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in Ecosystem Research

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Abstract:

While it is assumed that ecosystem function and biodiversity are related, evidence is hard to find. Here, two sets of studies were undertaken. The first related high plant species richness from scales of 0.01m² to catchment to soil moisture, as inferred from measurements of a network of fixed sensors; early indications in scale-dependent relationships between these two variables needs further analysis. The second investigated relationships between phenology and greening of beech forests to environmental drivers at scales of km² and above using wavelet analysis, and showed that the greatest influence of particular drivers were seen at particular scales. This kind of study remains difficult, because both biodiversity and ecosystem processes must be measured across the same scales in the same areas, which is very rarely achieved with current technologies. Ecosystem researchers should look to include new technologies, including drones, to provide observational data between the scales of point and small area measurements and data derived from satellites.

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1. Background

One of the challenges of relating environmental change to ecological responses is that the relationships are scale-dependent. The vision of ExpeER is to be able to assess environmental change and its ecological impacts across multiple scales using the infrastructure that is available. It is therefore important to be able to upscale and downscale between scales that are observable using ExpeER infrastructure. This workpackage seeks to provide “operational upscaling frameworks in space and time for biogeochemical fluxes (water, C, N,...)”, “upscaling tools for determining species density and functional diversity based on data-oriented statistical models” and “new monitoring strategies (the amount and type of data, and the sampling strategy) so that the prediction of the ecosystem response with respect to climate change improves”.

Here we focus on biodiversity upscaling, reporting on Task 10.2.2: “Select, test and refine up-scaling methods for ecological patterns: for assessing species density and ecological interactions at multiple scales using Species-Area approaches (UNIVLEEDS) and for upscaling functional biodiversity by using wavelet methods (UFZ).” This work is not simply aimed at a better understanding of how biodiversity scales, as ExpeER seeks to consider “how far results from the upscaling of biogeochemical fluxes and biodiversity patterns are complementary to each other”. This is important as it impinges on the problem of how biodiversity contributes to ecosystem function, affects the choice of relevant scales at which to measure such effects, and thus is needed to help shape the design of integrated ecosystem research platforms.

We explore two approaches to the analysis of scaling of biodiversity and ecosystem function in relation to environmental drivers of change. The first focussed on small spatial scales, from below 1m^2 to small catchment areas, focusing on relating plant species richness to soil function. The second approach deals with much larger spatial scales, relating vegetation phenology to land cover and weather patterns applying the statistical approach of wavelet analysis.

2. Biodiversity and ecosystem functions, from sub- 1m^2 to catchment scales

2.1. The Challenge

The general relationship between species number (a common measure of biodiversity) and area is well understood to be non-linear. Suppose one was to record the number of higher plant species in a patch of grassland of size A , and then expand the survey to include twice as large an area ($2A$). While the larger patch may be expected to have roughly twice as many individual plants as the smaller one, it is unlikely to have twice as many species, because a lot of the additional plants will likely be of species that were already present in the smaller patch (Wiens, 1989). This is very different to some ecological goods; for example, the soil carbon content of a patch of uniform grassland is directly proportional to its area; if the patch is doubled, so is the amount of carbon. These observations suggest that relationships between biodiversity and ecosystem function are likely to depend on scale. The design of an ecological infrastructure needs to take this scale-dependence into account.

In order to test this hypothesis, all that is needed is to measure biodiversity and other ecosystem functions in the same places at different spatial scales. This turns out to be a major challenge. It's not

difficult to measure biodiversity directly at different scales up to a few hectares for herbs and grasses. However, measurement techniques for other ecosystem properties are often fixed at a single scale, the size of gas chamber, the reach of a flux tower, the water quality of a stream.

2.2. Methods

2.2.1. Site selection

Site selection therefore depended on the potential availability of both biodiversity and ecosystem function data across the same spatial scales. An initial assessment of EXPEER infrastructure revealed that there were three sites that had the potential to support this experiment. This potential was confirmed by site visits by Les Firbank (University of Leeds) during June 2012. The sites are two grassland sites in Germany, involving highly instrumented small catchments, and an instrumental Boreal woodland area in Finland. Both are involved in larger networks of sites; the German sites are part of the TERENO network of instrumented ecosystems in Germany, while the Finnish site is part of the ICOS network of sites focussing on gaseous fluxes.

SMEAR II, Hyttiälä, Finland

The SMEAR II site is boreal forest. The topography is very variable at the small scale, consisting of lots of rocks of different sizes, with patches of soil on and around them. These undulations form mini-catchments, but they are very small and hard to discern on the ground. At the larger scale, the area slopes down towards a lake. The habitat is boreal forest, managed by clear cutting; the SMEAR II site was last clear-cut over 30 years ago. No management is applied to this habitat other than occasional thinning and clear cutting.

The SMEARII site at Hyttiälä is better instrumented for gaseous fluxes, and part of the ICOS network, with a flux tower that captures emissions from around 500 m radius, as well as networks of locations for CO₂ sampling using chambers. There are soil moisture sensors close to the tower. The site includes detailed forestry records, and has fixed quadrats radiating away from the tower for detailed growth data (and chemodiversity) of trees. The site is close to a forestry field station with excellent accommodation, labs and offices, around 2.5 hours from Helsinki. Because this site is part of Helsinki University, there is a lot of scope for using e.g. Masters students for some aspects of the work.

The habitat is boreal forest, which is relatively uniform at larger scales, but the forest floor shows considerable small scale variation, with rocks and hollows creating complex microtopography (Fig 1). Field sampling includes soil flux measurements and some hydrology measurements as well as data from the flux towers. The soil gaseous fluxes are measured only at two scales; within small gas chambers at soil level, and by the flux tower sampling across a zone around 500 m in radius. It is not possible to measure gas fluxes directly at intermediate scales, and interpolation is made difficult because of the complex nature of the terrain at small scales and the need to correct for fluxes from the trees. Comparisons between biodiversity and ecosystem function would depend on the choice of interpolation methods, which is not a satisfactory situation. For this reason, it was decided not to use this site for this study.



Figure 1. The SMEAR II site in Finland, at ground level (left) and canopy level (right), showing flux tower.

TERENO catchments, Germany

The two TERENO sites within ExpeER are agricultural grassland in the uplands of Germany; both are at similar altitude, and both are small stream catchments that narrow towards the bottom, resulting in a small valley a couple of hundred meters across. They are both highly instrumented for hydrology.

The Schaeferfel site is in the uplands south of Berlin, and has less rainfall than Rollesbroich. The site is owned by a single farmer, who combines grassland with arable farming. Oilseed rape and wheat are grown on the upper slopes, but the wheat area does not extend to the end of the valley. The grassland areas are managed very lightly, with annual grazing and no fertilisation. This has not been reseeded, so represents a low disturbance grassland site. There are no linear features. The vegetation visibly varies from slopes to the stream at the valley bottom, which appears to reflect water availability (Fig 2). There is an underground dam cutting across the valley, stopping groundwater movements down the valley.

This site is highly instrumented for hydrology, but in two networks. There is a network of fixed soil sensors crossing the catchment where it narrows (in the area visible in Fig 2, Left). There is also a set of sampling positions for time domain reflectometric (TDR) measurements that covers the whole catchment.



Figure 2. The Schäfertel site in Germany, towards the outflow of the catchment looking along the valley bottom (left); and looking in the opposite direction along the stream towards the oil seed rape and wheat fields (right).

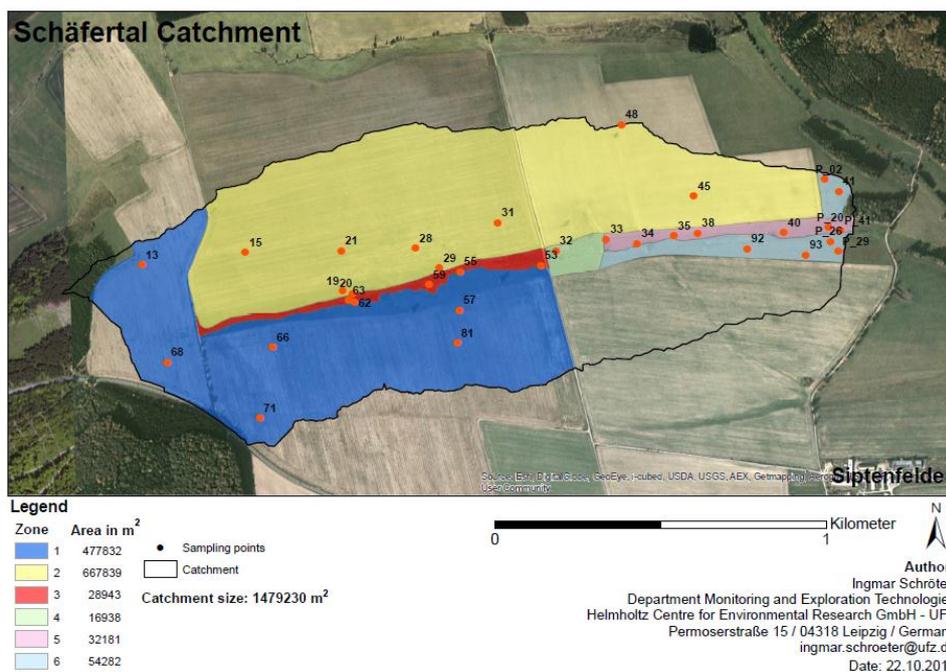


Fig 3. Map of Schäfertel catchment, showing zones identifying oil seed rape (Zone 1), wheat (2) and grassland zones, along with sample locations.

The Rollesbroich site is the more fertile, and is managed more intensively. The top of the catchment is an open area of damp grassland, close to a minor road and some housing. The valley bottom was used for arable agriculture during the 1930s, but is now grassland for hay (and possibly for silage) and cattle grazing. The valley is subdivided by hedges and ditches into distinct fields, managed differently, with an area of woodland higher on one side (Fig 4). The vegetation appears to vary in structure (if not in species), but according to land management, which also depends on the rather fragmented land ownership, rather than because of natural processes.

The Rollesbroich site is highly instrumented with a network of fixed soil moisture sensors, eddy covariance tower and meteorological station (Fig 5). This rich set of sensor data, coupled with the relatively homogenous vegetation within the individual fields, made this site an appropriate choice for this study. There were no comprehensive biodiversity data available before this study.



Figure 4. The Rollesbroich site in Germany, towards the head of the catchment with eddy covariance tower (left), and towards the steeper valley at the catchment outflow (right)

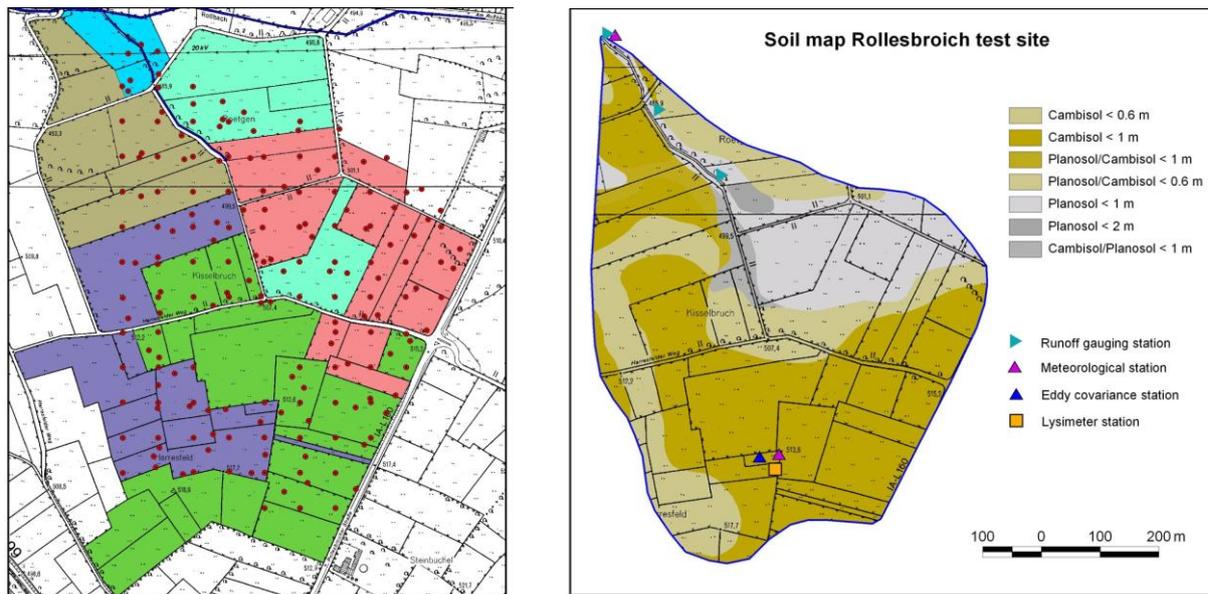


Figure 5. The Rollesbroich site in Germany, showing the map of land ownership (left, each owner is a different colour) and positions of soil moisture sensors (red dots) and soil type (right). Note that some land lacks sensors, either because it is outside the catchment boundary (shown on the right) or access was denied by the farmer.

It was concluded to use the two German field sites for this study.

2.2.2. Biodiversity data collection

The intention was to sample both plant diversity and some measure of ecosystem function at different scales within the two catchments. These measurements were to be co-located, to enable comparison of how biodiversity and ecosystem function jointly scale. The network of soil sampling points at both sites gave an appropriate set of sample positions. A nested quadrat approach was planned for the biodiversity measurements, where a quadrat was centred close to a randomly selected sensor position, and species richness recorded over quadrats increasing by orders of magnitude from 0.01m² to 1000m². The next higher scales were given by subdividing the catchments into 'zones' that sought to separate the catchment into areas that appeared to be botanically similar. At Rollesbroich, these areas corresponded to land ownership (Fig 3, left), while at Schäfertal they corresponded to land cover, which split the grasslands into different zones according to visible differences in vegetation, linked to position along the wetter valley bottom and drier sides (Fig 5).

Six quadrats were selected in each zone sequentially by first selecting a sensor location at random, ensuring that the quadrat did not touch the zone boundary, then selecting a second sensor as long as it did not overlap with the first, etc. Some zones were too small for this, so fewer quadrats were selected, and sometimes losing the larger quadrat sampling sizes.

Biodiversity was recorded once at each field site in early summer 2013, before the grass was cut. The only exception was the oil seed rape areas at Schäfertal, which was too dense to be surveyed then, and sampling took place in September 2013. Sampling involved recording higher plants in nested quadrats, ranging from 0.01m² to 1000 m² in 10 fold size steps. Species presence was recorded in all quadrats, and cover (using the Raunkier scale) was recorded at the 0.01m², 0.1m² and 1m² quadrat nests. Finally, the whole zone, including boundary and other features not sampled by the nested quadrats, was searched for additional plant species not encountered in any quadrat. Species richness of the whole catchment is given by combining the data of all zones. Biodiversity recording was undertaken by local experts.

2.2.3. Ecosystem function data collection

The only ecosystem functions that are being monitored at small scales across both catchments relate to soils¹. Soil moisture, and its resilience after a rainfall event, is an indicator of the soil function of regulating water fluxes through landscapes. Here we focus on the Rollesbroich catchment. The hydrology of this site was modelled using a new version of TOPMODEL (Beven and Kirkby, 1979) that is fully spatially-distributed (Gao et al., 2015), which models the outflow of a catchment in relation to the input from precipitation, the topography, and can account for the characteristics of the soil and vegetation. TOPMODEL used the hourly discharge and weather data and a 1m² spatial resolution digital terrain model; this early stage of the work does not involve soil characteristics. The model was fitted using data from a single rain event against soil moisture data recorded at all sensor locations, where soil moisture is recorded at depths of 5cm, 25cm and 50 cm. Bulk density and other soil data were collected at each sensor location during their installation. TOPMODEL therefore generated a

¹ Gaseous exchange measurements have been taken at some locations at Rollesbroich, but these did not coincide with positions of the botanical quadrats

surface of soil moisture, with a resolution of 1m^2 . This make it possible to consider soil hydrology at the locations used to assess biodiversity at sample sizes of 1m^2 , 10m^2 , 100m^2 and 1000m^2 , by sampling the modelled surface using ArcMAP. The values of the 1m^2 cells within the quadrat sample area were simply summed, to give an integrated estimate of the overall soil moisture at the same scale as the botanical quadrats.

2.3. Results

Results are available for the biodiversity assessments. The ecosystem function data are still being analysed at the time of writing: here we give summary biodiversity data for Schäfertal, and more detailed biodiversity data and preliminary ecosystem function findings for Rollesbroich.

2.3.1. Biodiversity at Schäfertal

The increase of plant species richness with sample area differed substantially between the cropped areas (oilseed rape and wheat) and the grassland zones. The rate of increase in species number differs among the grassland zones, with the plots in the very wet central valley floor having fewer species in the smaller plots (Fig. 6).

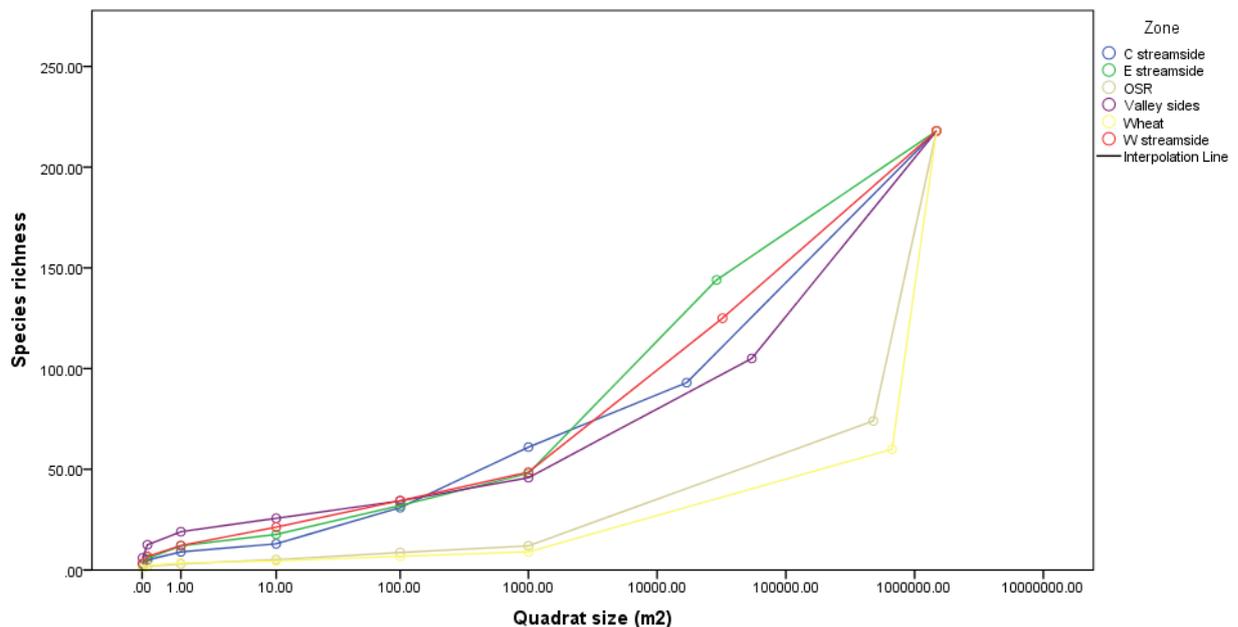


Fig 6. Plant species richness in relation to scale of sampling at Schäfertal grouping the data into the zones shown in Fig 3. Note that the species richness data inevitably converge, as there is only one value of species number for the whole catchment

2.3.2. Biodiversity at Rollesbroich

Plant species richness differed among the zones at the scales covered by the quadrats, presumably due to differences in times since re-seeding, fertiliser use etc. Species richness was much higher at the whole zone and catchment scales, as it is here that plants in ditches, hedgerows etc are recorded (Fig 7).

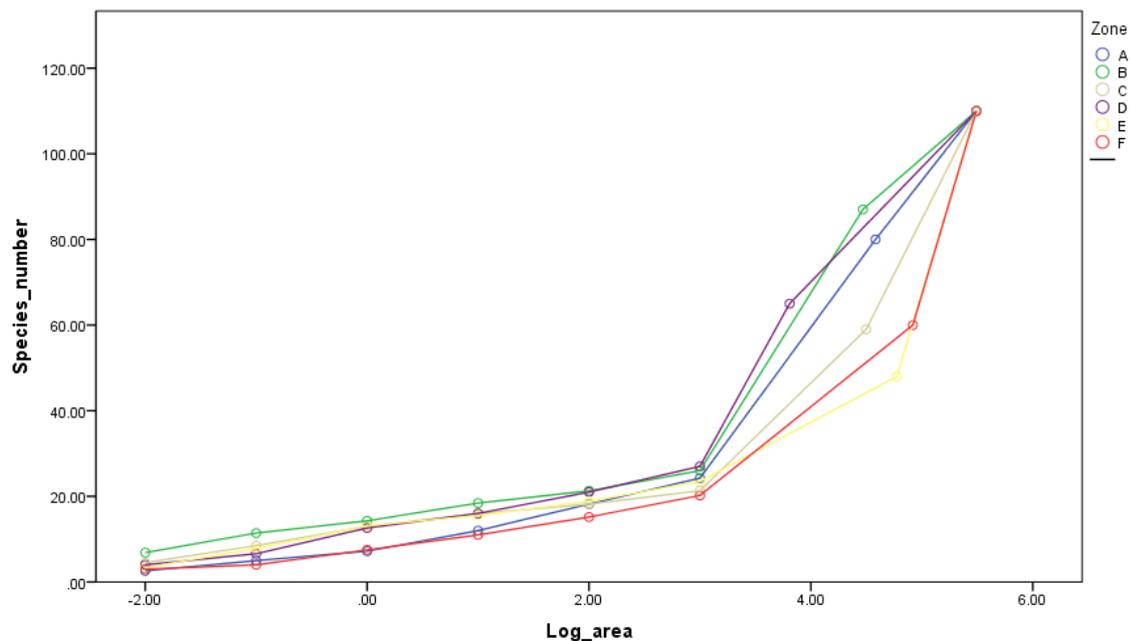


Fig 7. Plant species richness in relation to scale of sampling (on a \log_{10} scale) at Rollesbroich grouping the data into the zones shown in Fig 5. Species richness among the zones diverges at larger scales because of the inclusion of linear features. Note that the species richness data inevitably converge, as there is only one value of species number for the whole catchment

2.3.3. Soil function at Rollesbroich

Here we relate soil characteristics to biodiversity.

2.3.3.1. Soil carbon and bulk density

We found no evidence that soil carbon or bulk density as measured at the soil sensor locations were related to plant species richness in the 1m^2 around the sensor (Fig 8).

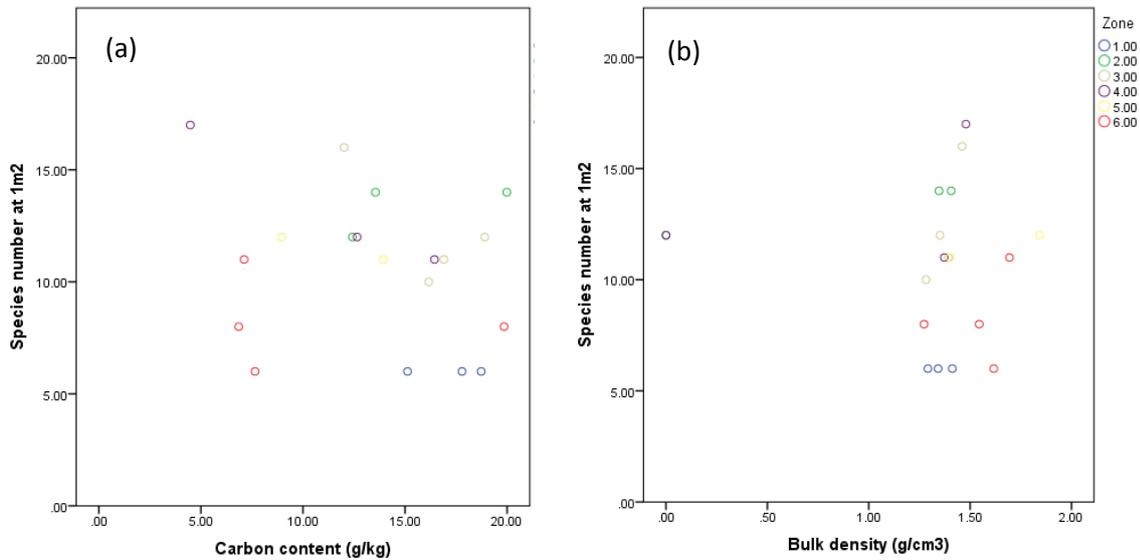


Fig 8. Plant species richness at 1m² in relation to (a) soil carbon and (b) soil bulk density. There are no significant correlations between species richness and these variables (with carbon, $r = 0.245$, with bulk density $r = -0.94$).

2.3.3.2. Soil moisture

A multi-scale analysis shows a statistically significant difference in relationship between plant species richness and the integrated measure of soil moisture from TOPMODEL (Fig 9). The effect of quadrat on soil moisture is inevitably highly significant, given that the soil moisture measure is integrated over the number of cells that equates to the quadrat size. More importantly, there are also significant effects of species number on soil moisture ($p < 0.001$), and there is a significant interaction between these two variables ($p < 0.001$) (Fig 10). This result suggests that the relationships between biodiversity and other ecological processes may be scale dependent.

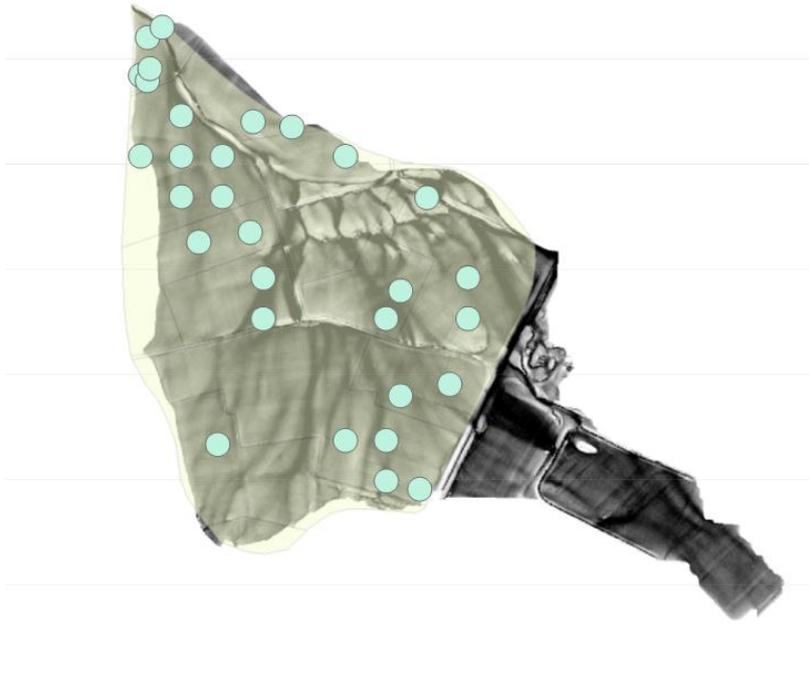


Fig 9. TOPMODEL outputs of the expected variation in soil moisture, using data from the set of soil moisture sensors. Locations of the sensors used for biodiversity assessments are given by the circles, scaled at 1000m².

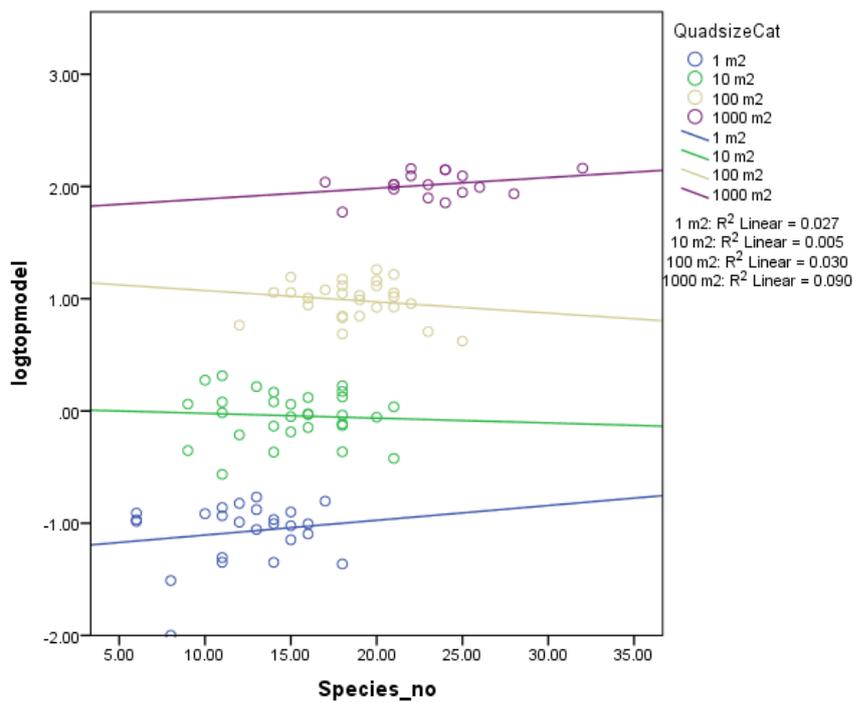


Fig 10. Relationship between plant species richness and integrated soil moisture measure (from TOPMODEL), showing the effects of sample size.

2.4. Next steps

At the time of writing, the joint analysis of ecosystem function and biodiversity needs further development. The field season for biodiversity data collection was delayed by a year, which has also delayed the modelling and analysis, longer than was anticipated. The next steps are to use a more advanced soil moisture modelling approach that takes soil characteristics and depth into account as well as a measure of soil ecological function, most likely return time of soil moisture after rainfall. The same approach is to be undertaken at the Schäfertal catchment. It may well be the case that relationships between biodiversity and soil function are easier to see in the lightly managed grasslands at Schäfertal than the intensely fertilised and reseeded grasslands at Rollesbroich.

3. Use of wavelets to relate vegetation phenology to changing weather patterns

3.1. Introduction

ExpeER addresses the better understanding of ecological responses to environmental change. Many of these responses are highly scale dependent, as are many environmental variables themselves. Simple linear upscaling from small-scale studies struggle to cope with such scale dependence. Therefore, WP10 considers an alternative approach, describing multi-scale spatial and temporal data using 'wavelets' (Kumar and Foufoula-Georgiou, 1997).

A function that describes a multi-scale process can be described using combinations of wavelets. A wavelet is an oscillating function whose amplitude diminishes to zero within a certain interval of space or time. Any function can be produced by a combination of wavelets, which can be visualised to reveal behaviours at the selected scales of space and time; knowledge of the wavelet coefficients gives perfect knowledge of the original function. Spatial patterns can be transformed into a matrix of wavelet coefficients, which show patterns of variation horizontally, vertically and diagonally. Once calculated, the wavelet coefficients are powerful tools for relating environmental change to ecological response.

3.2. Relating vegetation greening to both climate and land cover

It is well understood that patterns of biodiversity are related to both land cover and climate, and that land cover influences predominate at smaller scales than climate. In this study, land cover and climate were related to the ecosystem process of vegetation greening, at scales from $0.01 \times 0.01^\circ$ resolution (approx. 1×1 km), covering an area of 1024 cells square, across Central Europe (Fig 11).

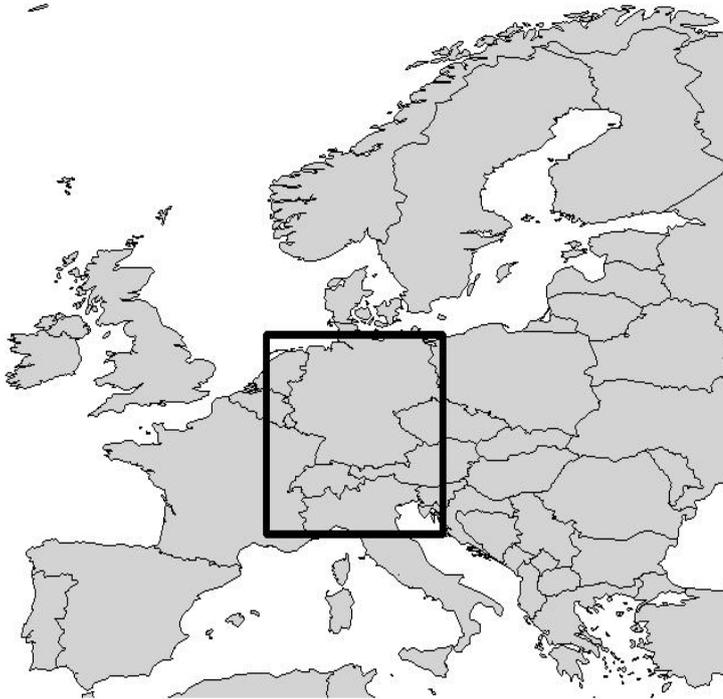


Fig 11 – Map of Europe showing the area of analysis relating greening to land cover and climate

Data on vegetation greening were derived from remotely sensed data. Archived data were used from the NOAA satellites, yielding full resolution AVHRR channel data on a daily basis from 1989-2007. Changes in the Normalised Difference Vegetation Index were calculated, using dynamic filtering to correct for cloudy conditions, and the greening periods estimated for each pixel. Land cover data were obtained from the Corine Land Cover 2006 vector data, while climate data were obtained from the WorldClim database, that gives average temperatures and precipitations from 1950 to 2000.

The data are decomposed into scale-specific subcomponents by means of wavelets, allowing multiple regressions linking vegetation greening, climate and land cover at each scale. Models are ranked using multi-model inference, and the importance of a variable in the regressions is indicated by the sum of Akaike weights over the models that include the variable. Spatial resolutions studied ranged from the finest (level 0) to approx. 250,000 km² (level 9; note that sample size falls with scale, making results from levels 7-9 less reliable than the others).

The results show that land use variables are clearly more important at scale sizes 2 (approx. 16 km²) to 4 (approx. 256 km²), while the other, climate-related, variables are more important at levels 5-6 (Fig 12). Note also that temperature is also important at the finest scale.

Full details of this study are given in (Carl et al., IN prep).

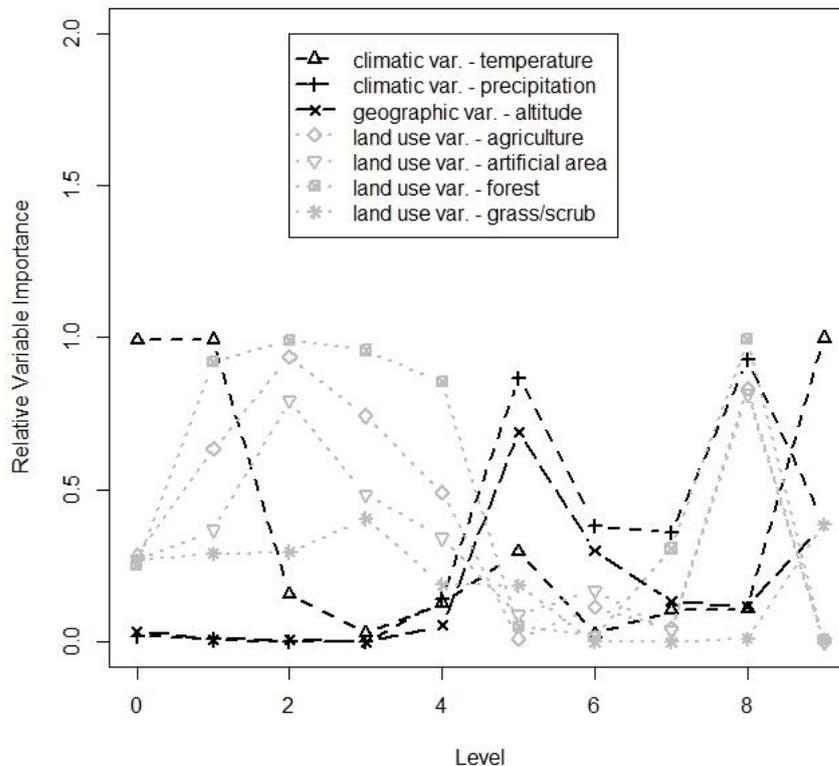


Fig. 12. Relative variable importance (measured as Akaike weights) as a function of scale. The analysis is based on scale-specific regressions capturing only detail components as scale-specific subcomponents. Land use variables are indicated by gray lines and symbols, all the others are indicated by black ones.

3.3. Relating the phenology of beech forests to changes in temperature

This analysis focuses on the relationship between forest phenology and temperature changes, as this is an important indicator of ecosystem change in response to global climate change. While the previous study focused on a large spatial area, this study focuses on the time series of both temperature and vegetation changes in a large beech forest occupying a grid cell of the NOAA spatial database in Germany. Thus the NOAA data show the phenology, in terms of greening, of what is very close to a single-species stand of beech. Weather data come from a meteorological station close to the site, that match the NOAA temporal coverage of 1989-2007.

Data are decomposed by means of wavelets for periods of 1 year, $\frac{1}{2}$, $\frac{1}{4}$ and $\frac{1}{8}$ years. Comparisons of the vegetation cover and temperature wavelet patterns show a marked 'phase locking' effect, in that beech phenology is strongly related to the temperature about 300 days earlier, an effect which is most evident using the wavelets at the $\frac{1}{8}$ period.

This work is presented in more detail by Carl et al. (2013) (Carl et al., 2013).

4. Discussion

Ecological processes are driven by living organisms, and so it is intuitively obvious that ecosystem functions are related to biodiversity, and that understanding these relationships will enhance our capacity to forecast changes in ecosystem processes in response to the impacts of global environmental change on biodiversity. We have revealed large scale relationships between different environmental drivers and the plant function of greening, and are finding indications of scale-dependence of biodiversity and soil processes at sub-catchment scales. Yet by and large, these relationships remain hard to elucidate. One of the problems is that biodiversity and ecosystem functions vary across scales, meaning that their interrelationships are highly scale dependent, and single-scale studies can generate misleading results. This ExpeER workpackage have helped show why such studies have rarely (if ever?) been undertaken: there are very challenging mismatches in in scales in measuring and analytical methods for biodiversity and ecosystem processes.

One of the challenges of this task was to find situations where both biodiversity and ecosystem function data could be collected across the same range of scales, within the same system. Data should be collected directly at each scale, as any interpolation uses some form of model, which imposes scale-dependent relationships, rather than enabling the detection of underlying ones. We found this challenge more difficult than we anticipated.

We undertook direct sampling of plant species richness using nested quadrats up to the 1-10 ha scale; even here, there were not the resource to provide cover and abundance data at scales above 1m², nor was complete spatial coverage of species occurrence attempted at scales up to and including 1000 m². At larger scales still, it is rarely practical to record biodiversity in particular research campaigns, instead biodiversity atlas data are typically used, with resolutions of 1 -10 km², usually with complete coverage of large areas (including countries and the whole of Europe). By contrast, for ecosystem processes, ground-based instruments typically measure processes at a single scale, ranging from a few cm for soil sensors, through under 1m² for gaseous exchange in chambers, to flux towers integrating data over hundreds of m². Spatially explicit data of some ecosystem processes is available using remotely sensed data, with typical resolutions of hundreds of m², but with up to continental-scale coverage.

The potential to address the interaction between biodiversity and ecosystem processes across scales is therefore currently very limited. For the small scale biodiversity study, the intention was to develop simple models of the relationships between biodiversity and function across scales. None of the ExpeER sites allowed this to be undertaken using independently measured ecosystem function data at each scale. Therefore, attention was focussed on TERENO catchments where soil data was available at multiple points, allowing the interpolation of ecosystem function at small spatial scales, creating a response surface from which larger samples can be taken. The use of the full set of soil moisture sensors for TOPMODEL gives a degree of independence from the biodiversity data, but the use of interpolated data cannot be avoided. Furthermore, soil moisture sensors do not measure ecosystem processes directly, and the refinement of TOPMODEL that is required is still in progress. Nevertheless, the ability to model hydrological functions at scales of 1m² and above hold out the promise of addressing biodiversity and ecosystem function at scales between 1 m² and habitat/catchment units, here 1000 m².

The use of wavelet analysis allows for much more sophisticated investigation into the relationships between biodiversity and ecosystem function across scales. However, the cost is that both data sets need to be available across the selected range of scales using large numbers of spatially explicit and

contiguous data points. In order to use this approach at Rollesbroich, both species and ecosystem function records would have been required at an appropriately small spatial scale (1-10 m²?) for the entire area, and not just for 30 sample locations. Such intensity of sampling is not practical using current techniques. The wavelet analyses studies were therefore undertaken using remotely sensed data, giving a large number of contiguous sample areas, using beech forests, giving good homogeneity of conditions. Even then, the choice of variables was constrained by the available data to a monospecific response (greening) to a particular environmental driver (weather).

The challenges of integrating ecosystem function and biodiversity data are currently technological. But environmental monitoring technology is developing rapidly. For example, the use of drones will allow spatially-explicit sensing at sub 1m² scales of at least some ecosystem functions, and at least some measures of biodiversity. One of the challenges of ANAEE is to ensure that ecosystem infrastructure includes the use of sensing systems that truly cross scales.

5. References

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