Disentangling and ranking the influences of multiple environmental factors on plant and soil-dwelling arthropod assemblages in a river Rhine floodplain area

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Abstract

Floodplains of large rivers are among the most dynamic and diverse, yet most threatened ecosystems on earth. For a solid underpinning of river conservation and rehabilitation measures, it is critical to unravel the influences of the multiple stressors affecting floodplain ecosystems. Using canonical correspondence analysis (CCA) with variance partitioning, we disentangled and ranked the influences of three floodplain ecosystem stressors (land use, flooding and soil contamination) on terrestrial plant and soil-dwelling arthropod assemblages in a floodplain area along the river Rhine in The Netherlands. We included five biotic assemblages: plant species (73 taxa), ground beetle species (57 taxa), ground beetle genera (29 taxa), beetle families (32 taxa), and arthropod groups at taxonomic levels from family to class (10 taxa). Plant as well as arthropod assemblages were primarily related to land use, which explained 19% to 30% of the variation in taxonomic composition. For plant species composition, flooding characteristics were nearly as important as land use. Soil metal contamination constituted a subordinate explanatory factor for the plant assemblages only (3% of variation explained). We conclude that the taxonomic composition of terrestrial plant and

arthropod assemblages in our study area is related to land use and flooding rather than soil metal contamination.

Key words

Carabidae; Coleoptera; canonical correspondence analysis (CCA); flooding; land use; metal contamination; variance partitioning; vegetation

Introduction

Floodplains of large rivers are among the most dynamic and diverse ecosystems on earth (Tockner et al. 2010; Tockner and Stanford 2002). However, being located in low-lying areas, where human population densities are disproportionally high (Cohen and Small 1998), floodplains are also among the most threatened ecosystems (Tockner and Stanford 2002). Particularly in Europe and North America, vast floodplain areas have been reclaimed for agricultural, industrial and urban activities, resulting in the modification and eradication of natural floodplain habitats (Nienhuis et al. 2002; Tockner and Stanford 2002). Along with the reclamation of riverine land, natural river flow regimes have been substantially distorted by the construction of dams, embankments, groynes and diversions (Jansson et al. 2000; Stanford et al. 1996). This has reduced the hydrological connectivity between the river channels and adjacent floodplains, leading to reduced floodplain rejuvenation, less pioneer habitats, and decreased heterogeneity and biodiversity (Cabezas et al. 2009; Stanford et al. 1996; Ward et al. 1999). Particularly in lowland river reaches, chemical pollution may pose an additional threat to floodplain ecosystems, due to the downstream transport and subsequent overbank deposition of sediment-bound contaminants originating from the upstream catchment (Hendriks et al. 1995; Leuven et al. 2005; Schipper et al. 2012; Van den Brink et al. 2003).

For a solid underpinning of floodplain conservation and rehabilitation measures, it is critical to quantify the influences of the multiple stressors that affect floodplain ecosystems. This is particularly relevant because a focus on single stressors may lead to erroneous management priorities and failing rehabilitation efforts, for example when effects observed are ascribed to the wrong stressor or more important stressors are overlooked (Klok et al. 2007; Tockner et al. 2010). A simultaneous analysis of the multiple stressors that affect floodplain ecosystems may help to attribute effects to particular stressors and place the impact of each stressor in a realistic perspective (Loos et al. 2010; Tockner et al. 2010). For example, it has been shown that macro-invertebrate communities in river Rhine floodplain lakes in The Netherlands were related to the oxygen content of the water rather than the metal contaminations in the sediment

(Van Griethuysen et al. 2004). Yet, many studies regarding floodplain ecosystem stressors focus on one type of stressor at a time, for example interference with the hydrological regime (Bayley and Guimond 2008) or chemical pollution (Rozema et al. 2008).

The goal of the present study was to disentangle and rank the influences of multiple floodplain ecosystem stressors on terrestrial plant and soil-dwelling arthropod assemblages in a river Rhine floodplain area in The Netherlands. The river Rhine is one of the longest rivers in Europe, flowing from the Swiss Alps to the North Sea via Germany and The Netherlands. Just downstream of the border between Germany and The Netherlands, the river Rhine splits into three main channels i.e., Waal, Nederrijn and IJssel (Fig. 1). The channels have been regulated by weirs, sluices and groynes for flow regulation and flood defence and the majority of the floodplains have been embanked and cultivated (Nienhuis et al. 2002). During the past century, particularly during the 1930a and the 1950s, the deposition of sediments contaminated with metals has resulted in elevated metal concentrations in the floodplain soil (Middelkoop 2000). Hence, the lowland river Rhine floodplain areas are subject to at least three anthropogenic floodplain ecosystem stressors: land use, interference with the hydrological regime, and floodplain soil contamination.

We sampled terrestrial plant and soil-dwelling arthropod assemblages as well as environmental conditions pertaining to land use, flooding and contamination in a floodplain area along the river Nederrijn (Fig. 1). We analysed the relationships between the biotic assemblages and environmental conditions with canonical correspondence analysis (CCA) using the variance partitioning approach. With variance partitioning, variation in taxonomic composition can be ascribed to particular environmental variables by 'factoring out' the effects of other environmental variables (Borcard et al. 1992; Peeters et al. 2004; Volis et al. 2011). Thus, effects of multiple environmental factors on biotic communities can be disentangled and ranked.

Methods

Study area and sampling sites

Data collection took place in the 'Wolfswaard' floodplain area, which is located along the north side of the Nederrijn channel (Fig. 1). The major part of the study area is in use as pasture for cattle. A relatively small part of the area is used for sheep grazing and contains some scattered fruit trees. The sheep grazing area is separated from the cattle by a hedgerow consisting mainly of common hawthorn (*Crataegus monogyna*). A minor embankment parallel to the river, at a distance of approximately 200 m from the middle of the channel, protects a part of the study area against minor floods. Data collection took place at 30 sampling sites, which were selected to cover differences in land use (sheep grazing, cattle grazing, hedgerow) and hydro-topographic setting (distance to the river, elevation, position with respect to the embankment).

Biotic assemblages

At each of the 30 sampling sites, terrestrial plant species composition was recorded in a 3x3 m plot in May 2008 (Schipper et al. 2010; 2011). In total, 73 species were recorded (Table S1 in Supplementary Material). The abundance of each plant species was estimated according to a modified Braun-Blanquet scale (Barkman et al. 1964). A pitfall trap was placed at the centre of each sampling site to collect soil-dwelling arthropods (Schipper et al. 2010). The traps were filled with ~ 3.7% formalin and a drop of detergent lotion to reduce surface tension. Traps were sampled monthly from May through October 2007 and were opened two weeks prior to each sampling event, i.e., the trap duration was 14 days. Arthropods were identified to order level (Aranea, Coleoptera, Dermaptera, Hemiptera, Isopoda, Opiliones), except for the mites and ticks (subclass of Acari), myriapods (classes of Chilopoda and Diplopoda) and ants (family of Formicidae). The beetles (order of Coleoptera) were further indentified to the taxonomic level of family, and the ground beetles (family of Carabidae) were identified to genus and species level. Thus, we distinguished four arthropod assemblages, comprising ground beetle species (57 taxa), ground beetle genera (29 taxa), beetle families (32 taxa), and groups of arthropods at taxonomic levels ranging from family to class (10 taxa). Per arthropod assemblage, we

calculated the average abundance based on the six monthly pitfall trap samples (Table S2-S5 in Supplementary Material).

Environmental characteristics

At each of the 30 sampling sites we quantified flooding characteristics, land use, vegetation structure, physical-chemical soil properties, and soil metal contamination levels (Table 1). The distance to the river (m) was calculated per sampling site as the Euclidian distance to the middle of the channel. The surface elevation of each sampling site (m amsl) was derived from The Netherlands' 5x5 m digital elevation model (www.ahn.nl). The average yearly flooding duration (days/year) was derived from the frequency distribution of daily river water level data covering the period 1999–2008 (Schipper et al. 2010; 2011). Land use was quantified as a categorical variable with three levels: sheep grazing, cattle grazing, or hedgerow. Vegetation structure was described by the total cover (%) and height (m) of the vegetation (herb layer). Soil samples were collected in August 2007. Three soil samples collected within 1 m from the centre of each sampling site were pooled, mixed and air-dried for 48 h at ambient room temperature. The soil pH was measured in a suspension of 10 g air-dried soil in 25 ml deionized water (<10 µS/cm), mixed 24 h before the measurements. Soil organic matter content (%) was determined from the weight loss upon ignition (4 h at 550 ^{o}C) of 10 g oven-dried (i.e., 24 h at 105 ^{o}C) samples. The particle size distribution of the soil was analyzed with laser diffraction (Malvern Master Sizer 2000 with Hydro 2000 G) performed on oven-dried samples sieved over 2000 µm. Prior to this analysis, samples were treated with 30% H_2O_2 and 10% HCl for detaching coagulating particles and dissolving organic matter. To determine the soil metal concentrations, 0.2 g dw of each sample was weighed on a Sartorius LA310S mass balance and digested in a mixture of 4 ml 65% HNO_3 and 1 ml 30% H_2O_2 using a Milestone Ethos-D microwave. Total concentrations of arsenic (As), cadmium (Cd), chromium (Cr), copper (Cu), nickel (Ni), lead (Pb) and zinc (Zn) were determined with ICP-MS (X Series; Thermo Electron Cooperation). Dissolved concentrations of Cd, Cu, Pb and Zn were calculated based on their total soil concentrations

combined with soil pH and soil organic carbon (SOC) content (Sauvé et al. 2000), whereby SOC was derived from SOM based on a conversion factor of 2 (Pribyl 2010). The mean and range of all but the categorical land use variable are provided in Table 1.

Data analysis

We investigated the relationships between the biotic assemblages and the environmental characteristics with canonical correspondence analysis (CCA) using Canoco for Windows 4.56 (Ter Braak and Šmilauer 2002). Braun-Blanquet units used to describe plant species abundance (r, +, 1, 2a, 2b, 3, 4, 5) were converted to ordinal values ranging from 1 to 8 (Ter Braak 1987). The arthropod abundance data were square-root transformed, which is considered the most appropriate for count data (Lepš and Šmilauer 2003). Vegetation cover and height were included as potential explanatory factors for both plant and arthropod assemblages, as vegetation not only responds to the environment but also modifies it (Økland and Eilertsen 1994; Volis et al. 2011; Wiser and Buxton 2008).

First, we conducted exploratory CCA analyses for each of the five biotic assemblages in order to identify and rank significant ($p < 0.05$) explanatory environmental characteristics. This was done with the manual forward selection procedure as available in Canoco. The significance of each explanatory variable was evaluated with Monte Carlo permutation tests (1000 permutations). Once the significant environmental variables were identified, we quantified their relative influence on the biotic assemblages with the variance partitioning method. With this approach, variation in taxonomic composition is attributed to specific environmental variables by including other potentially relevant environmental variables as covariables (Borcard et al. 1992). For each of the five biotic assemblages, we first performed a CCA including all significant environmental characteristics as explanatory variables. This yielded the amount of variation in the biotic data explained by all significant environmental variables of concern. Then, the environmental variables belonging to a specific category (land use, flooding, soil metal contamination, vegetation structure, or physical-chemical soil properties; Table 1) were used as

explanatory variables while all other environmental variables were included as co-variables. This was done for each category of environmental variables. Thus, we isolated the effect of each category of environmental variables by 'factoring out' the effects of the others. Finally, we assessed how much of the variation in the biotic assemblages was due to joint effects of environmental variables belonging to different categories. This so-called 'shared variation' was assessed by summing the variation attributed to the various categories and subtracting this sum from the total variation explained as assessed with the first CCA, i.e., the analysis based on all significant environmental variables together. The significance of each category of explanatory variables was evaluated with Monte Carlo permutation tests (1000 permutations).

Results

The forward selection procedure yielded two to seven significant ($p < 0.05$) explanatory variables per biotic assemblage (Fig. 2, Table 2). Variance inflation factors (VIFs) of these variables were all well below 10 (Table 2), indicating limited collinearity and hence little redundancy between the selected variables (Field 2005). The total variation in the biotic assemblages explained by the significant explanatory variables ranged between 31% and 55% (Fig. 2, Table 3).

For the terrestrial plant assemblages, significant explanatory variables were land use, flooding characteristics (distance to the river, flooding duration, elevation), vegetation height and the total soil concentration of As (Table 2). Land use and flooding characteristics were clearly more important than vegetation height and contamination (Fig. 2; Table 3). Arthropod assemblages were primarily related to land use variables (Table 2), which accounted for 22% to 30% of the taxonomic variation (Fig. 2, Table 3). In addition, vegetation structure was selected as a significant explanatory factor for all four arthropod assemblages, accounting for 4% to 13% of the variation. Flooding duration was selected as significant but subordinate explanatory factor for the ground beetle assemblages. None of the arthropod assemblages was significantly related to physical-chemical soil properties or soil metal concentrations.

Discussion

Methodological issues

Using canonical correspondence analysis (CCA) with variance partitioning, we disentangled and ranked the influences of multiple environmental factors on terrestrial plant and soil-dwelling arthropod assemblages in a river Rhine floodplain area. Before interpreting the results, a few methodological aspects are to be addressed. First, we used a large number of potential explanatory variables relative to the number of sampling sites included in our study. This increases the probability of chance correlation, i.e., it inflates the Type I error (Blanchet et al. 2008; Freedman et al. 1992). On the other hand, the correlations between our potential explanatory variables probably reduced the risk of false inclusion: if multiple highly correlated variables are included in a stepwise selection procedure, they compete with each other for inclusion, and if one is selected, the others will be left out. If correlations are very high (> 0.9), as were observed among the soil metal concentrations or among the grain size distribution parameters (Supplementary Material, Table S6), this may even result in the explanatory variables being less likely to be selected than can be expected based on the chosen level of significance (Freedman et al. 1992). Thus, in an exploratory forward variable selection procedure like we applied here, the *p*-values levels do not provide rigorous levels for rejecting or including an explanatory factor as significant. In addition, it should be noted that in CCA the total variation explained is affected by the number of explanatory factors (Blanchet et al. 2008) as well as the total variation within the biotic dataset, represented by the total inertia (Økland 1999). This implies, for example, that we cannot conclude that vegetation structure is more important for the arthropod groups than for the ground beetles in our study area, as the arthropod group dataset was characterized by smaller total inertia (Table 3). Despite these limitations, however, the variation explained by the various environmental characteristics can be compared within one dataset to assess the relative importance of the environmental factors (Økland 1999). Further, the stepwise forward selection procedure selects the 'best' variable at

each consecutive step, and hence the order in which the explanatory variables are selected also provides a ranking of their relative importance within one dataset (Ter Braak and Verdonschot 1995).

Ranking of environmental factors for plant assemblages

The results of our analyses suggest that plant species composition in our study area depends mainly on land use, closely followed by flooding characteristics (Table 3). The hedgerow included 10 plant species absent from the sheep and cattle grazing fields (Supplementary Material, Table S1), such as common hawthorn (*Crataegus monogyna*), oak (*Quercus robur*), common ash (*Fraxinus excelsior*) and elder (*Sambucus nigra*), which may explain why the hedgerow ranked first among the explanatory variables for plant species composition. Sheep grazing was also selected as significant explanatory factor (Table 2), indicating distinct differences in plant species composition between sheep and cattle grazing sites. This may result from a difference in animal density and hence grazing intensity, but also from a difference in grazing behaviour, as sheep are more selective than cattle (Sýkora et al. 1990). Sheep control the dominant grasses, thus allowing lower growing herbs to thrive (Sýkora et al. 1990). This may explain why species like common daisy (*Bellis perennis*) and white clover (*Trifolium repens*) were present almost exclusively in the sheep grazing fields (Supplementary Material, Table S1).

Despite the human interference with the hydrological regime of the river Nederrijn, flooding characteristics were nearly as important as land use for plant species composition. Segregation of plant species along a hydrologically defined gradient is a well-described phenomenon (Silvertown et al. 1999; Sýkora et al. 1988; Van Eck et al. 2004). Tolerance to flooding strongly differs between plant species and has been shown to range from 6 to over 60 days of total submersion for a selection of 20 grassland species commonly occurring in lowland river Rhine floodplains (Van Eck et al. 2004). Due to such differences in flooding tolerance, spatial variation in flooding duration is generally well reflected by differences in species composition. Our observations agreed well with flooding tolerance differences as observed by

Van Eck et al. (2004). Species identified as flood-tolerant, like *Elytrigia repens*, *Potentilla anserina*, *Potentilla reptans* and *Rumex crispus*, tended to occur mainly on the most flood-prone sites, whereas more sensitive species, like *Festuca rubra* and *Rumex acetosa*, occurred on less flood-prone sites (Supplementary Material, Table S1).

The forward selection procedure resulted in the total soil concentrations of As being selected as subordinate explanatory factor for the plant assemblages (Table 2). This does not necessarily imply that As has larger explanatory power than the other metals, as the soil metal concentrations were highly mutually correlated (Supplementary Material, Table S6). Moreover, the significant correlation between plant species composition and As could be a spurious one, given the relatively large number of potential explanatory variables relative to the number of sampling sites (see above). This would match the observation that the As soil concentrations measured in our study area (Table 1) are below the no-observed effect concentrations (NOECs) for plants that have been established for various European soils (Song et al. 2006). In order to be conclusive on the potential effects of metal contamination on plant species composition in river Rhine floodplain areas, a follow-up study would be needed.

Ranking of environmental factors for soil-dwelling arthropod assemblages

The terrestrial arthropod assemblages in our study area responded primarily to land use (Fig. 2). This is probably the result of indirect effects, i.e., via vegetation characteristics, as was shown in several previous studies (Garcia et al. 2010; Stoner and Joern 2004). As vegetation structure characteristics were included as separate explanatory variables in our analyses, the land use effect in our study may have been mediated by plant species composition. This hypothesis matches with a recent study showing that plant species composition consistently outperformed abiotic conditions as well as vegetation structure in explaining the taxonomic composition of arthropod assemblages (Schaffers et al. 2008).

Flooding explained a subordinate part of the variation in the ground beetle assemblages. This seems in contrast with other studies showing clear responses of ground beetle assemblages to flooding regimes (Bonn et al. 2002; Moran et al. 2012). However, these other studies covered considerable gradients in flooding influence, ranging from occasional to prolonged inundation. In the river Nederrijn, river dynamics are strongly reduced due to the sluices and groynes. Hence, clear flooding influence in our study area was present at the river margin only, and the majority of our study sites were hardly inundated (Supplementary Material, Table S1).

None of the arthropod assemblages was significantly related to soil metal contamination (Table 2, Fig. 2). Limited impacts of metal contamination on invertebrate fauna in river Rhine floodplains have been found before, for ground-dwelling organisms as well as burrowing invertebrates like earthworms (Ma et al. 2004; Rozema et al. 2008). Metal exposure concentrations for terrestrial invertebrates were generally below or close to (tentative) toxicity thresholds (Hobbelen et al. 2004; Notten et al. 2005; Schipper et al. 2008). This indicates that current bio-available metal concentrations in the floodplain top-soil are too low to induce detectable toxic effects in the organisms exposed. Flooding lowers the redox potential and increases the pH of the soil, notably through the deposition of carbonate-rich sediments (Kashem and Singh 2001). This reduces the bioavailability of sediment-bound heavy metals, thus limiting accumulation in biota and diminishing toxicological effects (De Jonge et al. 1999; Hobbelen et al. 2004; Hobbelen et al. 2006; Kashem and Singh 2001).

Concluding remarks

Summarizing, we used canonical correspondence analysis (CCA) and variance partitioning to disentangle and rank the influences of multiple environmental factors on terrestrial plant and soil-dwelling arthropod assemblages in a lowland floodplain area of the river Rhine in The Netherlands. Plant as well as arthropod assemblages were primarily related to land use, which explained 19% to 30% of the variation in taxonomic composition. For plant species

composition, flooding characteristics were nearly as important as land use. Soil metal contamination was selected as explanatory factor for the plant assemblages only (3% of variation explained). We conclude that the taxonomic composition of terrestrial plant and arthropod assemblages in our study area is related to land use and flooding rather than soil metal contamination.

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Tables

Table 1: Environmental characteristics measured in the 'Wolfswaard' river floodplain area (n = 30).

Category	Variable	Mean	Min	Max
Flooding characteristics	Distance to river (m)	225	102	347
	Elevation (m amsl)	8.41	7.00	9.64
	Flooding duration (days/year)	10	1	79
Physical-chemical soil properties	Clay content (< 2 µm; %)	6.6	1.8	11.3
	Silt content (2 - 64 µm; %)	59.4	17.3	84.0
	Sand content (> 64 µm; %)	7.9	7.9	80.9
	Median grain size (d50; µm)	54	9	292
	pH	7.6	7.3	8.0
	Soil organic matter (SOM; %)	11.4	5.3	16.1
Vegetation structure [a]	Vegetation cover (%)	91	40	100
	Vegetation height (m)	0.31	0.05	1.10
Soil metal contamination	As (mg/kg dw)	8.17	3.30	14.7
	Cd (mg/kg dw)	1.18	0.30	3.20
	Cr (mg/kg dw)	42.8	12.8	103
	Cu (mg/kg dw)	35.9	12.3	76.8
	Ni (mg/kg dw)	21.8	10.8	35.6
	Pb (mg/kg dw)	77.4	29	148
	Zn (mg/kg dw)	205	66.3	413
	Cd - dissolved (mg/l)	0.189	0.0392	0.481
	Cu - dissolved (mg/l)	11.1	4.66	21.6
	Pb - dissolved (mg/l)	1.09	0.508	1.64
	Zn - dissolved (mg/l)	24.6	7.11	45.8

[a] Vegetation cover and height refer to the herb layer of the vegetation.

Table 2: Significant explanatory variables ($p < 0.05$) for terrestrial plant and soil-dwelling arthropod assemblages in the 'Wolfswaard' floodplain area, according to a CCA with manual forward selection procedure as available in Canoco.

Biotic assemblages	Step	Explanatory variables [a]	F-statistic	*p*-value [b]	VIF [c]
Plant species	1	Hedgerow	5.77	0.001	2.17
	2	Flooding duration	4.11	0.001	6.26
	3	Sheep grazing	3.65	0.001	3.10
	4	Elevation	2.41	0.001	5.35
	5	Vegetation height	2.29	0.001	1.58
	6	Distance to river	1.73	0.025	4.51
	7	Total As concentration in soil	1.70	0.035	3.69
Ground beetle species	1	Cattle grazing	4.39	0.001	1.95
	2	Sheep grazing	2.94	0.001	1.85
	3	Flooding duration	3.08	0.001	1.22
	4	Vegetation height	1.53	0.043	1.09
Ground beetle genera	1	Cattle grazing	5.88	0.001	1.90
	2	Sheep grazing	3.61	0.001	1.79
	3	Flooding duration	2.47	0.003	1.23
	4	Vegetation height	1.65	0.042	1.09
Beetle families	1	Cattle grazing	5.19	0.001	1.64
	2	Sheep grazing	3.09	0.002	1.71
	3	Vegetation height	2.33	0.005	1.06
Arthropod groups	1	Hedgerow	12.18	0.001	1.32
	2	Vegetation cover	6.30	0.006	1.32

[a] Vegetation cover and height refer to the herb layer of the vegetation.

[b] The significance was evaluated with Monte Carlo permutation tests involving 1000 permutations.

[c] VIF = variance inflation factor

Table 3: Variance partitioning results for terrestrial plant and arthropod assemblages in the 'Wolfswaard' study area.

Biotic assemblage	Explanatory variables [a]	Sum canonical eigenvalues	Sum unconstrained eigenvalues [b]	Variance explained (%)	*p*-value
Plant species	all	1.33	2.61	55	0.001
	flooding	0.16	1.75	17	0.001
	land use	0.42	1.78	19	0.001
	vegetation	0.12	1.40	5	0.006
	contamination	0.09	1.27	3	0.035
Ground beetle species	all	0.66	1.92	34	0.001
	flooding	0.16	1.15	8	0.016
	land use	0.42	1.68	22	0.001
	vegetation	0.09	1.34	4	0.043
Ground beetle genera	all	0.43	1.13	38	0.001
	flooding	0.07	0.78	6	0.008
	land use	0.31	1.02	27	0.001
	vegetation	0.05	0.75	4	0.047
Beetle families	all	0.17	0.56	31	0.001
	land use	0.13	0.52	24	0.001
	vegetation	0.04	0.42	6	0.009
Arthropod groups	all	0.05	0.12	43	0.001
	land use	0.04	0.10	30	0.001
	vegetation	0.02	0.08	13	0.005

[a] 'All' refers to all explanatory variables that were selected as significant ($p < 0.05$) in the exploratory CCA analyses (see Table 2).

[b] The sum of the uncontrained eigenvalues with all environmental variables included represents the total inertia.

Figures

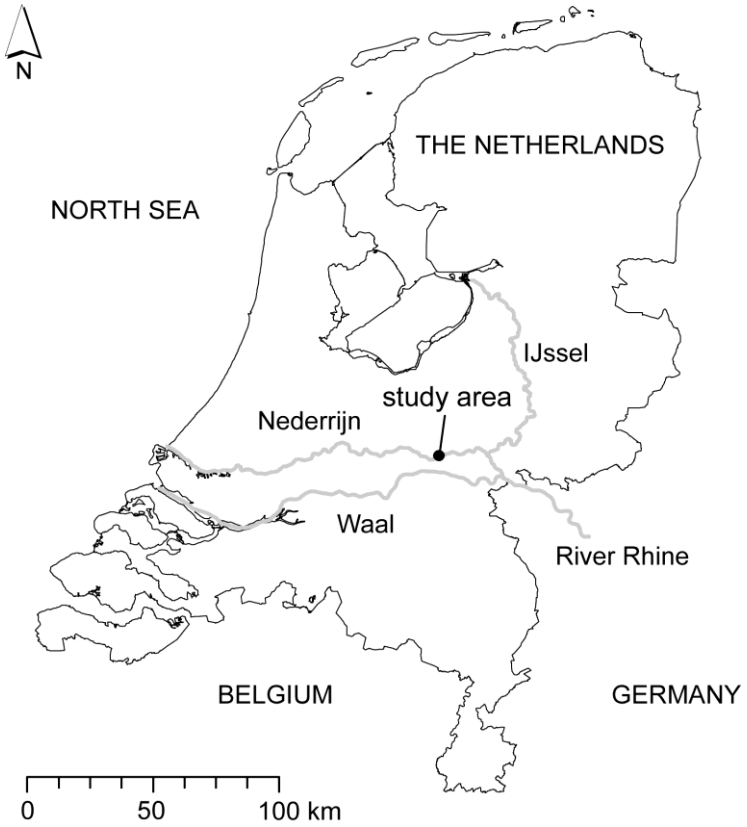

Fig. 1: Location of the 'Wolfswaard' study area.

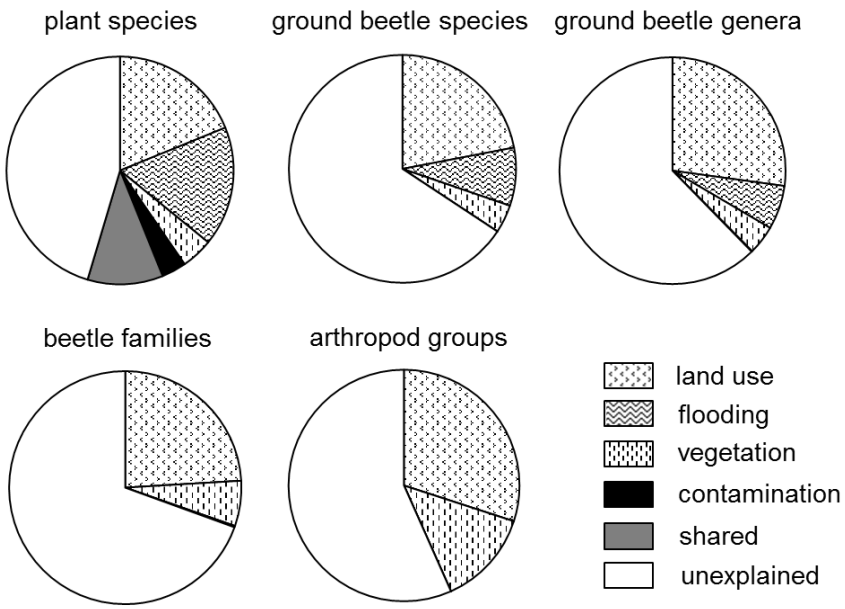

Fig. 2: Variance partitioning with canonical correspondence analysis (CCA) for terrestrial plant and soil-dwelling arthropod assemblages in the 'Wolfswaard' study area. 'shared' refers to variation in taxonomic contribution attributed to joint effects of environmental factors belonging to different categories.