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Vegetation diversity and geographical heterogeneity across multiple spatial scale

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Report 1

Acknowledgement

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For me, it has been stimulating to work with such enthusiastic and open minded supervisors as Edwin Peeters and John Stuiver. The chats in which we discussed possibilities how to continue the research had one thing in common: too much to know, too less to grasp.

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Levinus Boxhoorn

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Executive summary

This research addresses the relationship between vegetation diversity in ditches and geographical heterogeneity at multiple spatial scale (discharge and WB21 areas). Furthermore, correlation between geographic heterogeneity and vegetation diversity is investigated.

What is the relationship between vegetation diversity (alpha, beta and gamma) and spatial scale?
As a general pattern, results suggested a positive relation between vegetation beta and gamma diversity and spatial scale. This was stressed by general positive but weak relations between area and beta and gamma diversity per spatial scale for both terrestrial and ditch vegetation while at multiple spatial scale stronger correlations were observed.

What is the relationship between geographical heterogeneity (based on landuse, soiltype and a combination of both) in Holland and spatial scale?
Based on these results, it is not suggested that heterogeneity has a significant and strong relationship with area or spatial scale.

Is there a relationship between vegetation diversity and geographical heterogeneity on discharge area scale?
Results suggested a possible optimum in the potential maximum between heterogeneity and diversity. However, this suggestion was only supported by ditch results. Because the distribution of diversity also had an optimum shape, this suggestion could also be an artefact generated by the dataset used.

Is there a relationship between vegetation diversity and geographical heterogeneity on WB21 area scale?
Results suggested no specific relationship between heterogeneity and diversity. However, this suggestion could also be an effect of the small number of observations.

Is there a relationship between vegetation diversity and geographical heterogeneity on one or multiple spatial scale?
No specific relationship between vegetation diversity and geographical heterogeneity on multiple scale has been identified.

Table of Content

1. Introduction

The past decennia, much research has been put into how to conserve and stimulate biodiversity. Biodiversity relates, besides the many values it has, to the functioning of its ecosystem. This relationship has been one of the main issues within ecological research (Chapin, Sala et al. 1998). However, in spite of all the effort which has been put into this matter of conserving and stimulating biodiversity, there are still many factors determining biodiversity which are unclear.

One of these factors thought to determine biodiversity is heterogeneity. More specific, the idea of a positive relationship between environmental heterogeneity and diversity is one of the oldest in ecology (McIntosh 1985).

As environmental heterogeneity influences biodiversity, biodiversity influences the ecological functioning of its ecosystem.

Therefore, by investigating the relationship between biodiversity and environmental heterogeneity within the specific ecosystem of ditches, more insight is created about the ecological functioning of these ditches. This is the main aim of the PLONS-project (Langjarig Onderzoek Nederlandse Sloten: Longstanding Investigation Dutch Ditches).

This research is part of the PLONS-project and aims at more understanding about the relationship between geographical heterogeneity, vegetation diversity and spatial scale within Dutch ditches.

Ditch

A ditch is a line shaped waterbody, meant for drainage and hydrologic transport. In its normal proportions, a ditch has a maximum wideness of 8 meter and a maximum depth of 1,5 meter. In most cases, flow of water is not visible, temporarily and can change of direction. Furthermore, characterizing is its relative small volume for its size of the shore surface, soil-water and air-water boundary layer (CUWVO. Werkgroep 1988).

Ditches were mainly constructed for their water containing capability and for agricultural use. Many parts of The Netherlands, for instance polder and peat areas, would be uninhabitable without ditches retaining the water or transporting it from these areas. Moreover, in many cases ditches serve as a boundary of property or as fence, limiting both humans and animals. Their imaginary importance, with an approximate length of 250.000 kilometre, is considerable for the water rich Dutch polder scenery (Loorij 1985).

Likewise, their ecological functioning comes more in the picture. As research reveals, ditches are no 'deserts for aquatic biota' but serve as important habitats for e.g. several species of macrophytes and macro-invertebrates, accommodating many organisms (Davies, Biggs et al. 2008). Characterizing for the ditch community is, instead of ditch-specific species, the mix of species. Species within this mix are also encountered in other aquatic environments (CUWVO. Werkgroep 1988). In this all-round concept, ditches do considerable contribute to the agricultural biodiversity (Peeters 2007).

Biodiversity

Biodiversity is, besides its direct value by e.g. nutrition, medicines and industrial products (Gaston and Spicer, 2004) essential for the functioning of ecosystems. Processes crucial for human beings to live on earth (climate, biogeochemical etcetera) are impossible without biodiversity, i.e. without diversity in its organisms.

Within an ecosystem, biodiversity can be seen at three levels (Lévêque, Mounolou et al. 2003):

Intraspecific diversity: Genetic variability within populations. This genetic variation is one of the tools with which species are able to react directly on changes in their surroundings.

Diversity among species: Diversity in ecological functioning of species within their ecosystem. Species differ among each other in many ways. By their different ways to interact with each other, species contribute altogether to the dynamics of their ecosystem.

Ecosystem diversity: This diversity is joint with the variety of habitats and their variability over time. Species richness is often seen as a function of habitat diversity and the amount of available ecological niches. By their biodiversity, ecosystems play a global role in the regulation of geochemical and hydrological cycli.

Many concepts have been written about biodiversity and ways to examine biodiversity (Peet, 1974); (Wilson and Shmida 1984); (Loreau, 2000).

This is because biodiversity contains two elements, namely variety and abundance (relative richness) of species. Biodiversity can therefore be calculated in three ways: richness of species, abundance of species and a combination of both (Magurran, 1988).

The scale at which biodiversity is examined is of high importance. As Ricklefs (Ricklefs et al., 1977) stressed, local diversity has a noticeable dependence upon regional diversity. This dependence has often been failed to notice. Observations have suggested noticeable effects of historical and regional processes on local community structures, besides the importance of local circumstances at a certain moment.

To measure biodiversity on different spatial scales, or along a environmental gradient, Whittaker (Whittaker, 1972) and (MacArthur and Wilson 1967) stressed the importance of partitioning overall (gamma) diversity of a region in alpha and beta diversity. Alpha diversity represents species richness of a community within its niche or habitat, beta diversity represents how much these communities differ among each other within a certain geographic area and gamma diversity represents species richness within this certain geographic area (see Methods, 2.C). This way, values of beta diversity can be used to compare habitat diversity on different spatial scales (Wilson and Shmida 1984); (Weiher, Howe et al. 2003); (Clough, Holzschuh et al. 2007). High β-diversity values indicate large differences between locations in encountered species identities.

The beta diversity index should describe two things (Magurran, 1988):

species richness (i.e. number of species)

evenness (i.e. how equally abundant the species are, sometimes known as equitability).

Several studies have already been performed to compare and evaluate beta diversity measures (Shmida and Wilson 1985); (Magurran 1988); (Koleff, Gaston et al. 2003). However, in spite of its clear contribution to knowledge, still many studies do not take into account this difference in means of diversity. This has resulted in many studies concerning the pattern of alpha diversity while beta diversity has received far less extensive studies (Harrison, Ross et al. 1992). Analyses of α-diversity alone may misrepresent contributions of between-diversity (β) to total diversity (γ) (Clough, Holzschuh et al. 2007).

Geographical heterogeneity and spatial scale

Natural habitats are formed by environmental factors (climate, soiltype or topography), natural succession, and the frequency and type of natural disturbances. Types of species present in a habitat are dependent on habitat type (Wagner, Wildi et al. 2000). Therefore, by evaluating biodiversity of a certain habitat, the landscape in which it is situated is of explaining value. Forman (1995) stated that in most cases larger patches (or habitats) have more species than smaller patches (or habitats) and that area is a better explaining variable than many other variables.

In addition, one of the cornerstones of ecology is the 'habitat heterogeneity hypothesis' or 'mosaic concept' (Duelli, 1992); (Duelli, 1997) which assumes structural complex habitats to offer more niches and ways to consume sources of nutrition thereby causing higher species diversity (Simpson 1949); (MacArthur and Wilson 1967); (Lack 1969); (Bazzaz 1975). This is also hypothesized for plant species diversity (Ricklefs 1977); (Jeremy T. Lundholm 2003).

However, a standardised method to estimate this heterogeneity still does not exist. Also Tews (Tews, Brose et al. 2004) indicated this problem and stressed the dependence of habitat heterogeneity on landscape structural variables (like landuse, vegetation cover, soiltype, ditch-density etcetera) and the taxonomical group to which the studied organism belongs. Spatial scale therein places a valuable role.

How spatial scale and geographical heterogeneity are related is not that much investigated (Cooper, Diehl et al. 1998). Since heterogeneity in most cases is approached by its causal nature (Murwira and Skidmore 2005); (Brakman and van Marrewijk 2009) not much is known about how heterogeneity is dependent on other variables like spatial scale.

Tools within Geographical Information Systems (GIS) were thought to be of help to collect, structure, process and analyse the amount of spatial, geographical and vegetation information available.

Problem definition

Since ditches were considered to be 'aquatic deserts' and thereby of low ecological importance, not that much research has been assigned to investigate the ecological functioning of ditches. However, observations does suggest an increase of biodiversity of this landscape by its high species richness landscape (Patrick D. Armitage 2003); (Brose, Martinez et al. 2003); (Hinojosa-Garro, Mason et al. 2008), hereby increasing the natural value of agricultural. As it happens, several researches have shown the determining factor of vegetation structure in a ditch for diversity of amphibians, reptiles, macro-invertebrates and fishes (Peeters 2007).

An important aim of water management is conserving and stimulating biodiversity. Ditch cleaning, dredging, water refreshment and keeping it in shape are among the topics concerned (Nijboer, Verdonschot et al. 2003). Frequency and method of maintenance appear to be of great importance on ditch biodiversity, the precise relationship however is still unknown (Peeters 2007). Even less is known about correlation between geographical heterogeneity and vegetation biodiversity within ditches and how this possible correlation varies with spatial scale levels on which biodiversity is measured. This research aims at clarifying more about these topics.

Research questions

Objective

This research addresses the relationship between vegetation diversity in ditches and geographical heterogeneity at multiple spatial scale (discharge and WB21 areas). Furthermore, correlation between geographic heterogeneity and vegetation diversity is investigated.

This research can be summarized by the following main and sub questions:

Is there a relationship between vegetation diversity (alpha, beta and gamma) within Dutch ditches and geographical heterogeneity on different spatial scale?

1) What is the relationship between vegetation diversity (alpha, beta en gamma) in Dutch ditches and spatial scale?

2) What is the relationship between geographical heterogeneity and spatial scale?

3) Is there a relationship between vegetation diversity and geographical heterogeneity on multiple spatial scale?

Hypotheses

It is expected that the relationship between vegetation diversity and spatial scale is a positive one. This is due to the positive relationship between vegetation diversity and area. Area is directly related to spatial scale, hence a positive relationship.

Also a positive relationship is expected between geographical heterogeneity and spatial scale. This is because the amount of geographical types is expected to be positively related to area while geographical heterogeneity is partly estimated by the amount of geographical types.

At last, the relationship between vegetation diversity and geographical heterogeneity on multiple spatial scale is expected to be a positive one. This is due to both the expected positive effects of heterogeneity and of spatial scale which are described above.

2. Methods

A. Flowchart

To have a overview of the information necessary to answer the research questions, a flowchart was made (Fig. 1).

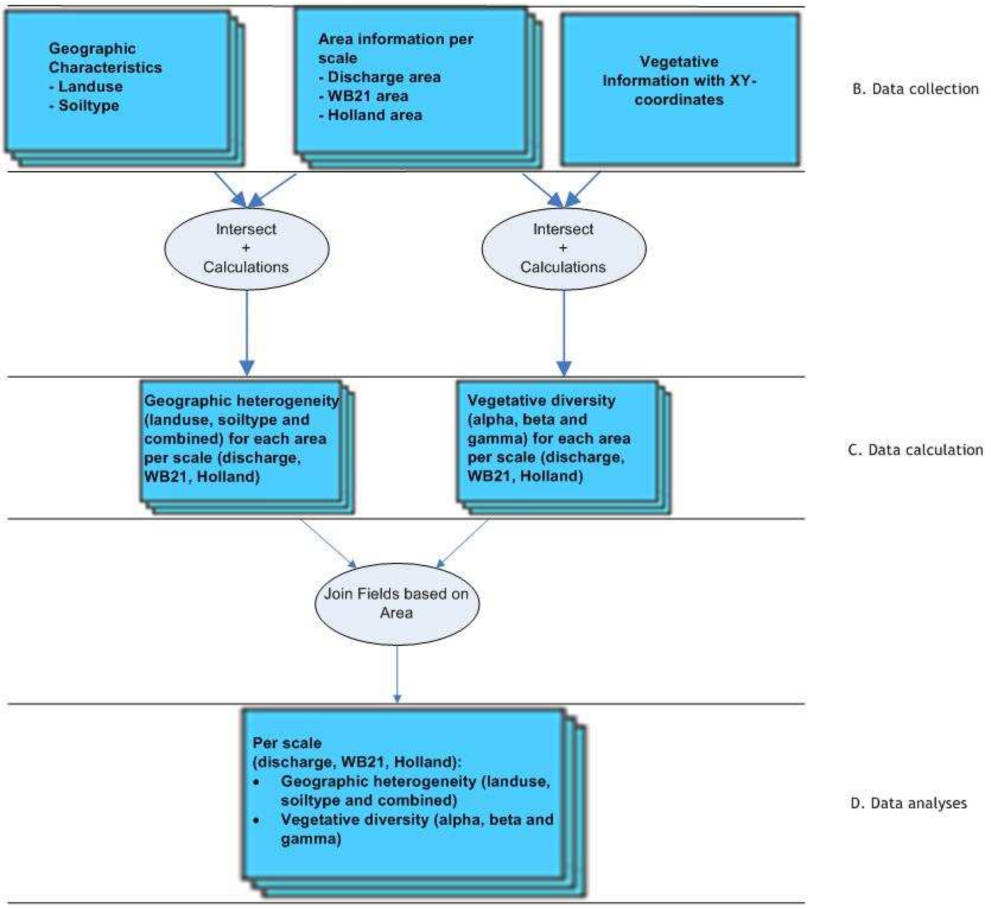

Fig. 1 Flowchart for operations

The following actions were performed using ArcGIS 9.2 (Fig. 1).

The collected data (see 2B) was put in multiple datasets. Geographical, vegetation and area-information was intersected. This intersection functioned as a query (Date 1981) and resulted in a selection of areas in which both geographical and vegetation information was available. In this way, areas in which no vegetation observations were recorded were excluded from the data set.

Subsequently, for each area per scale, both heterogeneity and diversity were calculated as explained in 2C. Eventually, these datasets were joined (based on the joined variable 'area') so geographical and diversity information were available for each area per spatial scale. By having the geographical and diversity together per area, statistical analyses were possible (see 2D).

B. Data collection

For this research, vegetation (ditch, terrestrial) and geographical (area, landuse, soiltype) data was used.

Vegetation data (ditch)

Since approximately 1980, records of the quality of Dutch surface waters by chemical and biological measurements have been collected in the dataset 'Limnodata Neerlandica' (www.nlbif.nl).

Data was collected according Tansley. Because sometimes only hydrophytes and water depending flora was recorded and other times all species on the waterside, it was hard to define a clear border between ditch and waterside. However, most records also contained information whether species were found in the water or on the water side. Mainly vascular plants but also chlorophytes and charophytes were recorded.

Vegetation data (terrestrial)

From point-records, only terrestrial vegetation records were selected (no hydrophilic vegetation). About 100.000 point-records remained. From these point-records, about 10.000 point-records were randomly selected.

This terrestrial vegetation dataset was created to compare results of ditch vegetation diversity with terrestrial vegetation diversity. For instance, a positive relationship between heterogeneity and diversity would be more likely to accept if this relationship was observed for both ditch and terrestrial vegetation.

Geographical information themes

From GeoDesk, four GIS-maps were used:

1. Discharge areas: Holland divided in approximately 9000 discharge areas, comparable with municipalities;
2. WB21 areas: Holland divided in 21 areas according to main legislative and geographical characteristics, comparable with provinces.
3. Landuse (Corine based, 5 main classes, in total 44 types);
4. Soiltype (10 types).

C. Data preparation

Select and group observations per area per spatial scale (discharge, WB21, Holland):

Discharge area borders were the main criteria of selection and grouping of observation. To estimate vegetation beta diversity, at least two observations are necessary. Therefore, minimum number of observations within a discharge area was two.

The same counts on a higher spatial scale. At least two discharge areas within one WB21 area are necessary to estimate vegetation beta diversity of concerned WB21 area.

In Fig. 2, the dots represent observation locations. A lot of observations were recorded in the provinces North- and South Holland. However, Brabant, Limburg and Achterhoek had less data points.

Most observations were recorded in the north and west of Holland, within the river area (between Meuse and Rhine) and at the 'Head of Overijssel'. In total 943 locations were used for this research.

Fig. 2 Observations in Dutch ditches

Estimate vegetation alpha, beta and gamma diversity per area per scale.

Alpha (α): mean species richness per observation within area (within diversity)
Gamma (γ): total species richness per area

To estimate alpha diversity, mean number of species richness per observation was calculated for each area per scale.
Gamma diversity was estimated by calculation of the total number of species within an area.

Three ways to calculate beta diversity are Whittaker's, Shannon's and Additive Partitioning.
Whittaker: $\beta = (\gamma / \alpha) - 1$
Shannon: $\beta = -\Sigma \rho \text{ Ln } (\rho)$
Additive Partitioning: $\beta = \gamma - \alpha$

Beta diversity calculated according to Shannon was supposed to be the most representative and therefore was used as default index for beta diversity. Beta diversity (additive) is used to compare the proportion of alpha and beta diversity to gamma diversity. Beta diversity (Whittaker) is not used in this research.
Magurran (1988) gives an explanation and an example how beta diversity should be calculated according the to Shannon method.

In this research, beta diversity was calculated by firstly estimate the proportional importance of local diversity to regional diversity (ρ) per species, subsequently multiply this proportional importance by the natural logarithm of this proportional importance per species and thereafter sum these values for all species and multiply by negative one (Tab. 1).

Tab. 1 Example information ordered to calculate vegetation beta Shannon-index for one area

Species	Number of observations where species was present (n)	ρ * LN (ρ)[1]
A	2	2/22 * LN(2/22) = -0.22
B	4	4/22 * LN(4/22) = -0.31
C	3	3/22 * LN(3/22) = -0.27
D	0	0
E	6	6/22 * LN(6/22) = -0.35
F	3	3/22 * LN(3/22) = -0.27
G	4	4/22 * LN(4/22) = -0.31
Species richness (S)	7	
Sum number of observations where species was present (N)	22	$\beta = -\Sigma \rho \text{ LN}(\rho)$ = 0.22 + 0.31 + 0.27 + 0 + 0.35 + 0.27 + 0.31 = 1.74

[1] $\rho = n/N$

Also the proportional importance of alpha versus beta diversity was calculated. With the proportional importance of diversity is meant how much the alpha or beta component explains of the total diversity (gamma). A trend in this proportional importance could indicate useful information concerning the relationship between vegetation diversity and other variables. This proportion is indicated by the percentage of alpha and beta (% alpha, % beta).

Vegetation diversity is different on multiple spatial scale. In the following example (Fig. 3, Tab. 2) it is tried to explain how vegetation diversity can be compared upon multiple spatial scale.

In North-Holland, vegetation observations were made at locations indicated with a dark-blue spot on Figure 3. In the example of Fig. 3, A1 – A3 are discharge areas and North-Holland is a WB21 area. This case provides the following options (see Tab. 2):

Scale 1 Discharge area (A1, A2 or A3)
Alpha: mean species richness per observation within A1, A2 or A3
Beta: vegetation diversity among observations
Gamma: species richness of discharge area A1, A2 or A3

Scale 2 WB21 area (A1, A2 and A3)
Alpha: mean species richness per A1, A2 or A3
Beta: vegetation diversity among areas A1, A2 en A3
Gamma: species richness of WB21 area North-Holland (sum of A1, A2 and A3)

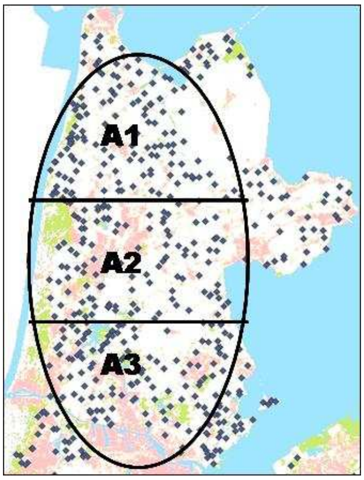

Fig. 3 Alpha, beta and gamma diversity

Scale 3 Holland
Alpha: mean species richness per WB21 area
Beta: vegetation diversity among WB21 areas
Gamma: species richness of Holland (sum of all WB21 areas).

Tab. 2 Alpha, beta and gamma levels on multiple spatial scale:

Scale level	Alpha	Beta	Gamma
1	Ditch observations (dots in A1)	Ditch observations among each other within discharge area	All ditches within discharge area (A1)
2	Discharge areas (A1)	Discharge areas among each other within WB21 area	All discharge areas within WB21 area (A1 + A2 + A3)
3	WB21 (A1 + A2 + A3)	WB21 areas among each other within Holland	Holland

Estimate geographical heterogeneity (landuse, soiltype and combined) per area per scale.

Geographical heterogeneity per area can also be calculated with the Shannon method (Forman 1995). The methodology is similar to how beta diversity is calculated (see previous section), however, unique species were replaced with an unique geographical type.

Firstly estimate the proportional importance of a certain geographical type of a region (ρ) per geographical type, subsequently multiply this proportional importance by the natural logarithm of this proportional importance per geographical type and thereafter sum these values for all geographical types and multiply by negative one (Tab. 3).

Tab. 3 Example how to order information to calculate geographical heterogeneity for one area in line with Shannon's index

Geographical type	Area (m^2)
A	2
B	4
C	3
D	0
E	6
F	3
G	4
Number of geographical types (S)	7
Total Area (m^2)	22

Geographical heterogeneity was estimated using landuse and soiltype in such a way that each type of landuse with each type of soiltype formed an unique combination. Based on these combinations heterogeneity (combined) was calculated. This index was supposed to be the most representative and therefore mainly used.

Geographical heterogeneity indices were indicated as follows:
- Heterogeneity based on landuse: h-landuse;
- Heterogeneity based on soiltype: h-soiltype;
- Heterogeneity based on both landuse and soiltype: h-combined.

The frequency of geographical types within an area is also an indication of its geographical heterogeneity. In this research, these frequency indices were indicated as follows:
- Frequency of landuse types within an area: f-landuse;
- Frequency of soiltypes within an area: f-soiltype;
- Frequency of an unique combination of landuse and soiltype within an area: f-combined.

D. Data analyses

Test for correlation (by Pearson) between geographical heterogeneity, vegetation diversity and spatial scale.

Test for equality of variances (by Levene's Test) between discharge, WB21 and Holland scale.

The Pearson-test of PSAW (SPSS Inc, PSAW Statistics 17) was used to estimate correlation between geographical heterogeneity variables, vegetation diversity variables and spatial scale. The number of discharge areas (N) was 252. Variables analysed were:

Area;
Beta diversity (Shannon);
Beta diversity (Additive);
Number of observations;
H-landuse;
H-soiltype;
H-combined;
F-landuse;
F-soiltype;
F-combined;
Gamma diversity (species richness);
Alpha diversity (mean species richness);
% Alpha;
% Beta.

Also the proportional importance of alpha versus beta diversity was calculated. With the proportional importance of diversity is meant how much the alpha or beta component explains of the total diversity (gamma). A trend in this proportional importance could indicate useful information concerning the relationship between vegetation diversity and other variables. This proportion is indicated by the percentage of alpha and beta.

3. Results

3.1 What is the relationship between vegetation diversity (alpha, beta en gamma) and spatial scale?

3.1.1 Vegetation diversity in ditches for discharge areas

Tab. 4 A few examples from the dataset concerning number of observations, area and diversity

Area name	Number of observations	Area (km2)	Alpha diversity	Beta Diversity (S)	Gamma diversity
S-Auvergne polder	2	10.6	1.5	0.35	2
NL37_E	2	53.5	2.5	0.35	3
NL37_H	7	104.8	8.71	7.83	29
RNWE_1759	2	8.9	20	6.24	29
RNWE_POL412	4	7.5	14	8.23	29
RNWE12_34	46	165.7	12.28	13.38	62
FR_900158022	4	10.4	36.75	15.50	63
RO_90	10	66.1	20.9	19.87	65
RO_144	20	73.2	19.95	18.53	67
NL35_07	9	74.2	30.89	19.74	72

Because not all variables of one discharge area could be presented together, a selection is presented in Tab. 4. These 10 discharge areas represented high variability in how area, number of observations and diversity were related. Area NL35_07 with the highest gamma diversity of the whole dataset did not have a exceptional large area nor a high number of observations. Area NL37_H had about the same number of observations and a larger area while gamma diversity was about half of gamma diversity from Area NL35_07. Fig. 4 shows how alpha, beta and gamma diversity were distributed. The diversity indices were not normal distributed.

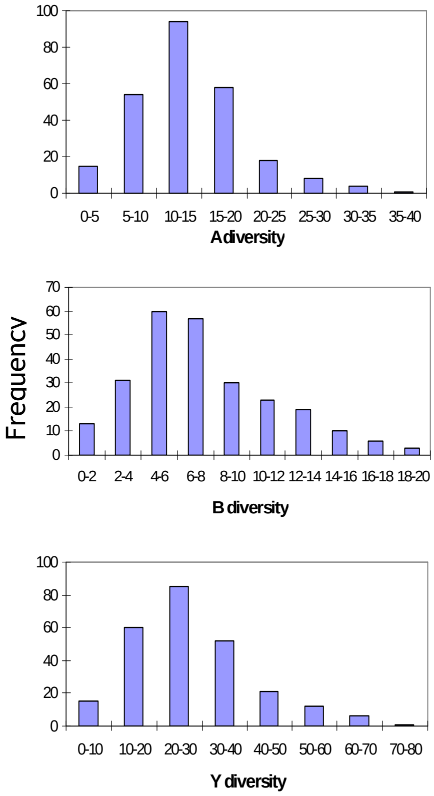

Fig. 4 Frequency graphs of classes of α, β and γ diversity in discharge areas (N=252).

Since number of observations correlated with number of species (R^2=0.63, P<0.05) this difference in number of observations had an effect on species number observed. The range for number of observation laid between 2 (the minimum) and 62 per discharge area (Tab. 5).

Tab. 5 Descriptive statistics of number of observations and area on discharge area scale

	Number of observations	Area (km2)
Average	4.89	29.13
Minimum	2	0.52
Maximum	62	165.67
Total number	252	252

The area (km^2) of the 252 areas differed from 0.52 km^2 to 165.67 km^2 with an average of 29.13 km^2 (Tab. 5).

Area correlated only weakly but significantly with alpha and beta diversity (α: $R^2 = 0.04$, β: $R^2 = 0.02$; $P < 0.05$). Also Log(Area) did not correlate strongly with diversity indices.

Highest observed species number (gamma diversity) within a discharge area was 72, lowest was 2. Alpha diversity ranged from 1.5 to 36.75, beta diversity from 0.35 to 19.87.

Tab. 6 Descriptive statistics of ditch (N=252) and terrestrial (N=924) vegetation in discharge areas

	Alpha diversity ditch	Beta diversity ditch	Gamma diversity ditch	Alpha diversity terrestrial	Beta diversity terrestrial	Gamma diversity terrestrial
Average	13.78	7.48	28.20	19.23	21.41	84.34
Minimum	1.50	0.35	2	1.50	0.35	2
Maximum	36.75	19.87	72	45.50	61.56	445

(Tab. 6) Compared with ditch vegetation, terrestrial vegetation contained much higher species richness (maximum gamma diversity ditch: 72, terrestrial: 445).

Noticeable is the relationship between alpha, beta and gamma diversity. As already concluded, gamma diversity was much higher for terrestrial vegetation. However, alpha diversity did not differ that much between ditch and terrestrial vegetation. Therefore, beta diversity explained much more of total terrestrial species richness. In other words, compared with ditch vegetation, average species richness per discharge area was not that much higher for terrestrial vegetation but encountered species per discharge area differed more among discharge areas (higher beta diversity) resulting in a higher total species richness (gamma diversity).

Diversity indices were strongly correlated among each other ($R^2 > 0.5$, $P < 0.05$).

3.1.3 Vegetation diversity for WB21 areas

Tab. 7 Descriptive statistics of ditch vegetation diversity in WB21 areas (N=13)

	Alpha diversity	Beta diversity	Gamma diversity
Average	18.56	18.53	74.15
Minimum	10.67	11.95	41
Maximum	29.22	27.52	113

(Tab. 7) Compared with discharge areas, especially beta and gamma diversity were higher for WB21 areas. More explicit, an up-shift of the lower boundary caused a change in average and minimum for all diversity indices (see Fig. 5 and 6). However, maximum did only increase for beta and gamma diversity.

Tab. 8 Descriptive statistics of terrestrial vegetation diversity in dischargeWB21 areas (N=19)

	Alpha diversity	Beta diversity	Gamma diversity
Average	71.78	109.51	666.74
Minimum	27.62	46.86	203
Maximum	167.42	193.15	1004

(Tab. 8) Maximum alpha diversity decreased, probably because the number of discharge areas within one WB21 area is in general higher than the number of locations within one discharge area. This negative impact was probably larger than the positive impact of higher species number.

Terrestrial diversity of WB21 areas was much higher than ditch diversity, for gamma diversity this difference was almost a factor ten.

Terrestrial diversity was significantly but weakly correlated with area on discharge area scale ($R^2 < 0.1$, $P<0.05$) and not correlated on WB21 area scale ($P>0.05$).

Ditch beta diversity on WB21 area scale did correlate significantly and strongly with area ($R^2 = 0.52$, $P < 0.05$). However, no correlation was observed between area and alpha and gamma diversity.

3.1.3 Vegetation diversity on multiple spatial scale

Ditch vegetation diversity correlated with area on multiple scale (β diversity: $R^2 = 0.2$, $P < 0,05$) (Fig. 5).

Equality of variance on discharge and WB21 scale was tested with Levene's Test. For area (F=310,62; P=0.000) and gamma diversity (F=15.03; P=0.000) equality of variance was rejected while for alpha (F=3.06; P=0.081) and beta diversity (F=0.62; P=0.434) equality of variance was accepted. This meant that area and gamma diversity differed significantly per spatial scale and that those differences could not be explained by their variances.

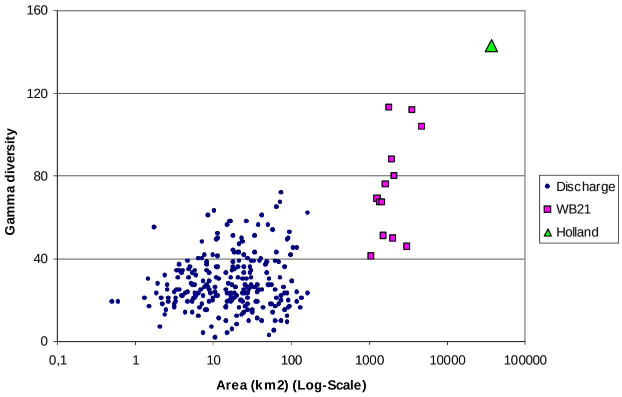

Fig. 5 Ditch gamma diversity versus area on three spatial scales (discharge, WB21, Holland)

Terrestrial vegetation diversity correlated with area on multiple scale (β-diversity: $R^2 = 0.56$, $P < 0,05$) (Fig. 6).

Equality of variance was tested with Levene's Test for discharge and WB21 areas and rejected for area (F=545.98; P=0.000), alpha diversity (F=271.58; P=0.000), beta diversity (F=163.39; P=0.000) and gamma diversity (F=191.75; P=0.000). Therefore, all these variables differed significantly per spatial scale and those differences could not be explained by their variances.

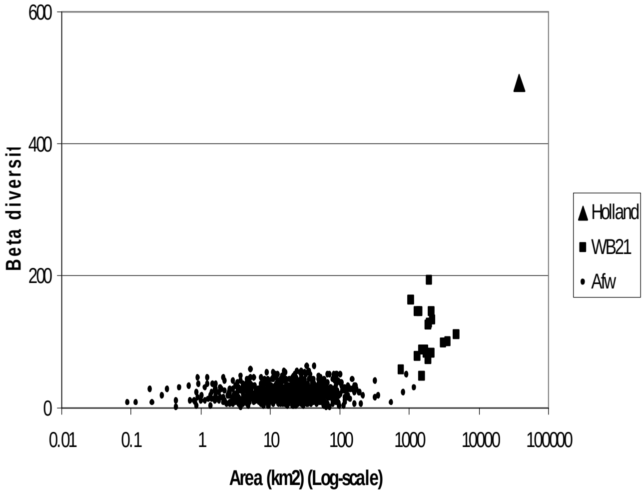

Fig. 6 Terrestrial beta diversity (S) versus area on three spatial scales (Holland, WB21 and discharge)

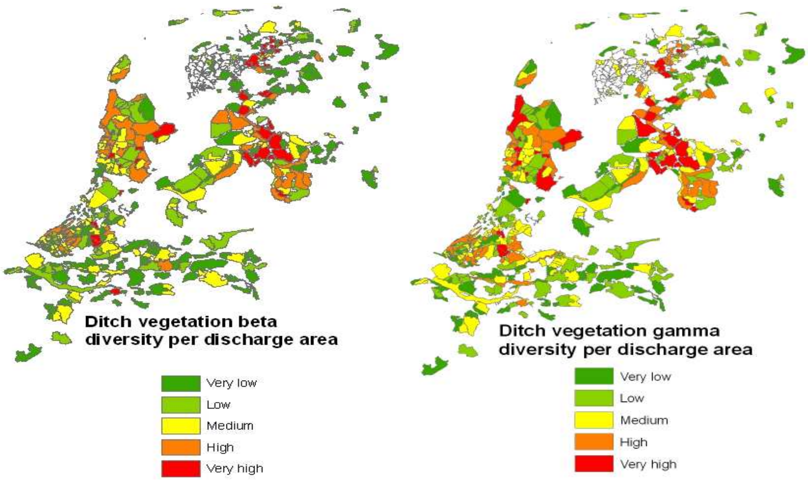

Fig. 7 Ditch beta and gamma diversity per discharge area. Discharge areas having the highest beta and gamma diversity appeared to be mainly situated in the 'head of Overijssel', parts of Friesland and North-Holland.

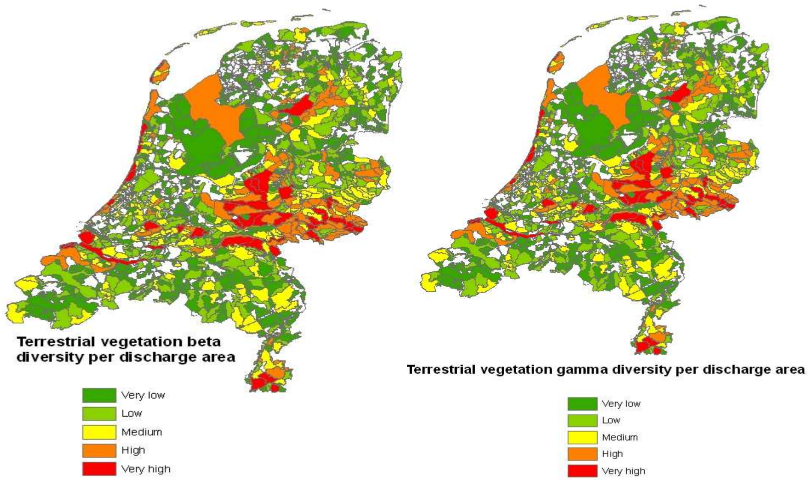

Fig. 8 Terrestrial beta and gamma diversity per discharge area. Discharge areas having the highest beta and gamma diversity appeared to be mainly situated at the Veluwe and Achterhoek. Also the south of Friesland, the south of South-Holland and the south of Limburg contained high diversity values.

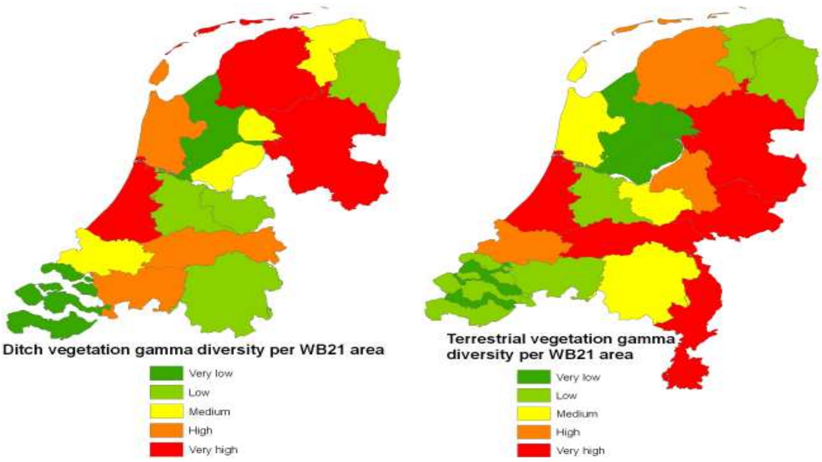

Fig. 9 This pattern was also observed for vegetation beta diversity on WB21-scale. Low vegetation beta diversity was calculated for Zeeland, East-Groningen, East-Brabant and Gelderse Vallei.

3.2 What is the relationship between geographical heterogeneity and spatial scale?

Tab. 9 Descriptive statistics of geographical heterogeneity on discharge area scale

	F-Landuse	H-Landuse	F-Soiltype	H-Soiltype	F-Combined	H-Combined	Area (km2)
Average	6.70	0.92	5.69	1.02	23.61	1.71	29.13
Standard deviation	3.24	0.50	1.71	0.43	14.85	0.63	31.21
Minimum	1	0.00	1	0.00	3	0.10	0.52
Maximum	20	2.25	10	1.87	101	3.32	165.67

Tab. 9 shows the high difference between heterogeneity index values. Standard deviation was in relation to their range. F-landuse and f-soiltype did have about the same average, landuse contained however twice as much types. F-combined contained 10 times more types than f-soiltype and 5 times more types than f-landuse. The average of f-combined was also much higher than for f-landuse and f-soiltype. Descriptive statistics for h-landuse and h-soiltype were similar, h-combined was a bit higher.

Based on Fig. 10, a general pattern of higher heterogeneity with larger area was expected, however this was not confirmed by Pearson's Test for correlation.

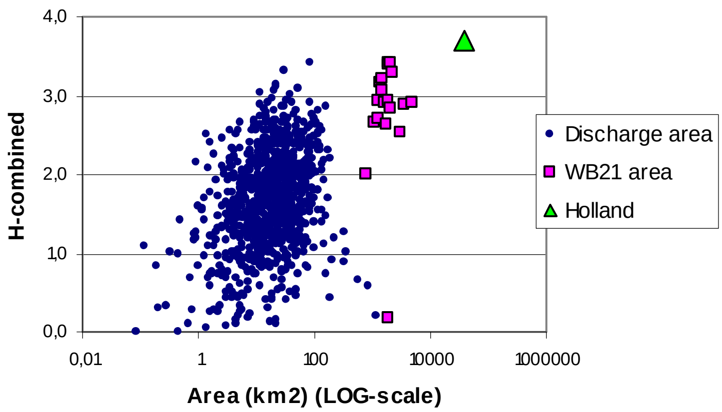

Fig. 10 Heterogeneity (combined) and multiple spatial scale (discharge, WB21 and Holland). No strong correlation was observed.

F-combined and f-soiltype were significantly correlated with area on discharge area scale (f-combined: $R^2 = 0.16$, $P < 0.05$; f-soiltype: $R^2 = 0.06$, $P < 0.05$). Furthermore, tests of correlation between area and heterogeneity on multiple scales (discharge, WB21 and Holland) resulted in significant but weak correlation ($R^2 = 0.02$, $P < 0.05$). On WB21-scale, correlation between area and f-combined was observed ($R^2 = 0.25$, $P < 0.05$). The Levene's Test revealed no significant difference in variance.

Fig. 11 shows the graphically results of the heterogeneity research (for h-combined on discharge and WB21 scale). On both discharge and WB21 scale high heterogeneity was observed in the river area. By comparing the heterogeneity map (Fig. 11) with the diversity map (Fig. 7-9), high heterogeneity did not necessarily coincide with high diversity.

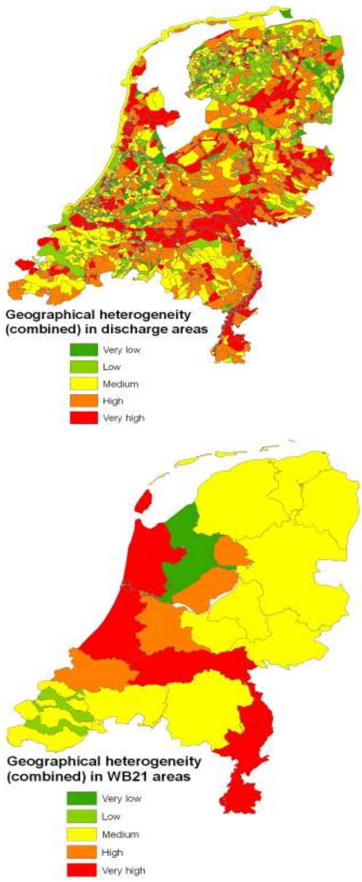

Fig. 11 Geographical heterogeneity (combined) on discharge (upper) and WB21 (lower) area scale.

3.3 Is there a relationship between vegetation diversity and geographical heterogeneity on multiple spatial scale?

3.3.1 Discharge area scale

Regression analyses of independent variables with dependent diversity are listed in Tab. 10. The vegetation diversity variables (α, β and γ diversity) did correlate strongly among each other (R^2 > 0,5; P < 0,05). Both beta and gamma diversity correlated significantly with number of observations, both alpha and beta diversity correlated significantly with area. Of the heterogeneity variables, none of them correlated strongly with one of the diversity variables. All significant correlations between diversity and heterogeneity were weak (R^2 < 0.1).

Tab. 10 Regression analyses (Ditch vegetation, discharge areas, N=252)

Dependent	Independent	R	R^2	Sig. F change
Beta diversity (Shannon)	Number of observations	0.426	0.18	0.000
	F-soiltype	0.172	0.03	0.006
	Area	0.136	0.02	0.031
	H-combined	0.042	0.00	0.502
	F-landuse	0.001	0.00	0.987
Alpha diversity (mean species richness)	F-landuse	-0.226	0.05	0.000
	H-landuse	-0.179	0.03	0.004
	F-combined	-0.167	0.03	0.008
	F-soiltype	-0.101	0.01	0.111
Gamma diversity (species richness)	Number of observations	0.467	0.22	0.000
	F-soiltype	0.140	0.02	0.027

For comparison the results of the regression analyses for terrestrial vegetation data are listed in Tab. 11.

Tab. 11 Regression analyses (Terrestrial vegetation, discharge areas, N=924)

Dependent	Independent	R	R^2	Sig. F change
Beta diversity (Shannon)	Number of observations	0.496	0.24	0.000
	F-soiltype	0.244	0.06	0.000
	Area	0.140	0.02	0.000
	H-combined	0.246	0.06	0.000
	F-landuse	0.303	0.09	0.000
Alpha diversity (mean species richness)	F-landuse	-0.176	0.03	0.000
	H-landuse	-0.133	0.02	0.000
	F-combined	-0.036	0.00	0.280
	F-soiltype	0.045	0.00	0.173
Gamma diversity (species richness)	Number of observations	0.749	0.56	0.000
	F-soiltype	0.221	0.05	0.000

The results of an extended Pearson test indicated significant but weak correlation among many variables involved in the project.

Terrestrial beta and gamma diversity correlated significantly with all heterogeneity variables. However, none of these correlations were strong. The correlation of beta and gamma diversity with number of observations was significant and stronger (R^2 = 0.24, resp. 0.56; P < 0.05).

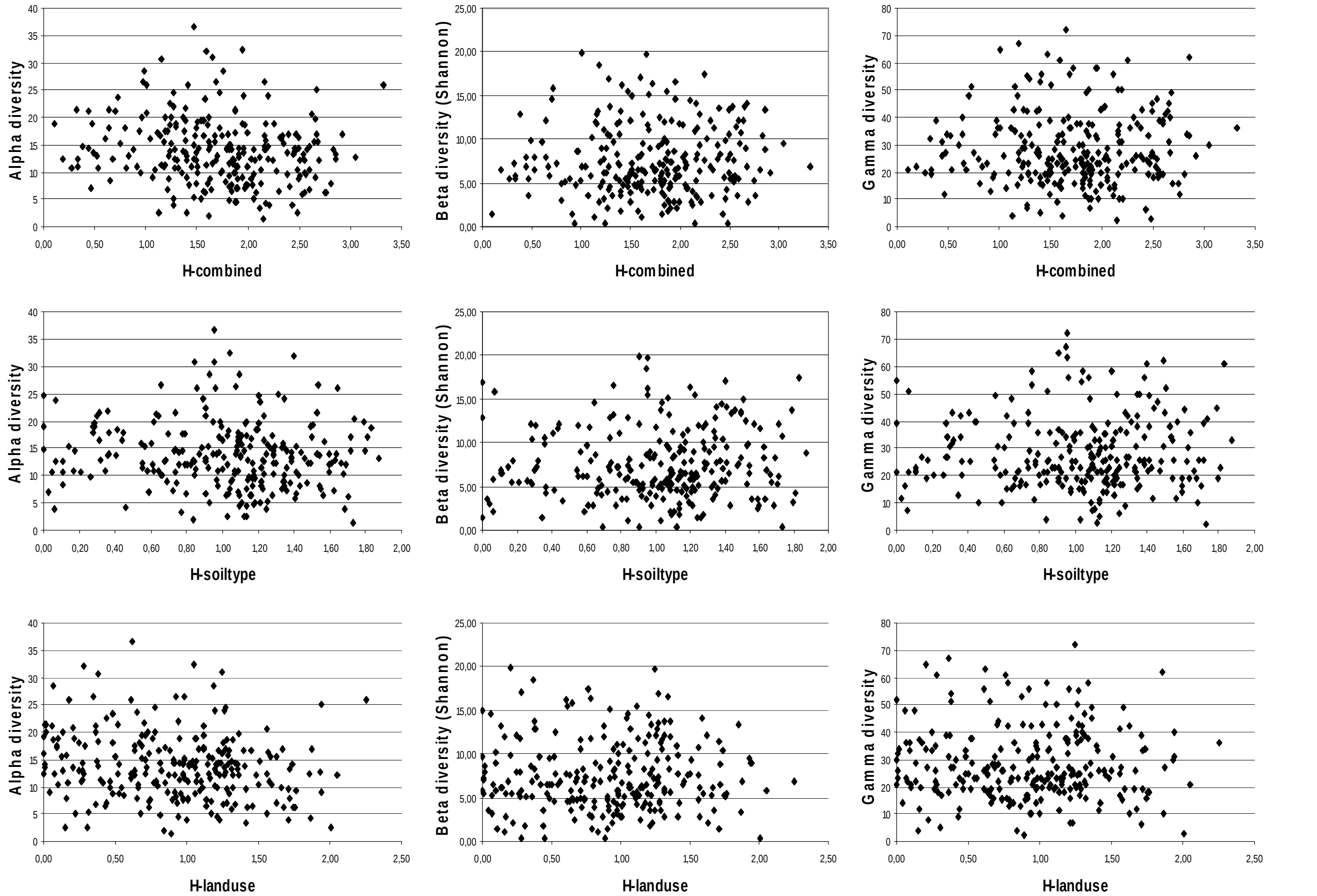

Fig. 12 Alpha diversity, beta diversity (Shannon) and gamma diversity versus geographical heterogeneity (combined, landuse and soiltype.

Heterogeneity variables h-combined, h-soiltype and h-landuse are plotted against alpha, beta and gamma diversity showing the relationship between heterogeneity and diversity for discharge areas in The Netherlands (Fig. 12). No significant linear relationship was observed, as concluded in the previous paragraph.

H-combined and h-soiltype did seem to have a kind of potential maximum at average heterogeneity values for diversity (alpha, beta and gamma). In other words, a high alpha, beta or gamma diversity was possible if h-combined or h-soiltype was at its optimum value (around its average). For h-landuse, results did not indicate a certain pattern with diversity values.

Potential maximum value of alpha, beta and gamma diversity is plotted against h-combined (Fig. 13). These graphs show a sort of optimum value suggesting the possibility of an optimum in potential maximum between heterogeneity and diversity.

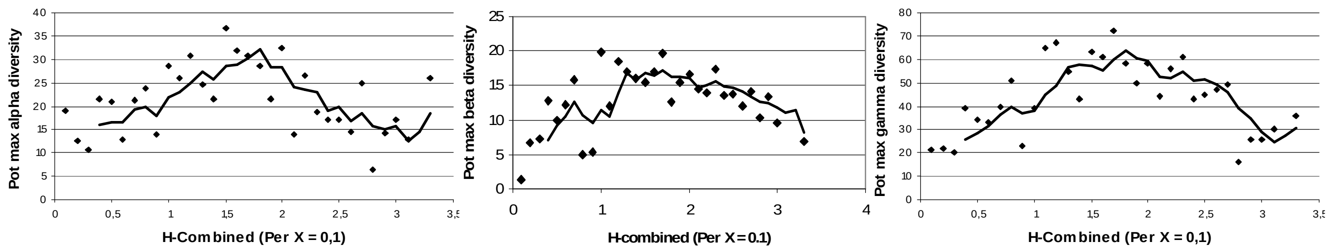

Fig. 13 Potential maximum of alpha (left), beta (middle) and gamma (right) diversity with geographical heterogeneity index h-combined. The line in the graphs is the moving average over four periods.

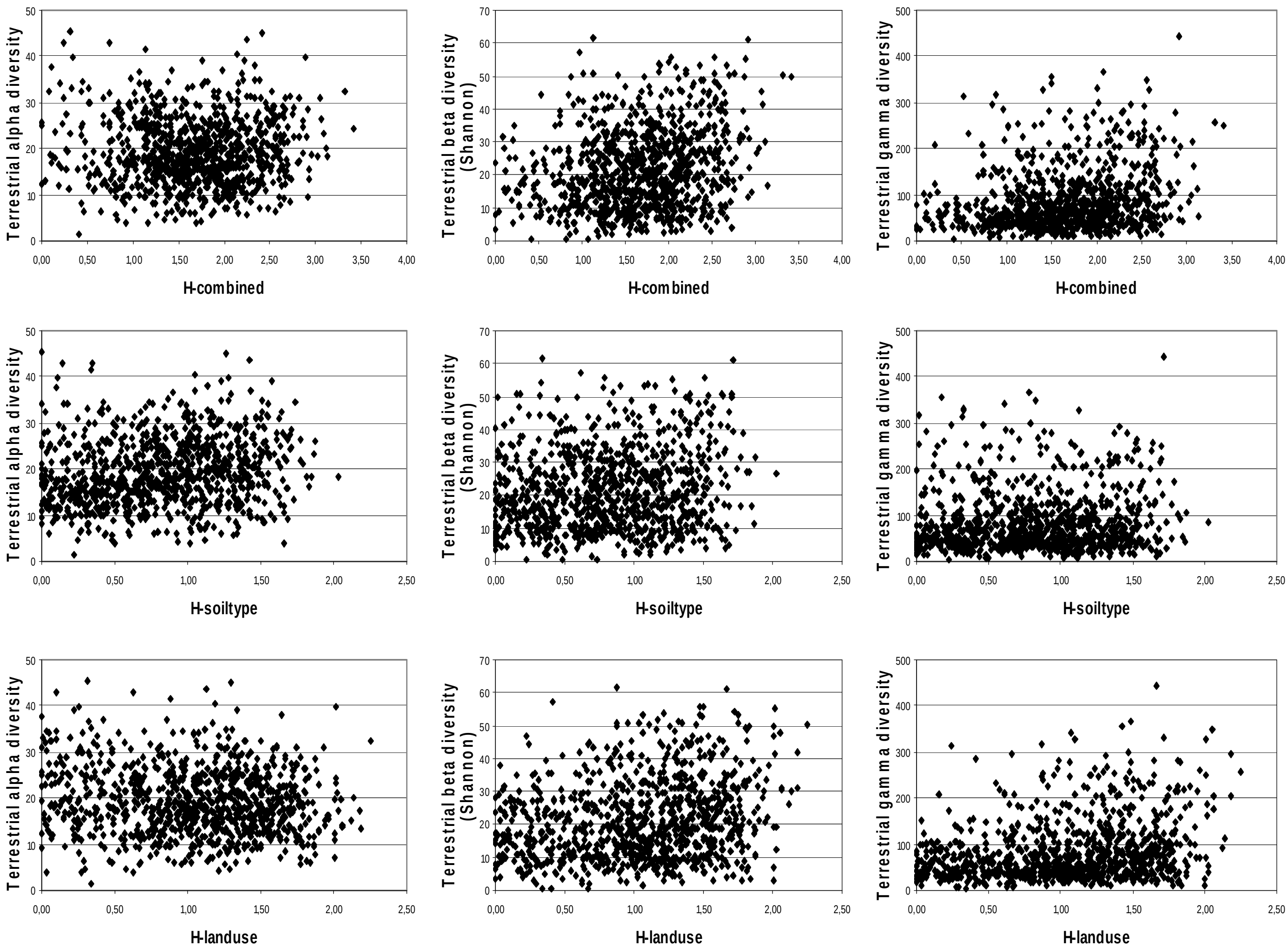

Fig. 14 Terrestrial alpha, beta and gamma diversity and geographical heterogeneity

In Fig. 14, heterogeneity (h-combined, h-soiltype and h-landuse) are plotted against diversity (α, β and γ), like in Fig. 12, but for terrestrial vegetation. The main observation was many values at the low diversity values, scattered over the heterogeneity scale.

A potential maximum graph was plotted (Fig. 15) to see whether this suggestion of an optimum in potential maximum between heterogeneity and diversity also might count for terrestrial vegetation. The graph of Fig. 15 did not support this suggestion.

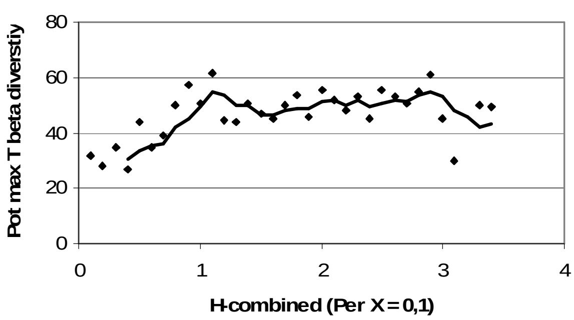

Fig. 15 Potential maximum of terrestrial beta diversity and h-combined

3.3.2 WB21 scale

At the scale of WB21 areas, area and number of observations appeared to be the most explaining variables for vegetation diversity. Taking them together as two independent variables predicting dependent beta diversity (Shannon), they significantly explained 73% of the observed variance (Tab. 12). Area and number of observations were the only variables correlating significantly with diversity variables. All heterogeneity variables did not correlate significantly with diversity.

Tab. 12 Regression analysis (Ditch vegetation, WB21, N=13)

Dependent	Independent	R	R^2	Sig. F change
Beta diversity (Shannon)	Area	0.718	0.52	0.006
	Number of observations	0.580	0.34	0.038
	H-combined	0.307	0.09	0.308
	F-landuse	0.280	0.08	0.354
	F-soiltype	0.240	0.06	0.431
	Area and Number of observations	0.853	0.73	0.002
Alpha diversity (mean species richness)	Number of observations	0.441	0.19	0.131
	F-combined	0.226	0.05	0.458
	F-soiltype	0.125	0.02	0.684
	F-landuse	0.021	0.00	0.945
Gamma diversity (species richness)	Number of observations	0.789	0.62	0.001
	F-soiltype	0.134	0.02	0.664

The results for terrestrial vegetation on WB21 scale were mainly similar to ditch vegetation concerning the heterogeneity variables. However, number of observation and area did not correlate that strong with terrestrial diversity as with ditch diversity. Some results of the regression analyses are shown in Tab. 13. Number of observations correlated strongly and significantly with gamma diversity ($R^2 = 0.5$, $P < 0.05$).

Tab. 13 Regression analysis (Terrestrial vegetation, WB21, N=19)

Dependent	Independent	R	R^2	Sig. F change
Beta diversity (Shannon)	Number of observations	0.237	0.06	0.329
	F-soiltype	0.158	0.02	0.517
	Area	0.026	0.00	0.916
	H-combined	0.352	0.12	0.140
	F-landuse	0.136	0.02	0.577
Alpha diversity (mean species richness)	F-landuse	-0.160	0.03	0.512
	H-landuse	0.232	0.05	0.339
	F-combined	-0.369	0.14	0.120
	F-soiltype	-0.132	0.02	0.589
Gamma diversity (species richness)	Number of observations	0.704	0.50	0.001
	F-soiltype	0.411	0.17	0.081

3.3.3 Multiple spatial scale

Tab. 14 Regression analyses h-combined versus vegetation diversity on multiple spatial scales

Independent	Dependent	R^2 ditch	Sig.
H-combined	Alpha	0.00	0.388
	Beta	0.09	0.000
	Gamma	0.10	0.000
		R^2 terrestrial	Sig.
	Alpha	0.03	0.000
	Beta	0.11	0.000
	Gamma	0.11	0.000

Regression between h-combined and vegetation diversity was also tested on multiple spatial scale for both ditch and terrestrial vegetation (Tab. 14). On multiple scales, vegetation diversity (ditch and terrestrial) showed weak but significant regression (except ditch alpha diversity) with h-combined.

Both ditch and terrestrial beta diversity are plotted against h-combined in Fig. 16. Although the Pearson test revealed a weak correlation, the graphs suggested the tendency of increasing diversity with h-combined. However, increasing diversity with spatial scale is higher than with increasing heterogeneity.

Furthermore, discharge area diversity values seemed to form the bottom of WB21 values, Holland is again a layer above. This may indicate certain layers of diversity determined by its spatial scale.

This same pattern can be observed for heterogeneity: the layer of discharge areas forms the bottom of the layer for WB21 areas.

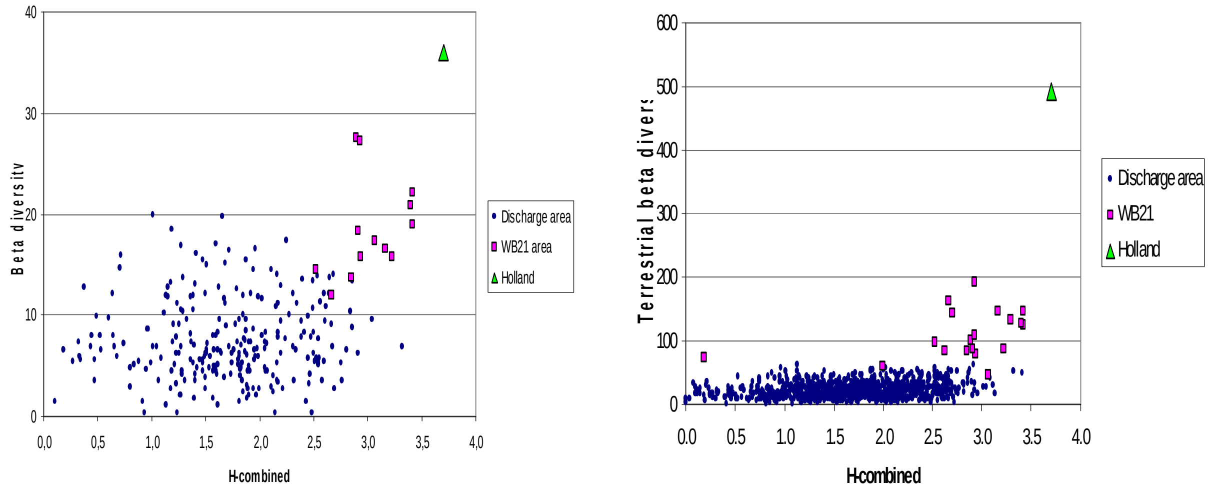

Fig. 16 Beta diversity (S) for ditch (left) and terrestrial (right) vegetation versus h-combined on three spatial scales (discharge area, WB21 area, Holland).

4. Discussion

Geographical heterogeneity – vegetation diversity

This research of the relationship between heterogeneity and diversity on multiple and one spatial scale has brought certain suggestions into notice.

Firstly, it appeared that separating vegetation diversity into alpha, beta and gamma diversity resulted in an enrichment of insight in diversity. By distinction between diversity on a location and diversity among locations, a more comprehensive idea of diversity of a region can be obtained. This was already stressed and argued by MacArthur and Wilson (MacArthur 1972) and Whittaker (1977). In this research, many areas with a high total diversity achieved this by a high beta diversity while local species richness (alpha diversity) was low. Similar results stressing the importance of beta diversity were easily to find in literature, for example Williams (Williams, Whitfield et al. 2004), Gabriel (Gabriel, Roschewitz et al. 2006), Scheffer (Scheffer, van Geest et al. 2006), Clough (Clough, Holzschuh et al. 2007) and Davies (Davies, Biggs et al. 2008). Measures of management by environmental agencies resulting in locally higher species richness therefore do not seem to be very sustainable and effective. And as Clough (Clough, Holzschuh et al. 2007) indicated, beta diversity accounts for a major part of species richness within agro-ecosystems. Scheffer (Scheffer, van Geest et al. 2006) suggested that it is usually more effective to stimulate situations of small populations differencing from each other (by for instance high fragmentation and isolation) resulting in an eventually higher species richness on higher spatial scale.

Furthermore, results suggested a strong explaining value in spatial scale (and therewith area) for diversity. MacArthur (MacArthur and Wilson) already argued that area is positive correlated with diversity. It was therefore of importance that areas compared were as equal as possible besides the variables to compare (diversity in this case). This counted also for area.

Therefore, spatial scale was taken into account by making a difference between regional (discharge), provincial (WB21) and national (Holland) areas. This difference might explain the weak correlation between diversity and area on discharge area scale. On WB21-scale, areas still did differ much among each other resulting in a higher correlation between diversity and area. By combining all areas for multiple spatial scale, area appeared to explain 20% of diversity variance. This observation was confirmed by similar results for terrestrial vegetation.

At last, these results suggested no measurable relationship between ditch vegetation diversity and geographical heterogeneity (based on landuse, soiltype and combined). Although studies confirmed the assumption of a positive relationship between these two variables (Lundholm, 2009), this positive relationship has not been found in this research. Some studies did also suggest no or a negative effect of heterogeneity on diversity (Lundholm, 2009). As Farina (Farina) observed, level of heterogeneity can also negatively affect some processes in which too much fragmentation may result in lower diversity. This coincides with our results suggesting an optimum in potential maximum between heterogeneity and biodiversity. The average of heterogeneity was the optimum value with highest measured diversity (Scheffer, van Geest et al. 2006). However, as heterogeneity tended to be normally distributed, most heterogeneity observations were also around this average. Therefore, most extreme diversity values were also expected to be around that average heterogeneity value. More research should reveal whether or how ditch vegetation diversity is influenced by its surroundings. Probably do chemical and physical factors play a more determining role (Biggs, Williams et al. 2005) by which the influence of heterogeneity of the ditch surroundings is not measurable. A possible solution could be to compare ditches which have the same phycho-chemical characteristics.

Important to notice is the external nature of heterogeneity in this research since heterogeneity of the surrounding (ex-situ) of the ditch was calculated instead of heterogeneity within (in-situ) the ditch. This might also partly explain why no relationship between heterogeneity and diversity was measured within this research.

This research has led to some specific suggestions.

For diversity measurement a distinction should be made between alpha, beta and gamma diversity.

Environmental agencies and waterboards should aim more at diversity among locations (beta) instead of biodiversity hotspots since beta diversity accounts for the major part of agro-system species richness. That way, regionally high species richness could be reached.

Spatial scale and area are important explaining factors

On multiple spatial scale, area appeared to be a significant explaining factor for both ditch and terrestrial vegetation diversity. Differentiation of vegetation diversity based on spatial scale was significant.

Optimum in potential maximum ditch vegetation

On discharge area scale, results suggested a possible optimum relationship in potential maximum ditch vegetation diversity (alpha, beta and gamma) and geographical heterogeneity (expressed as h-combined).

5. Conclusion and recommendation

As discussed in the introduction, ditches do have an ecological importance, their vegetation structure appears to be a determining factor in faunal diversity (Peeters 2007). This research was based on the postulate that terrestrial vegetation diversity increases with geographical heterogeneity (see Introduction) and in this research it is investigated whether this postulate also counts for ditch vegetation, on multiple spatial scales.

The main question addressed in this research was:

Is there a relationship between vegetation diversity in Dutch ditches and geographical heterogeneity on multiple spatial scale?

Subquestions:
What is the relationship between vegetation diversity (alpha, beta en gamma) in Dutch ditches and spatial scale?
What is the relationship between geographical heterogeneity (based on landuse, soiltype and a combination of both) in Holland and spatial scale?
Is there a relationship between vegetation diversity and geographical heterogeneity on multiple and one spatial scale?

Results of this research did not suggest a specific relationship between ditch vegetation diversity and geographical heterogeneity on multiple spatial scale.

This research results suggest a positive relationship between vegetation diversity and spatial scale.
This research results suggest no specific relationship between heterogeneity and spatial scale.
This research results suggest no relationship between vegetation diversity and geographical heterogeneity on multiple and one spatial scale.

Recommendations

I started this research telling about the efforts water boards put into conserving and stimulating biodiversity, also in ditches. I hope this research showed the importance of how this biodiversity is measured. Comparing areas to each other, factors such as number of observations and area are of importance. Furthermore, diversity numbers are surprisingly more informative (and interesting) if difference is made between alpha, beta and gamma diversity because that way a distinction can be made in how much diversity is due to local diversity within an area and how much diversity is due to diversity among locations within an area. Management scheme evaluations for conservation therefore needs to include β-diversity and subsequently implement measurements which do contribute to both alpha and beta diversity.

Further research could address how heterogeneity is of importance if other physical, chemical and biological factors do not play a role.

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Appendix

A. Short introduction of variables

F-Combined: Frequency (number) of combined-types (a unique combination of landuse and soiltype) within an area
F-Landuse: Frequency of landuse-types within an area
F-Soiltype: Frequency of landuse-types within an area
H-Combined: Heterogeneity (estimated following the Shannon formula) taking into account both landuse and soiltype within an area
H-Landuse: Heterogeneity (estimated following the Shannon formula) taking into account landuse within an area
H-Soiltype: Heterogeneity (estimated following the Shannon formula) taking into account soiltype within an area
Area: Amount of square meters of a discharge area of WB21 area
NoO: Number of observations within an area
α-diversity: Mean richness of all the locations within an area
β-diversity (Shannon): Diversity (estimated in accordance to Shannon formula) estimating the difference of present species among locations within an area
β-diversity (Additive): Diversity (estimated in accordance to Additive formula) estimating the difference of present species among locations within an area
γ-diversity: Total species richness of all locations within an area
%-alpha: Proportion of mean richness to total richness
%-beta: Proportion of difference of present species among locations (estimated in accordance to Additive formula) to total richness.