ORIGINAL RESEARCH

Unravelling direct and indirect effects of river-floodplain connectivity on biodiversity: insights from the Elbe River floodplains

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Abstract

River-floodplain connectivity is a critical ecological process influencing biodiversity and ecosystem functions. However, the impact of changes in this connectivity, particularly its loss, on biodiversity in floodplains remains insufficiently studied. This study aimed to assess how connectivity influences biodiversity metrics and whether it directly affects biodiversity indices for selected species groups, beyond its indirect influence through environmental variables. We used structural equation modelling to separate the direct effects of connectivity on plant and carabid beetle diversity from indirect effects mediated by flooding regimes, soil properties, and pollution in the Elbe River floodplains. We compared results from connected and decoupled floodplain sections to understand how these relationships change when connectivity is lost. Connectivity showed significant direct effects on most biodiversity metrics for both plants and carabids. For carabids, higher connectivity was associated with lower species richness and higher proportions of indicator species for wet grasslands, independent of intermediate factors such as flooding or soil conditions. For plants, higher connectivity was associated with higher species and functional richness, though only through indirect effects. Overall, connectivity had a positive impact on biodiversity, fostering higher species and functional diversity without leading to highly specialised, species-poor communities. Additionally, the models were largely consistent between connected and decoupled floodplains, suggesting that decoupling does not fundamentally alter the ecological mechanisms governing biodiversity, and that recovery through restoration is possible. Our findings highlight the complex role of river-floodplain connectivity in shaping floodplain biodiversity. Maintaining and restoring this connectivity is essential for promoting diverse and resilient floodplain ecosystems.

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Introduction

Floodplains, forming the ecotone between river and land, host a diverse array of both aquatic and terrestrial biota that have evolved to thrive under the exceptional conditions of recurrent flooding alternating with periods of drought. Understanding the intricate ecological dynamics of floodplain ecosystems is not only driven by a fundamental curiosity in the mechanisms that govern species distribution and diversity, but also has practical implications for management, conservation and restoration strategies of rivers and their adjacent land. This is increasingly relevant as floodplains are among the most threatened ecosystems, affected by river degradation and encroachment of intense land use (Koenzen et al. 2021; Tockner and Stanford 2002). Anthropogenic alterations to river morphology such as channelisation or dam construction have fragmented and decoupled floodplain systems from their natural hydrological regimes, challenging the integrity and resilience of floodplain ecosystems. Much attention in floodplain biodiversity research and the importance of river-floodplain connectivity has been focused on aquatic communities (Gallardo et al. 2009; Larsen et al. 2019; Paillex et al. 2009), while the impact of floodplain degradation and decoupling on terrestrial biota is less well understood.

Studies examining the effects of floodplain decoupling predominantly stem from the 1980 s and 90 s when the recognition of this phenomenon emerged (Bornette et al. 1996; Miller 1985; Bravard et al. 1997; Marston et al. 1995). They showed that river incision significantly reduces flooding disturbance (Marston et al. 1995) and can lead to the loss of pioneer species and an increasing terrestrialization of floodplain vegetation communities (Bornette et al. 1996; Marston et al. 1995). However, the methodologies and analytical tools available at that time were limited in their ability to comprehensively unravel the underlying mechanisms. In the following decades, studies examining the success and failure of restoration measures revealed the remarkable resilience and rapid recovery that terrestrial floodplain organisms exhibit following river restoration (Januschke et al. 2011, 2014; Pilotto et al. 2019). However, restoration success is not consistent across functional groups, metrics of biodiversity or scales of restoration (Göthe et al. 2016; Pilotto et al. 2019; Lorenz et al. 2018). While these studies explain the positive effects of restoration on biodiversity with the increased habitat heterogeneity following flooding dynamics, a positive heterogeneity-diversity relationship has not always been observed (Lundholm 2009). What exactly drives floodplain biodiversity and the impacts of degradation and restoration are not fully understood. With new computational methods that exist nowadays we have the chance to reconsider a principal question in conservation science: how does river-floodplain connectivity– and a lack thereof– affect the environmental conditions in the floodplain and ultimately species diversity?

River-floodplain-connectivity, i.e. lateral hydrological connectivity describes the transfer of matter, energy, and/or organisms between a river and the adjacent floodplain (Pringle, 2001; Ward, 1989). This transfer is obviously important for floodplain communities: a spot that is better connected to the river will be more frequently flooded; on patches close to the river and on frequently flooded spots plants will be removed more often through shear disturbance or suffocation. Flooding provides sediment, nutrients, pollutants and plant propagules or dislocated animals (Garssen et al. 2015; Poff et al. 1997). Repeated flooding can favour species adapted to high disturbance (Fournier et al. 2015). Contrarily, the decoupling of a floodplain from its river through an embankment or incision reduces hydrological dynamics

(Amoros and Bornette 2002), sedimentation and erosion (Amoros et al. 2005), thereby also modifying the vegetation, e.g. by allowing the colonisation of zones close to the shoreline or the disappearance of species adapted to alluvial dynamics (Santos et al. 1997). The dispersal and retention of plant propagules depend on flooding events but also on stream morphology and sedimentation (Bendix and Hupp 2000; Engström et al. 2009). Similarly, carabid communities in floodplains are governed by flooding regime and disturbance that create habitats and favour species with high dispersal capacity and larval stages outside the flood periods (Bonn et al. 2002). Soil characteristics and vegetation structure impact community composition (Schaffers et al. 2008), presence of rare riparian species (Lambeets et al. 2009) and functional richness of carabids (Pakeman and Stockan 2014). Pollution of the soil through toxins such as heavy metals or an excess of nutrients impact species richness and diversity of floodplain vegetation (Schipper et al. 2011). Altered vegetation can in turn affect arthropods by removing or adding host plants or prey animals symbiotic with certain plant species. These mechanisms are examples of *indirect* effects of connectivity on biodiversity, through changes in hydrology and soil properties. *Direct* effects act on the biological communities by interfering in biological processes such as competition or colonisation, without the mediation of any intermediate abiotic factors. However, in restoration efforts aiming to increase river-floodplain-connectivity, the impacts that are most commonly anticipated are those through indirect effects such as increased habitat heterogeneity. It remains unclear if and how increased connectivity directly affects floodplain biodiversity.

This study seeks to uncover how connectivity, flooding dynamics and local habitat conditions together shape terrestrial biodiversity in floodplains through direct and indirect pathways. It further addresses the impacts that river-floodplain decoupling has on these relationships. Species diversity is represented by plants and carabid beetles (Coleoptera: Carabidae) as model organism groups, as they differ in mobility and dispersal modes and are thus likely to be differently affected by floodplain decoupling. Both plants and carabids are valuable indicators for the ecological conditions of temperate floodplains (Scholz et al. 2009; Stammel et al. 2022; Gerisch et al. 2006). In temperate European floodplains, plant communities range from aquatic vegetation and flood-adapted riparian species to willow–alder–ash formations, oak–elm forests, shrubs, and a variety of grasslands (Ellenberg 1996). Each of these communities has distinct requirements regarding moisture levels, soil types, and nutrient availability, as well as varying tolerances to flooding. Similarly, while carabids are widely spread in floodplains, many species have narrow ecological niches with clear habitat preferences (Bräunicke and Trautner 2009).

To disentangle the direct and indirect effects of environmental variables on biodiversity and on each other we employed a structural equation modelling approach. We addressed five different biodiversity metrics of vascular plants and carabids in floodplain sections along the Elbe River in East Germany. We furthermore evaluated whether environment-biodiversity relationships varied between coupled and decoupled floodplain sections that differ in their degree of connectivity. The environmental variables considered included connectivity, flooding regime, soil properties, soil pollution, and, in the case of the carabids, vegetation structure. The biological metrics included species richness, functional richness, functional redundancy, indicators of periodically wet grassland and taxon rareness.

As disturbance-diversity relationships often peak at intermediate disturbance levels (Jurkiewicz-Karnkowska 2015; Tanentzap et al. 2013), increasing connectivity to the river and associated flood disturbance (in both frequency and/or intensity) may decline overall

species diversity (Zheng et al. 2021). At the same time, other biodiversity metrics may be positively related to connectivity and disturbance, e.g. the number of rare species specialised to disturbed conditions, or indicator species for wet habitats (Herben et al. 2018; Pedley and Dolman 2014). Functional richness describes the volume that all species of a community take up in multidimensional trait space. It is larger the more different the most "extreme" the traits of species in the community are (Villéger et al. 2008). In systems of very high disturbance intensity that exert a strong filter for only specific, well-adapted trait sets, functional richness can become smaller compared to low or moderate levels of disturbance (Mouillot et al. 2013). Functional redundancy, the extent to which species of a community have the same or similar trait sets, is typically high in frequently disturbed ecosystems (Biswas et al. 2023), because of the strong filter for specific trait sets (Mouillot et al. 2013).

In light of these considerations, we addressed the following hypotheses:

i)   Connectivity is not directly associated with plant and animal diversity, but indirectly via its influence on flooding regime and local environmental conditions such as soil properties.

ii)   Metrics of "general biodiversity", i.e., species and functional richness, are negatively associated with connectivity.

iii)   Metrics of floodplain or disturbance specificity, i.e. taxon rareness, indicator species of periodically wet grassland and functional redundancy, are positively associated with connectivity.

iv)   There are differences in the causal pathways between coupled and decoupled floodplains.

Methods

Field sampling

With a catchment area over 148,000 km², the Elbe River is the fourth largest river in Europe. Its mean annual discharge at the mouth measures 861 m³/s (Pusch et al., 2022). In contrast to many other floodplains in Germany, large parts of the Elbe's active floodplains remain in a near-natural state and can stretch several kilometres wide (Koenzen et al. 2021). Longitudinal dykes are typically positioned distant from the river; therefore, disconnections between the river and floodplain are primarily caused by incision due to river training and sediment deficits.

Our study focused on four study regions along the middle Elbe River: two decoupled floodplain sections ("Elsnig": river kilometres 167 to 168 and "Bösewig": kilometres 188 to 191), and two coupled sections ("Schönberg-Deich": kilometres 436 to 439 and "Jasebeck": kilometres 512 to 514). In Elsnig and Bösewig, upstream dams, bank reinforcement structures, and groynes have disrupted natural river dynamics, leading to significant riverbed incision in that stretch of the Elbe River (Faulhaber, 1995). Consequently, the riparian zones prone to frequent flooding are narrow and flanked by steep embankments, effectively disconnecting most of the floodplain from the river. Flooded areas in both regions primarily occur within a single cut-off meander in each region, while the more elevated, drier portions of the floodplain serve as mowing meadows and partially as cattle pastures. Conversely, the Schönberg-Deich and Jasebeck study regions further downstream exhibit a lower stream

slope, resulting in broader riparian zones that extend further inland. Here, river and flood-plain remain hydrologically well-connected. Both study regions feature frequently flooded patches, dispersed across oxbows and depressions throughout the regions.

In each of the four study regions, we sampled a total of 20 plots, resulting in 40 plots each for coupled and decoupled sections. Based on discharge data from the past 30 years and a digital elevation model (Weber, 2020), an inundation gradient ranging from 0 to >300 days per year was layered on top of all four study regions with the help of the R-package *hydflood* (Weber et al. 2023). This inundation gradient was broken down into three mois-ture classes through cluster analysis: dry floodplain ("dry"; 1–40 days/a inundated), wet floodplain ("wet"; 41–200 days inundated) and riparian zone ("riparian"; 201–355 days and located at the riverbank). The sampling plots were distributed across the whole floodplain area and evenly distributed among these three classes. Given that sampling plots were posi-tioned along the same inundation gradient in both the coupled and decoupled sections, the more natural flooding patterns in the coupled sections were not directly represented in our sampling design. Instead, by standardising our sampling approach across the same gradi-ent, we aimed to capture alterations in the regional species pool resulting from floodplain decoupling. Due to continuous rainfall during the spring and early summer of 2021, access to some plots for carabid sampling was restricted. Consequently, the total number of plots included in our analyses of carabids was only 78 ($n_{coupled}$ = 39, $n_{decoupled}$ = 39), while it was the total 80 for plants.

Biological data

Our sampling design mirrored previous field studies conducted along the Elbe River (Henle et al. 2006): on each study plot, we delineated a 25 m^2 rectangle for plant sampling and installed five Barber traps on a straight line, spaced 5 m apart, for carabid sampling. Plant surveys were carried out in spring and summer 2021 using an extended Braun-Blanquet Scale (Braun-Blanquet 1964). The Braun-Blanquet scale was transformed to numeric cover values for statistical analysis. The Barber traps, consisting of 200 ml plastic cups with a 7 cm opening diameter filled with 100 ml of 7% acidic acid and a small amount of detergent to reduce surface tension, were exposed for two weeks each in May and September 2021. The sampling periods in spring and autumn mirror the windows of activity for spring- and autumn breeding species, enabling the comprehensive collection of all present species. Ground beetles were then identified to the species level following Müller-Motzfeld (2006).

Abiotic data

On each study plot, a soil sample of the upper soil layer (0–10 cm depth) was taken, consist-ing of five randomly distributed subsamples excavated using an Edelmann auger (Hoyer and Weber 2022). Soil samples were sieved and separated into 12 grain size fractions. Topsoil metals (arsenic, lead, cadmium, chromium, copper, nickel, mercury, zinc) were analysed in the soil fraction <63 μm; organic micropollutants (polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs) and organochlorine pesticides) in the fraction <2 mm. For more detailed information see (Hoyer and Weber 2022). Using the *hydflood* and *elbe1 d* packages (Weber et al. 2023), abiotic variables were computed to describe the flood-ing regime and lateral hydrological connectivity of each plot. Hydrological connectivity and

flooding regime are, of course, closely related. We defined the flooding regime as variables describing the duration of inundation in a given spot, i.e. it is a summed-up measure of total received flooding. Contrary to this, variables of connectivity are of a more geographical nature, describing the morphology of the floodplain and thereby giving a measure of how easily water from the river reaches into the floodplain. A list of all environmental variables along with the scale at which they have been recorded and if they were computed or collected in the field, is given in Table 1.

Data analysis

Response metrics

Analyses were performed in R (R Core Team 2024). We built structural equation models (SEM) with five biodiversity metrics as responses for both plants and carabids, namely: taxonomic species richness, taxon rareness, indicator species for periodically wet grassland, functional richness and functional redundancy. Taxonomic species richness is simply the number of species present in a given study plot. Taxon rareness per plot was calculated analogous to the endemicity index proposed by Crisp et al. (2001) and Linder (2001). The index is calculated by weighting each species by the inverse of its range (the number of sites in which it is present) and summing the weights of all species present in a given site, before dividing this number by the total number of species in the site, thereby making the index independent of species richness. A list of indicator species for periodically wet grassland in the Northeastern ecoregion of Germany, in which the Elbe River is located, was taken from Januschke et al. (2023). As a response variable in our models, we calculated the share of these indicator species in the total community of a given plot and named this variable Ind-PWG. Functional richness is the amount of functional space occupied by the organisms of a sample unit (Mason et al. 2005). Higher functional richness values indicate a larger occupied trait space volume. If functional richness is low, the variation of the species' traits in the community is low. Functional richness was calculated from the framework by Villéger et al. (2008) as the volume in multidimensional trait space that the species of a community (one plot) take up. For this, we considered traits that reflect the adaptation to flooding disturbance of the species. For plants, that was CSR strategy (competitors - C; tolerant to stresses - S and ruderals - R) according to Grime (1974; 1979), lifespan (i.e., annual, biannual or poly annual), dispersal syndrome (i.e., the vector), and leaf anatomy. Trait data was derived from BIOLFLOR (Kühn et al. 2004) and LEDA (Kleyer et al. 2008) databases, retrieved through the TRY database (Kattge et al. 2020). To determine a single trait value for each species, we selected the most frequently occurring trait, excluding any "no entry" data. Entries representing similar trait manifestations were standardised into broader categories (e.g., "bal-lochoreous" and "blastochoreous" dispersal were both classified as "autochoreous"). For carabids, we selected the traits wing morphology (i.e., winged, wingless, or dimorphic), overwintering strategy (as larvae, as adult, or both forms occurring) and body size. A spe-cie's body size was calculated as the mean between the maximum and minimum body size found in the literature. Trait data was obtained from carabids.org with gaps filled in using additional literature (Andersen 2011; Lindroth and Bangsholt, 1985–1986; Matalin 2007). The lists of plant and carabid species traits used for further analysis can be found in Online Resource 1 and 2, respectively. Functional richness, as well as functional redundancy, were

Table 1 Environmental variables included in the analysis. Information is given whether a variable was recorded in the field (and/or result of subsequent laboratory analysis) or computed from a digital elevation model, and which composite variable for SEM Building they informed

Environmental variable	Unit/resolution scale	Recorded in the field or computed	Included in composite variable
Inundated area at discharge MHQ	[%]/hectometre	Computed	Connectivity
Difference in water levels between discharge MNQ and MHQ	[m]/hectometre	Computed	Connectivity
Distance to the water body at discharge MQ along the flow path	[m]/study plot	Computed	Connectivity
Airline distance to the river axis	[m]/study plot	Computed	Connectivity
Height above water level at discharge MHQ	[m]/study plot	Computed	Connectivity
Average inundation days per year in the last 30 years (1990–2020)	[d/y]/study plot	Computed	Flooding regime
Inundation days per year in 2021	[d/y]/study plot	Computed	Flooding regime
Fine gravel content in the upper soil (grain size fraction 2–63 mm)	[%]/study plot	Field recorded (soil sampling)	Soil properties
Sand content in the upper soil (grain size fraction 0.063–2 mm)	[%]/study plot	Field recorded (soil sampling)	Soil properties
Silt content in the upper soil (grain size fraction 0.002–0.063 mm)	[%]/study plot	Field recorded (soil sampling)	Soil properties
Clay content in the upper soil (grain size fraction <2 mm)	[%]/study plot	Field recorded (soil sampling)	Soil properties
Plant-available nutrients in the upper soil (phosphorus, potassium, magnesium, ammonium, nitrate)	[mg/100 g]/study plot	Field recorded (soil sampling)	Soil properties
Soil pH (in water)	/study plot	Field recorded (soil sampling)	Soil properties
Metal load in the upper soil (arsenic, lead, cadmium, chromium, copper, nickel, mercury, zinc)	[mg/kg dry matter]/study plot	Field recorded (soil sampling)	Pollution
Load of polyaromatic hydrocarbons in the upper soil (PAH; naphthalene, acenaphthylene, acenaphthene, fluorene, phenanthrene, anthracene, fluoranthene, pyrene, benz[a]anthracene, chrysene, benzo[a]pyrene, dibenzo[a, h]anthracene, benzo[b]fluoranthene, benzo[k]fluoranthene, indeno[1,2,3-cd]pyrene, benzo[ghi]perylene	[mg/kg dry matter]/study plot	Field recorded (soil sampling)	Pollution
Load of chlorinated diphenyls (PCB; PCB28, PCB52, PCB101, PCB118, PCB138, PCB153, PCB180, PCB6) in the upper soil	[µg/kg dry matter]	Field recorded (soil sampling)	Pollution
Load of organochloride pesticides (α-hexachlorocyclohexane, β-hexachlorocyclohexane, γ-hexachlorocyclohexane, o,p'-DDD, p,p'-DDD, o,p'-DDE, p,p'-DDE, o,p'-DDT, p,p'-DDT, 1,2,3-trichlorobenzene, 1,3,5-trichlorobenzene, 1,2,4-trichlorobenzene, 1,2,3,4-tetrachlorobenzene, 1,2,3,5-tetrachlorobenzene, 1,2,4,5-tetrachlorobenzene, pentachlorobenzene, hexachlorobenzene, hexachlorbutadiene) in the upper soil	[µg/kg dry matter]	Field recorded (soil sampling)	Pollution
Vegetation cover	[%]	Field recorded (vegetation sampling)	Vegetation structure

Table 1 (continued)

Environmental variable	Unit/resolution scale	Recorded in the field or computed	Included in composite variable
Average vegetation height	[cm]	Field recorded (vegetation sampling)	Vegetation structure
Vegetation species richness		Field recorded (vegetation sampling)	Vegetation structure

calculated using the R package *mFD* (Magneville et al. 2022). For the computation of functional redundancy, species are gathered in so-called functional entities, groups of species with the same trait values for categorical or ordinal traits (Mouillot et al. 2014). The index is then calculated as the average number of species per functional entity, i.e., reflecting how many species in a community perform similar functions.
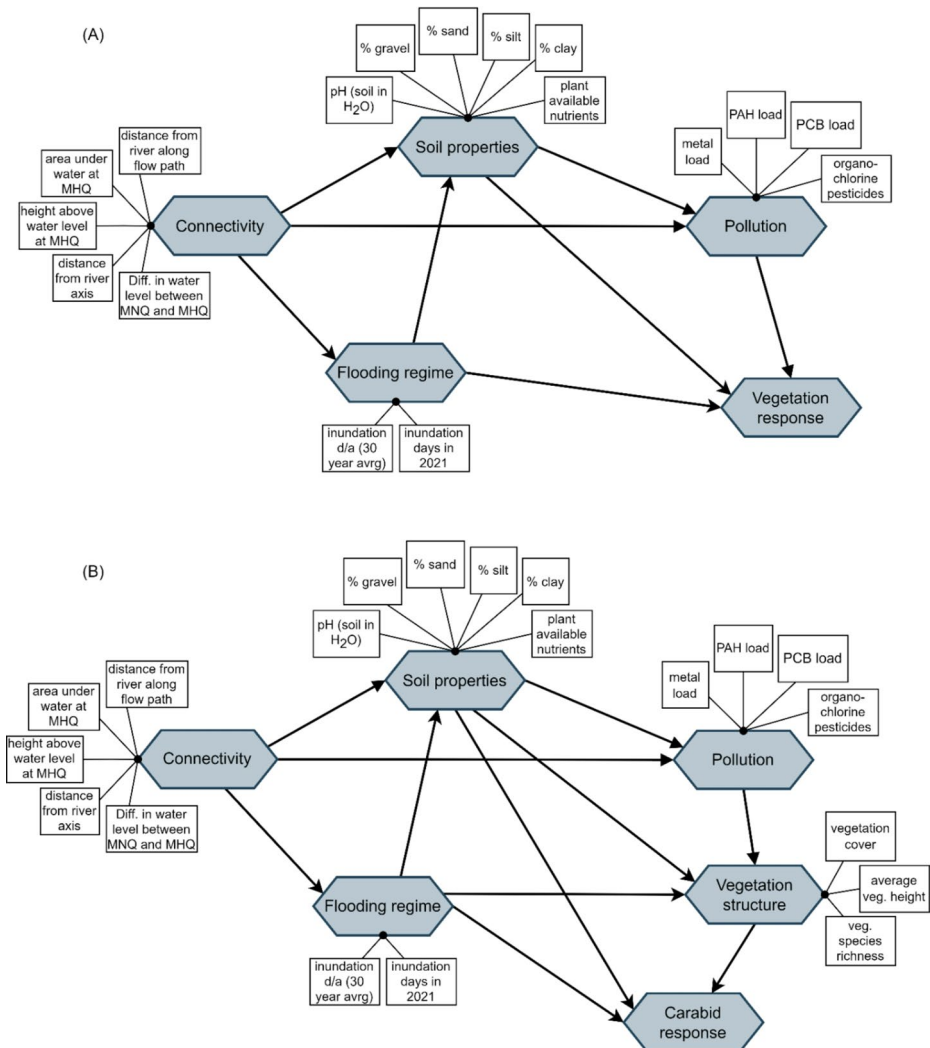
Structural equation models

Structural Equation Modelling (SEM) is a statistical technique used to analyse the complex relationships between variables. It allows users to examine and distinguish the direct as well as any indirect cascading effects of multiple independent variables on a dependent variable through multiple paths. SEM combines elements of factor analysis and multiple regression within a single framework, enabling the testing of theoretical models and hypotheses. These hypothesised relationships are commonly depicted in a path diagram where arrows show the directional association between observed or latent variables. There are three powerful differences to simple regression models based on correlation and regression coefficients: the paths in an SEM represent hypothesised *causal* associations (Pearl 2012), variables in the model can be both predictors and responses, and the effect of one variable on another can be distinguished into direct and indirect effect components.

To accommodate different non-linear relationships and the use of mixed effect models, we opted for a local, or piecewise, estimation approach (Lefcheck 2016; Shipley 2000). This contrasts the traditional, global estimation approach of SEMs in that each path in the model is modelled individually. This frees the analysis from the assumption that all observations are independent, enabling the use of different distributions and allowing for smaller sample sizes, as the degrees of freedom need only be enough to fit any single component of the model (Shipley 2000). We modelled the individual paths using generalised linear mixed models with moisture class ("dry", "wet", "riparian") as random effect to account for pre-selecting the sampling plots in those moisture classes. Models with environmental variables as response were modelled on a gaussian distribution, while in the case of biotic metrics we had to account for the different data structures and formation processes. Namely, species richness (count data) was modelled on a negative binomial distribution, taxon rareness and wet grassland indicators (percentages) on a gaussian distribution with a logit link, functional richness and functional redundancy (positive, continuous data) on a gamma distribution. Individual models were fitted using the *glmmTMB* package (Brooks et al. 2023) and evaluated using the *DHARMa* package in R (Hartig and Lohse 2017).

Structural equation modelling relies heavily on an informed hypothesised causal structure of the studied system. The analysis starts with the formulation of this hypothesised structure (Fig. 1). In a piecewise SEM approach, each drawn path is then calculated as a single regression model. A test of directed separation tests for the significance of so-called independence claims, i.e. the "claim" that two variables that do not have a direct path between them, are in fact independent from each other, while considering the indirect association they may have through another variable (Shipley 2000). If two variables have a significantly correlated error term, the test yields a p-value <0.05. In that case, the user

Fig. 1 Structure of the structural equation model performed with (**A**) five plant and (**B**) five carabid diversity metrics as response. Variables in rectangles are measured or computed variables that together inform composite variables depicted in grey hexagons. The missing paths between Connectivity and the response metric, between Flooding regime and Pollution, and between Connectivity and Vegetation Structure were modelled where appropriate but are not shown for clarity of the hypothesised effect structure

needs to make an informed decision whether this path is reasonable to assume, i.e., it is (potentially) ecologically meaningful and should therefore be included in the model, or whether the two variables are more likely to be structured by the same background process but without a causal association. If the latter is the case, the significant association between the two variables can be included in the model as a correlated error term. Another aspect that makes SEMs a powerful tool in ecology is that the method can accommodate the use of latent or composite variables, i.e. unmeasurable variables that distil several measured (manifest) variables into a discrete, conceptual variable. For example, pH, grain sizes and nutrient content are measurable variables that all represent the concept of physical soil characteristics. We created five composite variables ("connectivity", "flooding regime", "soil properties", "pollution" and "vegetation structure") by adding up the weights of all manifest variables comprising the respective composite. Weights were derived from generalised linear mixed models of each manifest variable and the respective biodiversity metric as a response. The composite variable "connectivity" was constructed using the distance from the river of a given plot both along the flow path of the water and from the river axis (airline), the area of the plot that is inundated during MHQ discharge, the height of the plot above water level during MHQ discharge, and the difference between water levels at a plot between MNQ and MHQ discharge. "Flooding regime" was constructed using the average inundation days per year in the last 30 years and the inundation days per year in 2021. "Soil properties" was constructed using pH, shares of gravel, sand, silt and clay and the sum of plant-available nutrients (phosphorus, potassium, magnesium, ammonium, nitrate). Pollution was constructed using the load in the soil of polycyclic aromatic hydrocarbons (PAHs), chlorinated biphenyls (PCBs), metals and organochloride pesticides. Lastly, the composite for "vegetation structure" for use in the carabid SEMs was constructed using vegetation cover, species richness and average vegetation height (Table 1). All environmental variables were scaled through z-transformation prior to analysis in the SEM to remove the influence of measuring units of the variables on the creation of composite variables.

SEMs were built using the *piecewiseSEM* package in R (Lefcheck 2016) to allow the local estimation of the models, i.e., the modelling of each path separately. To evaluate overall model fit we considered Fisher's C and looked at the R^2 value of the response metric to evaluate how well the total model could explain it. Indirect effects are computed by multiplying all path coefficients along the way from predictor to response variable and adding up the results from all possible ways that lead from the chosen predictor to the response. For the calculation of indirect effects, we considered all compound paths that had at least one significant path in them. We proposed that plant diversity metrics would be directly affected by flooding regime, physical soil characteristics and soil pollution (Fig. 1a). In the model for carabid diversity metrics, we included vegetation structure as a directly acting predictor, next to flooding regime and soil characteristics (Fig. 1b). In both models, however, we did not include a direct path from connectivity to the response metric, suggesting that connectivity acts only indirectly through cascading effects on the other environmental variables.

To test whether the path coefficients in the SEMs differed between coupled and decoupled floodplain sections, we employed a multigroup analysis of the models. In each path model individually, a grouping variable is included as an interaction term. If this interaction is significant, this particular model is free to vary between the groups provided by the grouping variable. In the present study, the grouping variable was "connectivity state" with the two levels "coupled" and "decoupled". If the interaction is not significant in a path model,

the estimate from the global model (without the grouping variable) is used. The decoupled floodplain sections are by definition less connected to the river than the coupled sections. However, since the study plots in each section are distributed across the whole floodplain covering also riparian zones and the banks of floodplain water bodies, even in the decoupled sections there is a gradient of connectivity between the plots that allowed us to perform the SEM modelling.

Results

In total 202 plant and 11,798 carabid individuals from 146 species were recorded.

Overall model fit

The structural equation models adequately reflected the main causal relationships between the environmental variables and the respective biological metric. Except for one, all models had adequate fit with non-significant Fisher's C statistics, i.e., the hypothesized (modelled) structure did not deviate significantly from the structure of the data (Table 2). The SEM with vegetation taxon rareness as response was fully saturated (all possible paths between variables were included) to resolve significant independence claims, making the calculation of Fisher's C impossible due to 0 degrees of freedom on the model.

The share of explained variation R^2 of the biological metrics ranged from 0.27 to 0.58 (Table 2).

Table 2 Goodness-of-fit measures for all SEMs including Fisher's C, the degrees of freedom and the overall p-value (significant p-value indicating that the postulated model deviates significantly from the data on which it is based). The share of explained variance for each biological response metric R^2 is given

	R^2 biological response	Fisher's C statistic	Degrees of freedom	p-Value
Vegetation				
Species Richness	0.58	4.98	4	0.289
Taxon rareness %	0.31	NA	0	NA
Indicators of periodically wet grassland %	0.5	3.897	2	0.143
Functional Richness	0.27	7.807	4	0.099
Functional Redundancy	0.29	2.081	2	0.353
Carabids				
Species Richness	0.56	2.033	4	0.73
Taxon rareness %	0.41	5.692	4	0.223
Indicators of periodically wet grassland %	0.32	4.1	6	0.663
Functional Richness	0.46	4.828	4	0.305
Functional Redundancy	0.48	1.949	6	0.924

Connectivity is directly associated with many biological responses

Significant correlated error terms between connectivity and the respective biological metric were identified in 8 of the 10 models, and between pollution and flooding in 4 models. Where significant, the missing paths were included in the model as it is reasonable to assume that the correlated error terms are actually based on causal associations. The only two metrics on which connectivity did not have a direct effect were taxonomic and functional richness of plants. The paths between vegetation structure and connectivity and between pollution and the carabid biological response, which were not included in the hypothesized model structure, did not yield a significant test of directed separation in any of the 5 carabid SEMs, indicating that they were rightfully excluded.

Differential effects of connectivity on biodiversity metrics observed

For plants, species richness and functional richness were positively correlated with connectivity (Table 3). Species richness was well explained by the model ($R^2 = 0.58$; Table 2) with the positive indirect effect of connectivity being governed by its cascading effect on flooding and soil. The positive effect of connectivity on functional richness ($R^2 = 0.27$; Table 2) was also entirely governed by its indirect effects (Table 3). Connectivity had a negative, mainly direct, effect on plant taxon rareness ($R^2 = 0.31$; Table 2) as well as on the share of indicator species for periodically wet grassland ($R^2 = 0.5$; Table 2) in the coupled floodplain sections (Table 3). Additional to the direct effect, connectivity also affected the share of indicator species in the coupled floodplain sections indirectly through soil and pollution. Conversely, connectivity had a positive, though non-significant, effect on the share of indicator species in the decoupled sections. Functional redundancy ($R^2 = 0.29$; Table 2) was positively affected by connectivity, mainly through its indirect effects (Table 3).

For carabids, connectivity had a negative effect on species richness ($R^2 = 0.56$; Table 2), governed by the negative direct effect and cascading effects through flooding regime and soil (Table 4). In contrast, connectivity had a positive effect on functional richness ($R^2 = 0.46$; Table 2), resulting from the direct effect as well as cascading effects, mainly through

Table 3 Direct and total (i.e., the sum of any direct and indirect paths between the predictor and the respective response metric) effects of abiotic variables on five different vegetation diversity metrics (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$)

Biodiversity metric	Model scope	Paths with significant interaction term [predictor:coupling state]	Connectivity direct	Connectivity total	Flooding direct	Flooding total	Soil direct	Soil total	Pollution direct	Pollution total
Species Richness	global	0	NA	0.233	0.418***	0.435	0.441***	0.571	0.265*	0.265
Taxon rareness	global	0	-4.533***	-4.831	-1.483	-0.454	0.846	1.123	1.968**	1.968
Indicators of periodically wet grassland %	coupled	2	-1.252*	-1.184	-3.308***	-3.690	1.062*	1.005	-0.157	-0.157
	decoupled		0.674	0.816	-3.101***	-3.460	1.678*	1.588	-0.415	-0.415
Functional Richness	coupled	2	NA	1.361	4.361*	3.972	-2.008	-3.745	-6.269***	-6.269***
	decoupled		NA	4.601	4.646*	7.364	-2.467	-4.870	-7.63***	-7.63***
Functional Redundancy	coupled	1	0.009**	0.009	0.007	0.015	-0.015	-0.022	-0.013	-0.013
	decoupled		0.033**	0.034	-0.021	-0.011	-0.013	-0.019	-0.013	-0.013

Green = positive effect, orange = negative effect of connectivity. IndPWG = Indicator species for periodically wet grassland. Total effects are only given if at least one of the paths between the predictor and the respective response metric was significant. Effects are based on standardised regression coefficients. For models that varied between coupling state (coupled/decoupled), the number of paths that exhibited a significant interaction term with coupling state are listed. Coefficients are different between "coupled" and "decoupled" even in the constrained paths because of the standardisation. Model scope "global" means no path had a significant interaction term with coupling State

Table 4 Direct and total (i.e., the sum of any direct and indirect paths between the predictor and the respective response metric) effects of abiotic variables on five different carabid diversity metrics (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$)

Biodiversity metric	Model scope	Paths with significant interaction term [predictor:coupling state]	Connectivity		Flooding		Soil		Pollution		Plant diversity	
			direct	total	direct	total	direct	total	direct	total	direct	total
Species Richness	coupled	2	- 0.059**	-0.224	- 0.259*	-0.391	-0.117	-0.138	NA	0.047	0.115	0.115
	decoupled		- 0.226**	-0.249	- 0.312*	-0.592	-0.131	-0.155	NA	0.049	0.15	0.15
Taxon rareness	global	0	- 2.623*	-5.522	1.577	2.014	- 4.139**	-4.269	NA	0.679	3.294**	3.294
Indicators of periodically wet grassland %	coupled	3	6.266***	6.412	4.533*	6.005	2.127	1.745	NA	1.803	3.18*	3.18
	decoupled		6.583**	7.016	4.2667*	5.211	2.513	3.481	NA	0.749	2.394*	2.394
Functional Richness	coupled	2	0.111**	0.134	0.003	-0.287	0.396*	0.396	NA	-	0.195	0.195
	decoupled		0.225**	0.285	0.004	-0.066	0.3*	0.300	NA	-	0.139	0.139
Functional Redundancy	coupled	1	- 0.064**	-0.117	0.013	0.275	- 0.217*	-0.250	NA	0.043	0.234**	0.234
	decoupled		- 0.134**	-0.229	0.011	0.233	- 0.171*	-0.197	NA	0.033	0.181**	0.181

Green = positive effect, orange = negative effect of connectivity. IndPWG = Indicator species for periodically wet grassland. Total effects are only given if at least one of the paths between the predictor and the respective response metric was significant. Effects are based on standardised regression coefficients. For models that varied between coupling state (coupled/decoupled), the number of paths that exhibited a significant interaction term with coupling state are listed. Coefficients are different between "coupled" and "decoupled" even in the constrained paths because of the standardisation. Model scope "global" means no path had a significant interaction term with coupling state

soil properties and pollution (Table 4). Connectivity also had a negative effect on carabid taxon rareness ($R^2 = 0.41$; Table 2), resulting from a combination of a direct and indirect effects through soil and pollution (Table 4). Connectivity had a positive, mainly direct, effect on the share of indicator species ($R^2 = 0.32$; Table 2), but a negative effect on functional redundancy, governed by both direct and indirect effects cascading through soil and pollution (Table 4).

Depictions of the SEMs and all standardized path coefficients can be found in Online Resource 3 for plants and Online Resource 4 for carabids.

Few differences between coupled and decoupled floodplains

The SEMs for plants had a total of nine or 10 paths, depending on whether the direct path between connectivity and the response metric was included or not. The carabid SEMs all had 13 paths. Out of the total of 113 modelled paths (five biological response metrics from two organism groups), only 11 paths varied between coupled and decoupled floodplains. In 7 out of these 11, this variation between groups came with a change of sign of the coefficient, i.e. the direction of the effect (compare Online Resources 3 and 4).

Plant species richness and taxon rareness of both plants and carabids was identically structured by the environmental variables in the coupled and decoupled floodplain sections, i.e. no significant interaction between the response variable within the model and the grouping variable coupling state was observed. In the other seven SEMs, at least one path had such a significant interaction term and was therefore modelled separately for the two groups. All paths that did not show significant interaction with coupling state were constrained to the global model. This means that the raw path coefficients are identical in both groups, but since the coefficients are standardized using the standard deviations of response and predictor, the standardized coefficients vary between the two groups as the standard deviations of only the respective group is considered. The path that varied most often, in five SEMs, between "coupled" and "decoupled" was the path between connectivity and flooding regime. The path between connectivity and the biological response did only

once vary between groups: in the share of plant indicator species, where it changed from a significantly negative effect in the coupled sections to a non-significant positive effect in the decoupled ones. This is especially interesting since this path was only included based on a significant test of directed separation on the global model. The present result of the multi-group analysis now indicates that while connectivity does have a direct (negative) effect on the share of indicator species in coupled floodplains, it does not have a direct effect on this metric in decoupled floodplains.

Discussion

Our study explored the direct and indirect effects of river-floodplain connectivity on plant and carabid beetle biodiversity using structural equation modelling (SEM). We aimed to understand how connectivity influences flooding regime, soil properties, and pollution, and how these factors, in turn, affect biodiversity.

Contrary to our initial hypothesis i), we found that river-floodplain connectivity had a significant direct effect on most biodiversity metrics for both plants and carabid beetles, in addition to the anticipated indirect effects mediated through flooding, soil properties, and pollution. This is consistent with the findings of Ye et al. (2024), where the inclusion of connectivity in a structural equation model explaining the effects of different floodplain environmental factors on riparian vegetation and arthropod assemblages greatly improved the explanatory potential of the model. To understand this direct effect, it is important to consider how this composite variable was derived. Contrary to the variable "flooding regime", the "connectivity" variable includes the morphology of the floodplain and how easily the water from the river reaches into the floodplain. In other words, it represents, though not measured directly, the frequency of flooding events. A plot with higher connectivity receives flooding earlier, quicker and therefore potentially with more force than a less connected spot. Water levels are higher in the well-connected spots during high discharge, at least until the water has had time to distribute more equally in the floodplain. It is widely accepted that the frequency and manner, in which floods occur, are crucial for floodplain-forming processes such as sedimentation or the creation of new open habitats (Tockner et al. 2000; Junk et al. 1989; Opperman et al. 2010). Our findings of a direct effect of connectivity on terrestrial biodiversity show that this "when and how" of a flood also directly interferes with biological processes, for example, competition or reproduction. Indeed, shallow flooding puts much less stress on plants, emerging seedlings or invertebrate larvae compared to deep flooding. Flash floods may drown terrestrial animals that could otherwise escape if the water levels were rising more slowly. For example, increases in flooding frequency in the Illinois River prevented the naturally occurring moist-soil plants from completing their life cycle in between floods, leading to a drastic reduction in these species (Ahn et al. 2004). Carabid beetle species exhibit little flooding resistance but remarkable resilience stemming from a high re-colonization ability (Gerisch et al. 2012b; Hering et al. 2004). During these times of re-colonization, the timing and severity of additional floods can have significant impacts. In the case of carabid beetles, flooding is especially critical at times when species are in their larval and pupal stages and cannot easily escape the rising water level (Hering et al. 2004). Mechanisms such as competitive exclusion by only a few, strong competitors may never be fully realised due to continuous disturbance, fostering the coexistence of many different

species (Whited et al. 2007). While we observed distinct effects of connectivity and the flooding regime, these two variables are inherently interlinked. In their effect on the floodplain they present different aspects of disturbance, with connectivity relating to intensity and extent, and flooding regime to duration. Together, they shape floodplain hydrology and, in turn, influence biodiversity. Further research is needed to disentangle their individual and combined roles. As such different aspects of disturbance can shape disturbance-diversity relationships differently (Miller et al. 2011), restoration efforts seeking to increase hydrological dynamics in the floodplain need to be precise about which of these aspects of disturbance they are aiming to change.

According to hypothesis ii), we further expected that connectivity would be negatively affecting the more general biodiversity metrics species and functional richness, while it would be positively affecting floodplain-specific biodiversity metrics, i.e. taxon rareness, indicator species for periodically wet grassland and functional redundancy (hypothesis iii). This overall pattern was not confirmed. The direction of the effect of connectivity on different biodiversity metrics was not uniform along these categories or organism groups. In three of the four SEMs with species or functional richness as response, connectivity had a positive effect. Only species richness of carabids had the expected negative association with connectivity. The positive effect of connectivity on plant species richness and functional richness of both plants and carabids suggests that the gradient of connectivity that is covered by our data does not create a level of disturbance that limits the species pool to a few, specialised species. Rather, the floodplain sections are affected by intermediate disturbance, where species richness is highest, according to the intermediate disturbance hypothesis (Grime 1973; Horn 1975; Connell 1978). Similarly, Friedman et al. (2022) showed that plant species richness was highest at intermediate inundation durations per year. High values of functional richness indicate a large functional space, i.e., relatively high differences in trait combinations. This would equally be favoured in an intermediate disturbance situation where many different trait sets are able to thrive. In high-disturbance systems, more species does not necessarily mean more different functions but rather more of the same (higher functional redundancy) (Biswas et al. 2023; Gerisch et al. 2012a). In systems that experience less disturbance, the association of species and functional diversity is stronger positive, i.e. more species do bring more functions (Biswas et al. 2023). Biswas and Mallik (2010) found that both species and functional richness of riparian plants peaked at intermediate disturbance levels, supporting that our finding of a positive effect of connectivity only represents the gradient of low to intermediate disturbance levels. Increased connectivity does not, however, only mean increased disturbance due to the water flowing into the floodplain more easily. In our study, connectivity also affected soil conditions and pollution levels, potentially creating new habitats and increasing microhabitat diversity, thereby facilitating the occurrence of more species. Similarly, Zhang et al. (2022) observed higher soil nutrients and, consequently, higher plant biomass in high-frequency wet-dry alternating (i.e., better connected) zones compared to low-frequency alternating zones. Additionally, closer spatial proximity to the river, one component of connectivity in this study, is likely to affect floodplain biota in that any influxes of biotic and abiotic agents, such as prey animals or nutrients, are more likely to come from the river and not from a terrestrial source (Ballinger and Lake 2006; O'Callaghan et al. 2013). In four of the six SEMs with taxon rareness, the share of indicator species or functional redundancy as response variable, connectivity had a negative effect, contrary to what we expected in hypothesis iii). Here again, the mechanism exclud-

ing the large pool of generalist species and favouring rare, specialised species, only comes into effect at high disturbance rates (Mouillot et al. 2013). Based on the selected response metrics, we cannot rule out, that higher connectivity does increase other floodplain-specific groups of species such as pioneer species or indicators for more open habitats, as the most connected plots in the well-coupled floodplain sections are often not actually periodically wet grassland but open sandy bars. Functional redundancy of plants was positively associated with connectivity as expected. In combination with the findings of increased species and functional richness with increased connectivity, this means that more species seem to be present in better-connected plots, and both new functions are added to the assemblage (increased functional richness) as well as many that were already present (increased functional redundancy). Contrastingly, carabid functional redundancy was negatively affected by connectivity. This again, could indicate that the disturbance caused by high connectivity is not yet so strong as to imply a strong filter for few trait sets on the community. Instead, changes to soil conditions and the plant community triggered by connectivity may have created the opportunity for a variety of trait sets to thrive, limiting the coexistence of species with similar functions. The effect that connectivity has on the floodplain and its biological communities is mainly that of creating disturbance. However, unmeasured confounding factors likely also shape the relationship between connectivity and the biological communities. Further studies are needed to integrate such factors into our postulated models, for example the fact that the floodplain can be used more intensely in less connected spots, or the amount of fragmentation in the floodplain enabling different community assembly processes.

We expected differences in the pathways of the SEMs between coupled and decoupled floodplains (hypothesis iv). This was only partly confirmed. In our SEM multigroup analysis, which tested for a significant interaction term of each modelled path with the grouping variable "coupling state", only 11 out of a total of 113 paths had such a significant interaction, meaning that the data were generally not better modelled when separated by coupling state. This in turn indicates that the mechanistic pathways of effects acting on environment and biota in the floodplain were not profoundly different in coupled and decoupled sections. This does not mean that there are no observable differences between communities of coupled and decoupled floodplains: Bauspiess et al. (2024) found that carabid species richness was higher directly at the stream bank than further away in near-natural stream conditions, but not so in degraded, embanked streams. In a previous study on floodplains of the Elbe River, both the taxonomic and functional diversity of plants, carabids and molluscs showed significant differences between coupled and decoupled floodplain sections (Wenskus et al. 2025). Instead, our findings indicate a large potential for restoration in the Elbe floodplains: decoupled floodplains have a noticeably different environment in terms of flooding regime or soil conditions. These modified conditions, input into an effect chain such as our SEM shows, will naturally lead to a different outcome in the biological communities compared to the environmental conditions of intact floodplains. However, with this effect chain intact, the restoration of the environmental conditions in decoupled floodplains is likely to lead back to the desired intact biological communities. How long this potential for recovery can last under heavy and continued degradation and if there are any tipping points-of-no-return, should be the focus of further research. More river systems will need to be analysed using our models to examine to what extent this stability in mechanistic pathways can be generalised beyond the Elbe River.

Conclusion

Lateral hydrological connectivity describes the transfer of matter, energy, and/or organisms between a river and the adjacent floodplain (Pringle, 2001; Ward, 1989). Through applying a structural equation modelling approach, we showed that not only the "matter" and "energy" but also the direct effects of connectivity, i.e. the transfer of organisms or the modification of competition, affect biota. In the studied floodplain sections of the Elbe River, the effects of connectivity on biodiversity are mainly positive, supporting the notion that high river-floodplain connectivity creates opportunities for coexistence of many different species, both through increasing habitat heterogeneity (an indirect effect) and through interfering in biological processes, for example inhibiting competitive exclusion processes by repeatedly resetting succession processes (a direct effect). The Elbe floodplains show a high potential for recovery of degraded habitats as effect chains remain the same even in the decoupled sections. Continued monitoring and restoration of these sections is crucial to not exceed the point where these effect chains, too, become disrupted.

Data availability The data that support the findings of this study are available from the authors upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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