understanding, mapping aim, data sources and methodology.

To quantify the accuracy of the maps, validation with independent data should be performed. However, monitoring of ecosystem services is often not possible or available, limiting a full validation. Many indicators for environmental issues exist that tell something about ecosystem service provision, but due to the differences in indicator definition, they are not comparable with modelled ecosystem service maps. Consequently, there are no accurate measures for ecosystem service map quality.

Agreement among four climate regulation maps and four erosion protection maps. The maps indicate how many of the underlying maps have values within the upper (hotspot) or lower (cold spot) quartile of the data distribution.

The large differences between ecosystem service maps have implications for policies aimed at ecosystem services. First, policies should clearly specify their target of interest to ensure that indicators on ecosystem services exactly fit this target and to minimise the risk of inconsistencies. Second, there is a need for independent validation data on ecosystem services. Third, a variety of ecosystem service maps from different sources could be applied to provide insight in the uncertainty margins of ecosystem service provision.

Reference


Link to paper

http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0109643
New paper on wild food in Europe

Dr C.J.E. Schulp

Wild food an iconic, sometimes debated, but also often enjoyed ecosystem service. Many people enjoy gathering wild plants, fruit or mushrooms, or like to go on a hunting trip. Even more people like to consume food from the wild. In recent years, the interest in wild food has increased in many countries: from celebrity cooks using and promoting wild plants via cooking magazines that feature more wild food in their recipes to a growing number of people who actually go in the field and collect wild plants.

So far, the gathering and consumption of wild food has received little attention in the quantification of ecosystem services, due to a perceived lack of data. In a new paper in Ecological Economics, a first EU-scale quantification of wild food as an ecosystem service is presented by CONNECT researchers Nynke Schulp, Peter Verburg and Wilfried Thuiller. Using data from a wide range of sources, from species distribution modelling to gastronomy, an inventory of the availability and values of wild food in the EU was made.

The inventory showed that more than 10% of EU citizens collect wild food and about 20% consume wild food regularly. A large variety of plant, mushroom and game species that are consumed were identified. The review of the motives for wild food gathering and the socioeconomic backgrounds demonstrate that wild food is particularly important as a cultural ecosystem service. It contributes to the connectedness people feel with the region they live in; and fruit and mushroom picking, gathering herbs and hunting are highly appreciated recreational activities.


CONNECT: www.connect-biodiversa.eu

Blog about the paper at Die Zeit: http://blog.zeit.de/gruenegeschaefte/2014/09/16/pilze-sammeln/
Sympathy for the commons: Developing funding & support communities for the cultural ecosystem services of individual nature areas

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The overall aim of the research project ‘Sympathy for the Commons’ is to investigate whether online communities can be an effective way to translate the strong appreciation of individuals for specific nature areas into new ways of community support and funding for these nature areas. The scientific starting point of the project is the Hotspotmonitor (HSM), an online survey tool in which respondents designate their most attractive natural areas on an online map. This tool has been developed since 2010 by the University of Groningen and PBL (Netherlands Environmental Assessment Agency), in cooperation with De Ontwikkelfabriek and Alterra-Wageningen (see Sijtsma and Daams, 2013). At the start of the research project Sympathy for the Commons around 5000 respondents had marked their favourite natural places on three levels: the neighbourhood, region and the Netherlands. The aim of the project is to take a next step and to investigate whether the strong appreciation of individuals for specific nature areas can be used to find new ways of community funding and support for these areas. The three main objectives are:

1. To involve a large number of respondents in the HSM;
2. To build standardised websites for a selection of nature areas which will serve as the basis for online communities;
3. To perform a series of experiments with online ‘Hotspot communities’ with the aim of finding effective ways of finance and support.

Hotspotmonitor

At the start of the project we made the choice to first develop the software for the online communities both conceptually and practically, before focusing on our first aim to involve a large number of respondents in the HSM. We made this choice to be able to lead the new respondents of the HSM directly to the new community software once they had completed the questionnaire. However, we still partly reached the first objective by cooperating with the Walterproject (Walterproject.nl) and focusing on the Wadden area. In this cooperation we also gave the HSM an international ‘twist’. We developed German and Danish versions in addition to the existing Dutch version and in total 7649 respondents from the Netherlands, Germany and Denmark marked their favourite natural places (Sijtsma et al. 2014). To be able to identify these international connections we added the ‘world level’ to the existing scale levels in the survey. We made this change because we acknowledged that nature areas can also have international fans. This strengthens the HSM database. But it also strengthens the future online communities potential since it makes the online communities more interesting as fans can have community activities in several areas on several scale levels. Figure 1 shows a map with the favourite places on the world level of the respondents in the three countries.
Segmentation is important for distinguishing different groups of fans. The existing segmentation in the HSM appeared not to be suitable for international use. After a review of the literature on this subject we developed a new section in the questionnaire for the segmentation, based on the short version of Schwartz Personal Values Scale.

A new step in the development of the HSM is the construction of a short version of the HSM, which has almost been finished. This short version makes the tool more suitable to use as a starting point for the online community tool. It is also using a different software technique, which makes it possible to show the markers of the participant directly on an online map. This in turn makes it easier to use the HSM as a starting point for the online community tool in which we want share the outcomes (i.e. the markers of other participants) on an online map with the participants.

**Online community software**

In addition to improvements in the HSM itself the focus is of course very much on developing the online community software. Based on useful discussions with our stakeholders in the project, both nature conservation organisations and software experts, but also through literature review and by visiting workshops on social media and participation, we have developed our ideas about this online community software. (See Figure 2 for an impression of the 0.5 Beta version).

At the moment the software developers of De Ontwikkelfabriek are working on it and we are planning to invite people to use it for the first time before the end of the year. For this we are cooperating with the Gooisch Natuurreservaat, a new partner in our project.
Figure 2 | Impression of the online community software.

Discover, enjoy and share ideas

An important building block in the community software is the sharing of our data with our participants. Until now the results of the HSM were in data files used by the University of Groningen and PBL. Over the past year we have worked on making the data available online through an online viewer. On this map with markers people can discover which natural places are highly appreciated and probably discover new fascinating natural places, as the viewer has an added photo layer, which offers the possibility to explore the places on the map even more. So when people enter the online community environment through the HSM and also later when they return, one of the key things they can do is discovering new natural places. Both through the map, as explained above, but also by getting suggestions for nature areas they might like.

Figure 3 | Impression of ‘photo discovery’.
The other main thing is that they can enjoy and follow what’s going on in their specific nature areas. They can get to know more about these areas and what is happening there and view beautiful pictures of the area (See Figure 3). This also offers the opportunity for nature organisations active in the areas to involve fans of the area more. For the fans it also offers the opportunity to share ideas, concerns and plans with other fans of the area. That is almost impossible at the moment because you do not usually know the other people who love the same nature area as you do.

Output

A major aim of the project is to have more data about preferences but also to make these data and this increased understanding relevant and usable for management, policy and research. This implies that the project is also about the ‘backside’ of the software: the goal is also to develop a management information system based on the HSM and the community data for nature conservation organisations for their nature areas. This system is developed in connection with the online community software and will also be tested as pilot with the Gooisch Natuurreservaat.

We have presented the project on several occasions, for instance during a workshop on Internet Research in the Netherlands and the European Regional Science Association Congress in St. Petersburg. We also wrote a paper (Bijker et al., 2014) about the conceptual and practical principles of the project that was published in a special issue of the open access journal Land.

Links

www.hotspotmonitor.eu
www.sympathyforthecommons.eu

Publications


Regional biodiversity and the patterns of spatial connectivity in ditch landscapes

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Project goal

The conservation of aquatic biodiversity is a central objective of Dutch nature conservation policy. In the face of ongoing land use changes, this endeavour is especially challenging due to the limited availability of space and resources. Management schemes for wetland ecosystems have traditionally focused on the level of individual water bodies (e.g. EU Water Framework Directive). An integrated, landscape-oriented approach, nevertheless, offers much better guarantees for the effective and sustainable conservation of regional aquatic biodiversity. However, scientific knowledge on how such an approach can best be implemented is lacking. It is essential that the limited resources available for nature conservation are allocated to measures which result in maximal effects. Land use potentially has strong effects on regional or gamma diversity through a variety of mechanisms. Intensive land use results in the deterioration of local habitat quality and leads to reduced local or alpha diversity. Large-scale intensive land use can also lead to a decline in beta diversity through homogenisation of the environment and changed connectivity patterns. We still do not know which of these alternative mechanisms have the strongest impact on regional biodiversity. However, such knowledge is a prerequisite if one wants to remediate negative effects of changing land use on aquatic biodiversity and develop an effective and affordable conservation strategy for agricultural landscapes.

The aim of the project is to (1) provide a mechanistic understanding of the factors that determine aquatic biodiversity in Dutch agricultural landscapes, with special attention for rare species, species of conservation concern and functional groups, (2) reveal the pathways through which land use change (agricultural intensification and de-intensification, urbanisation) can affect landscape biodiversity, (3) identify how the response patterns of ecologically contrasting groups of aquatic organisms differ and (4) use this information to develop a strategic framework for the cost-effective management of landscape biodiversity for multiple organism groups.

Study design

We selected the ditch networks of the Western Peat district as model system for our study. These ditches are home to a wide variety of aquatic plants and animals. Based on accessibility and prevailing land use, we selected regions of ±200 hectares each. Within each region, we sampled the ditch network at 24 localities, following a stratified random design. At each of these localities, we assessed the community composition and biodiversity of zooplankton (water fleas) and macrophytes and measured key environmental factors that are generally known to be important in driving the community composition and diversity of these organism groups (e.g., water and soil nutrients, turbidity, ditch morphology and fish presence). In cooperation with another ‘Biodiversiteit Werkt’-project (‘Linking microbial diversity to the functioning of soil food webs’ – Prof. P. de Ruiter), we are also be looking into the (functional) microbial diversity of ditch banks in some of the regions in our study. Over the course of three field seasons (summer 2012, 2013 and 2014) we sampled 21 different regions, accumulating data on over 500 ditch communities and their local environmental conditions. The replicated factorial design across meta-communities/regions allows for a more formal analysis of the effect of land use practices on the spatial structure of aquatic biodiversity.
Conceptual and analytical framework

Spatial patterns in meta-community structure can arise due to a spatially structured environment (for example, when high nutrient inflow from a local farm reaches only one part of an area and not another). Alternatively, meta-communities may also be shaped by dispersal limitation, as not all species may be able to reach all sites. From a management perspective it is essential to know how the regional community is shaped, as a system with strong dispersal limitation will require a different management strategy than a system with an overall poor habitat quality. A good spatial model describing the connections between sites in the landscape is imperative for an adequate study of the spatial patterns present in communities. Using Moran Eigenvector Maps analysis we constructed different spatial models describing alternative patterns of connectivity in the ditch landscapes of our study. More specifically, we constructed three models, one based on geographical distance between sites, one based on hydrological connectivity (width weighted distance via the ditch network) and one based on the number of hydrological barriers in the ditch network between sites (bridges, dams, sluices). Using a variation partitioning approach we tried to evaluate the relative ability of the three models to explain spatial patterns in our community data.

Figure 1 | Sampling macrophytes in the field in Polder Oukoop. Photography: Marlies Gräwe.

Results

Preliminary analysis of helophyte data revealed that in all of the regions studied, total regional biodiversity (gamma diversity) is largely determined by a beta diversity component, i.e. by differences in the community composition among sites (Figure 2). This implies a large spatial community turnover, caused by lack of dispersal between sites and/or high environmental heterogeneity. To further examine these differences in community composition we studied the spatial patterns in the helophyte community. As an illustration of future analyses, we present here the spatial patterns of a single region for helophyte community data (Figure 3). We observed clear spatial patterns in the communities (combined model adj$R^2$: 0.286, p<0.001) and all three spatial models (Geographical distance, Width weighted hydrological distance, Presence of hydrological barriers) were statistically significant. Only the model accounting for the hydrological network explained unique variation (non-overlapping parts of the circles). Together with the fact that the explained variation of the hydrological model is also much
larger than that of the other models (adjR²=0.0249) this indicates that in this region spatial patterns in the helophyte community are best described by the hydrological network model. The observed superiority of the hydrological network model is a likely cause of the mechanisms represented by this model. Patterns described by the geographical model may represent wind or waterfowl dispersal while patterns described by the hydrological network model may show the signature of water-based dispersal between localities. Our results shown here are in agreement with existing knowledge of water being an important dispersal vector for helophyte vegetation.

**Figure 2** | The regional species richness (gamma) of helophyte vegetation divided into its average local species richness per site (alpha) and the difference in richness between sites (beta) for each of the sampled regions A-U.

**Figure 3** | Venn diagram showing the variation partitioning of helophyte community composition within a region explained by different spatial models created using Moran Eigenvector Map analyses (Geographical distance, Width weighted hydrological distance, Presence of hydrological barriers). The values shown are adjusted R² values of whole models and individual partitions; symbols are used to indicate significance (*=p<0.05, **=p<0.01, ***=p<0.001).
Next steps

While the study of spatial patterns in itself gives some insights into how diversity is structured in our study landscapes, it is but a first step. To understand the underlying processes shaping these patterns it will be important to account for the local environment in these analyses. Part of the spatial signal will undoubtedly be due to environmental heterogeneity. In addition, by linking our spatial analysis results with known dispersal traits of species we will be able to further examine to what extent dispersal limitation may have been important as a driver of spatial community patterns (cooperation with Dr Merel Soons, Utrecht University). To make full use of our study design these analyses will of course be carried out on all of our study regions and organism groups (bank, helophyte and aquatic vegetation and zooplankton). Furthermore, differences between regions in meta-community structure will need to be identified and linked to land use practices and landscape structure. Such knowledge can then be used to make more informed management choices and to support the development of cost-effective strategies for the conservation of aquatic biodiversity in polder landscapes.

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Soil transplantations for nature restoration on former arable fields – next steps

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Nature restoration on former arable fields represent one of the few opportunities to not only protect nature, but strengthen it by providing new habitat and connecting existing nature areas. However, natural succession is a notoriously slow process that depends in part – as it is now becoming clear – on the interactions of plants with their soil communities. Soil biota are the crucial players in many ecosystem processes and the composition of this community is also subject to successional changes. Soil transplantation may provide an effective measure to shortcut natural succession if well-developed soil communities are transplanted to sites that are to be restored.

In the last Biodiversity works newsletter1 we introduced the large-scale soil transplantation experiment we conducted at the Reijerscamp - a former arable field on sandy soil. We showed that in combination with top-soil removal – to reduce the high nutrient loads – transplantation of heathland soil, in particular, resulted in a vegetation that was much more similar to the target vegetation within six years. Now we have also completed our belowground survey of bacteria, fungi, nematodes and mites – all of them major components of the soil food web. Surveys on belowground natural succession show that soil communities shift over time from bacteria- to fungal-dominated systems and our data show that with soil transplantation the fungal community is much richer in fungi than without. In addition, soil transplantation substantially rehabilitated the nematode and mite communities that suffered heavily from top-soil removal. In total we found 61 nematode (roundworms) genera, 22 springtail species and 16 other groups including beetles, spiders and various insects. All in all, there is a lot going on belowground!

The next question we are now tackling is whether the soil community drives the successful changes in vegetation we observed in the field. Transplantation of bulk soil not only leads to the transfer of soil organisms to the new site, but seeds are concomitantly introduced as well. This summer we set up a greenhouse experiment – that is still ongoing – where we sowed standardised seed mixtures of 30 plant species into pots that were inoculated with the different soil communities found in the field experiment (Figure 1). The selected plant species are all typical for vegetations on sandy soils, covering the entire range from early-successional ruderal plants to target species from species-rich grasslands and dry heathlands. Through the use of standardised seed mixtures, the seeds available for germination are the same across all treatments. Consequently, when we find clear differences in plant community composition, in line with those found in the field, then this is clear evidence of the potential of soil biotic communities to aid nature restoration through soil transplantation.

For nature managers the exact mechanism is much less relevant – as long as the method works. To share our results with our stakeholders and other parties that collected biodiversity data in the area we held a ‘data-meeting’ this year (Figure 2). During this meeting the observations on various groups of organisms were discussed and together they form the basis of an evaluation report, which we are working on, that syntheses the experience of our stakeholders and us with this large-scale experiment. In addition, we are also very happy with the exposure of our work in popular media, in books (Abels et al ‘Wild en bijster land. Planken Wambuis’), radio (Vroege vogels’) and television in the Netherlands (Labyrinth) and abroad (SAT3/nano ZDF).

1 http://www.nwo.nl/onderzoek-en-resultaten/programmas/onderzoeksprogramma+biodiversiteit+werkt/Nieuwsbrief
4 http://www.3sat.de/mediathek/?mode=play&obj=43441
Figure 1 | Although the soil transplantations were done slightly differently, this involved trucks and manure spreaders, a lot of soil still has to be collected for experiments in the greenhouse (left). However, after all that work there is only one image even more reassuring than seeing your plants growing and competing happily in their pots (right) – and that is seeing all the data in a spreadsheet.

As one of the next steps we will present our findings at the First Global Soil Biodiversity Initiative (GSBI) conference, one of the largest gatherings of soil ecologists worldwide, in December 2014. At that conference a large international group of early career scientists will present a statement on the critical need to consider and implement strategies for the sustainable management of soil biodiversity. We made important contributions to the drafting of that statement.

Next year, we plan to organise a national symposium on the science and practice of soil transplantations. We hope and think this will be a very successful meeting, especially since we have already identified 24 other projects in the Netherlands where soil transplantations are now being carried out.

In addition to our more applied science in the context of nature restoration, we are also working on improving our fundamental understanding of the consequences of plant-soil biotic interactions for plant communities in spatially explicit settings. While the results of this work are less easily translated into management practice, we nevertheless find the outcomes very interesting and hope to inform you on this in the future.

Figure 2 | During the ‘data meeting’ nature manager Machiel Bosch (Verenig Natuurmonumenten) introduces the history of the Reijerscamp, the site of the field experiment (left). At the end of the day there was time for a field excursion where, for example, the permanent quadrats of one of the participants were inspected (right).