ECOLOGY

Biodiversity recovery following delta-wide measures for flood risk reduction

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Biodiversity declined markedly over the past 150 years, with the biodiversity loss in fluvial ecosystems exceeding the global average. River restoration now aims at flood safety while enhancing biodiversity and has had success locally. However, at the scale of large river distributaries, the recovery remained elusive. We quantify changes in biodiversity of protected and endangered species over 15 years of river restoration in the embanked floodplains of an entire river delta. We distinguish seven taxonomic groups and four functional groups in more than 2 million field observations of species presence. Of all 179 fluvial floodplain sections examined, 137 showed an increase in biodiversity, particularly for fast-spreading species. Birds and mammals showed the largest increase, that is, +13 and +3 percentage point saturation of their potential based on habitat. This shows that flood risk interventions were successfully combined with enhancement of biodiversity, whereas flood stage decreased (−24 cm).

INTRODUCTION

Global biodiversity decreased over the past centuries at similar rates as during previous mass extinctions in Earth's history (*1*). Paradoxically, the systematic analysis of local assemblages over the past 40 years showed a large change in species composition, but no consistent loss (*2*), which led to the explicit inclusion of spatial scale in biodiversity trends (*3*). The trends in composition may be driven by the introduction of alien species, habitat degradation, and climate change. These changes do not take away the risk of local extinction for many threatened native species, and societal norms on the preferred species composition have been translated in many countries into laws and regulations that protect vulnerable and endangered species. As a subset of the global ecosystem, the fluvial ecosystems showed extinction rates of freshwater fauna that are five times higher than for terrestrial fauna (*4*). River corridors and deltas potentially maintain high species richness because the periodic flooding links the main channel to the floodplains, and because the river supplies the water and nutrients to sustain life (*5*, *6*). However, especially in Europe and North America, land use change and population increase contributed to floodplain degradation and the decline in freshwater biodiversity. This degradation is still ongoing in Southeast Asia and Sahelian Africa (*5*). Currently, habitats associated with 65% of the river discharge are classified as moderately to highly threatened (*7*), showing that the valuable ecosystems in the world's deltas are severely stressed (*8*, *9*). At a global scale, river impairment will continue in the near future (*10*), although the number of efforts to restore rivers at the scale of entire deltas is increasing worldwide (*11*). Costly river restoration projects aim at combining multiple objectives including flood safety, biodiversity, navigation, water supply, and recreation (*11*, *12*). The large investments in these projects justify the question whether these efforts are successful. Although pioneer vegetation rapidly restores the "naturalness" perceived by a casual observer, it remains unclear how successful these restoration measures are for biodiversity in general and for threatened species in particular.

The effects of river restoration on flood hazards are routinely evaluated using calibrated hydrodynamic models. In contrast, biodiversity recovery has been evaluated with a very limited set of species (*13*, *14*), or it is evaluated with partial spatial coverage, with inconsistent data, and for a limited number of intervention types. Recently, meta-analyses of restoration success suggested that river restoration positively influenced fish, macroinvertebrates, and aquatic plants, but only few assessments were based on consistent data sets (*15*). Long-term species observation data are key to determining restoration success over large areas (*16*), but inadequate monitoring of restoration success is still pervasive (*17*).

Unique to our study on the Rhine River is the systematic spatiotemporal assessment of biodiversity changes following river restoration covering an entire active river delta and a relatively long time span. River restoration led to changes in land cover due to cyclic rejuvenation of floodplain vegetation, side channel construction, and adaptive management of meadows that allows extensive grazing, to which we will refer jointly as "measures" (*18*, *19*). The measures carried out in the Rhine distributaries (Fig. 1A) (*20*) led to a mean reduction in the predicted water level of 24 cm during the design discharge, which is specified by national law as a flood event with an average return period of 1250 years (Fig. 1B). We assessed biodiversity changes (i) for all protected and endangered species together, (ii) for four functional groups in each of seven taxonomic groups, and (iii) as a result of implemented measures. We take advantage of the most detailed species observation data set known to us: the National Database Flora and Fauna (NDFF) of the Netherlands, comprising long-term distribution data of higher plants and animals in the entire river Rhine delta. Within the embanked floodplains of the Rhine distributaries (Fig. 1A), more than 2 million observations of species presence (1993–2014) were collected, validated, and stored in a database (see the Supplementary Materials). These observations bracket the starting year of 1997 for data availability on detailed land cover.

RESULTS

Mapping biodiversity changes

A large number of biodiversity indices exist depending on the type of diversity and the spatial scale (*3*). Here, we computed specific biodiversity indices for valuation of protected and endangered species

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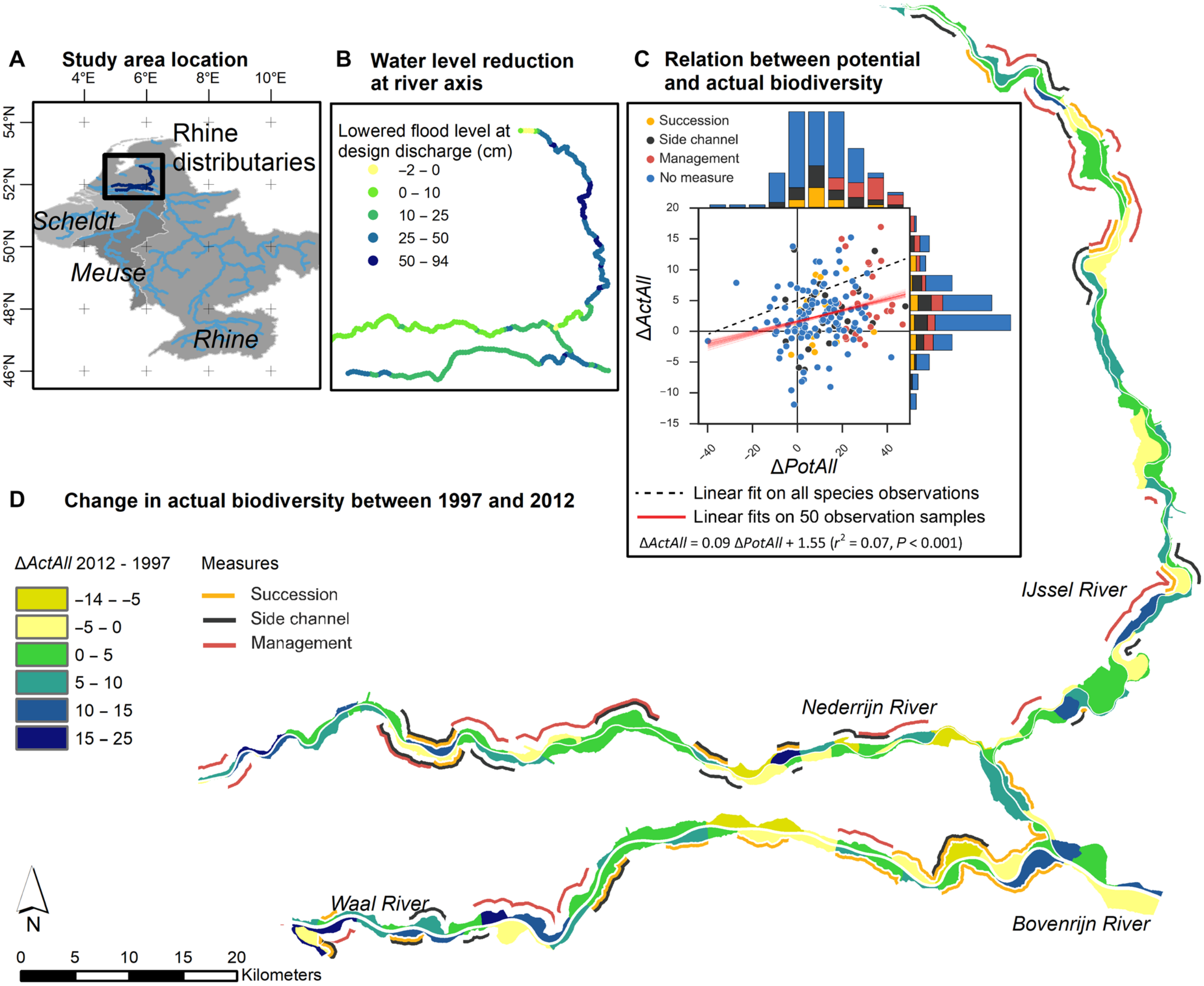


Fig. 1. Biodiversity changes in the embanked floodplains of the Rhine delta between 1997 and 2012. (**A**) Location of the distributaries of the Rhine delta within the drainage basin in northwest Europe, center at 5.5°E, 52.0°N. (**B**) Spatial distribution of the flood hazard reduction at the once-every-1250-year flood. (**C**) Bivariate distribution of changes in *PotAll* and *ActAll* between 1997 and 2012. (**D**) Spatial distribution of the changes in aggregated biodiversity (Δ*ActAll*) in all 179 floodplain sections. The colored lines alongside the sections indicate the measures implemented.

at the taxonomic level of order or higher for all species that are characteristic of river-floodplain systems. In addition, species were only selected if they were protected and/or regarded as endangered according to formal policy documents and legislation. These indices are referred to as "biodiversity" for brevity, although they include a subset of endangered species that are characteristic of fluvial systems and exclude nonprotected, nonthreatened, and invasive alien species. We chose this subset of protected and endangered species to exclude common native species that do not contribute to the signal of recovery. We used the BIOSAFE (Spreadsheet Application for Evaluation of BIOdiversity) model (*21*, *22*), which was adapted for automated mapping. BIOSAFE links 614 protected species in seven taxonomic groups (higher plants, dragonflies plus damselflies, butterflies, herpetofauna, fish, birds, and mammals) to 82 ecotope classes. Ecotopes are defined as "spatial landscape units that are homogeneous as to vegetation structure, succession stage, and the main abiotic factors that are relevant to plant growth" (*23*). The vector-based ecotope files were gridded to a 20-m spatial resolution for computational efficiency. To understand the effects of landscape changes on functional biodiversity, we classified the species according to their dispersal rate and specificity of habitat requirements, leading to four functional groups per taxonomic group: "slow-spreading generalist," "fast-spreading generalist," "slow-spreading specialist," and "fast-spreading specialist." We ran BIOSAFE for all 179 freshwater floodplain sections in the Rhine River distributaries (Fig. 1D) with ecotope maps of 1997, 2005, 2008, and 2012, as well as species presence data from the NDFF (*24*). We distinguish "best-case" results that are based on all NDFF observations and "worst-case" results that are based on subsampled observations to rigorously compensate for the possible increase in sampling effort. For data reduction, we calculated the following indices per floodplain section: *PotTax* and *ActTax*, the potential and actual biodiversity of protected and endangered species per taxonomic group, and *PotAll* and *ActAll*, which aggregate *PotTax* and *ActTax* over the investigated taxonomic groups. In addition, we computed the biodiversity saturation index as *SatTax* = *ActTax*/*PotTax* and habitat diversity as the fraction of suitable ecotopes present in the floodplain section per taxonomic group.

Between 1997 and 2012, the *PotAll* indices increased for 77% of the 179 floodplain sections and the *ActAll* indices increased for 82% based on the worst case (Fig. 1, C and D). Mean *PotAll* increased from 96 to 108, and mean *ActAll* increased from 9 to 13. The increase in *ActAll* is weakly related to changes in *PotAll* (Fig. 1C). For the worst case, we found a mean slope of 0.09 ($n = 50$), which indicates that actual biodiversity lags behind changes in ecotope composition. The standard deviation (SD) in slope, intercept, and explained variance of the regression equation was more than an order of magnitude smaller than the values themselves, which can be explained by reducing all sampled observations over the time periods to presence/absence vectors for BIOSAFE input. By comparison, the best-case regression showed both a higher slope (0.16) and a higher intercept (5.5) for the regression line (Fig. 1C, dashed line). Whether—and if so, how fast—potentials of a given area are fulfilled depends on species' dispersal and migration capacities, as well as on the distance to the nearest source population and the presence of barriers and corridors for dispersal and migration (*25–27*). The positive *y*-axis intercept can point to a regional recovery of biodiversity or a radiating effect of biodiversity recovery in neighboring floodplain areas. No regional recovery is known because terrestrial systems remained stable or declined in the Netherlands (*28*). This leaves the positive effects of measures and land cover change taken within the river system as the main explanatory factor for the *ActAll* increase.

Habitat diversity (Fig. 2, A and B) increased for all functional groups, except for fast-spreading generalists of the dragonflies plus damselflies, and generalist fish (fast and slow). The mean *SatTax* for the worst-case scenario increased between 1997 and 2012. The increase was most notable for birds and mammals. Large differences were found in the *SatTax* values and changes of this index over time. Functional groups with high dispersal rate (black and red lines, Fig. 2) showed the highest mean values and the largest increase. Mean saturation increased from 32 to 44% for birds and from 8 to 11% for mammals. Dragonflies plus damselflies, and fish showed a small increase in mean saturation (~2%), mostly due to the fast-spreading

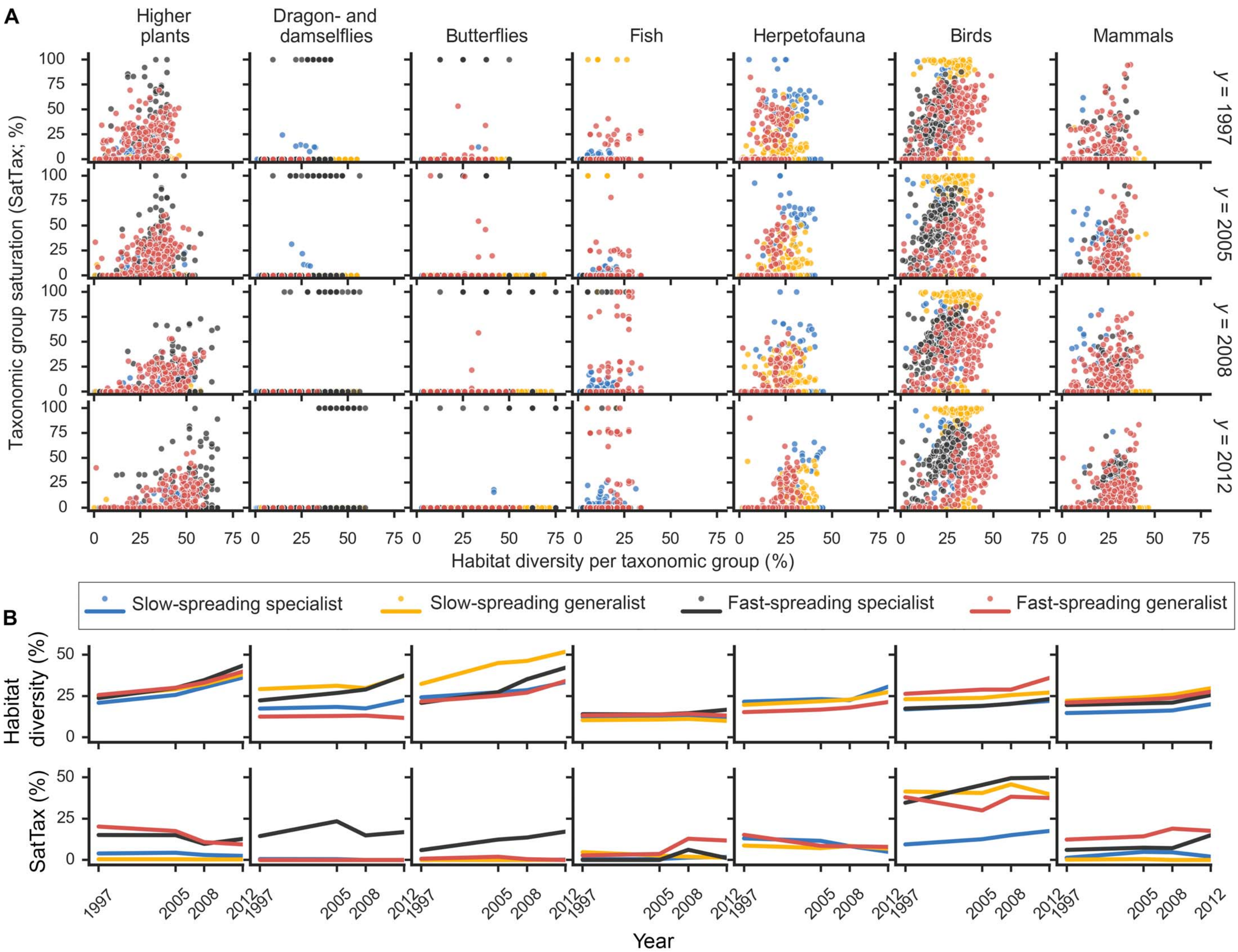


Fig. 2. Temporal overview of habitat diversity (*HabDiv*) and saturation (*SatTax*) for the subsampled species observations (worst case). (**A**) Biodiversity changes over all floodplain sections with more than one observation in all periods (1997, 2005, 2008, and 2012). The *x* axis represents habitat diversity for each taxonomic group (*HabDiv*; scale, 0 to 100%); the *y* axis indicates the biodiversity saturation (*SatTax* = *ActTax*/*PotTax*; scale, 0 to 100%). (**B**) Temporal development of mean *SatTax* and habitat diversity per functional group. Note that the *SatTax* values of functional groups with high dispersal rates are higher and increase faster than species that disperse slowly.

specialists. Conversely, *SatTax* decreased for herpetofauna and higher plants, whereas the habitat diversity increased. Even the fast-spreading generalist plant species decreased slightly. For the best-case scenario, the same patterns in *SatTax* were present (fig. S4), although the changes were larger compared to the worst case.

Fish species show a trade-off with reducing limnophilic species in formerly isolated water bodies in the floodplains and increasing rheophilic species for water bodies connected to the main channel by recently constructed side channels. However, the increasing saturation also shows that these newly available habitats were rapidly colonized by other species without losing much of the species that were already present. Similar results were found for bird species. By exchanging production meadows, which are beneficial for meadow birds and geese, for more natural habitats, the 6% increase in habitat diversity resulted in a 12% increase in saturation. Also, fast-spreading mammals and dragonflies plus damselflies profited from the measures taken. However, for the latter group, recovery is certainly not occurring in all floodplain sections. More than 50% of the floodplain sections showed a *SatTax* of zero for dragonflies plus damselflies.

Habitat diversity and *SatTax* (Fig. 2B) increased for the less mobile groups of higher plants, herpetofauna, and butterflies, but this did not translate in all cases to a higher saturation of their functional groups except for fast-spreading specialist butterflies (+11 percentage points). The decreasing saturation for herpetofauna and higher plants indicates that most species from these groups were not yet able to colonize the newly created habitats. Fifteen years of rehabilitation may not be sufficient yet to curb decades of habitat deterioration.

Effect of measures on biodiversity changes

Yearly overviews of the implementation dates of measures were unavailable. Therefore, we analyzed the changes in land cover to identify the floodplain sections where measures were carried out. These changes were detected by computing the transition matrix of 20 land cover classes, which consisted of aggregated ecotopes. The transition matrix contains the surface area for each transition in land cover between 1997 and 2012. The surface areas of transitions that represent specific measures were summed, and sections with large fractional changes were classified as "succession," "side channel," or "natural

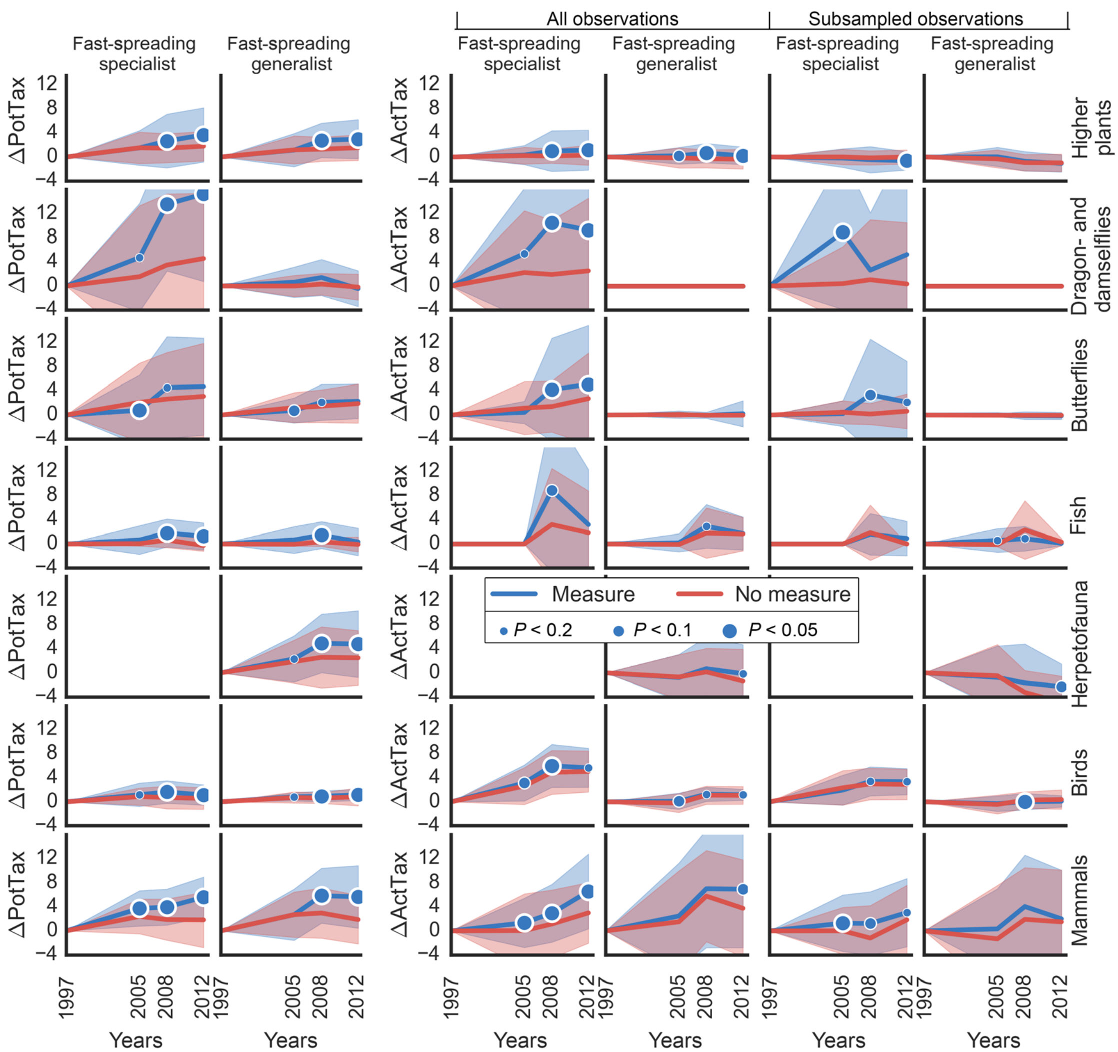
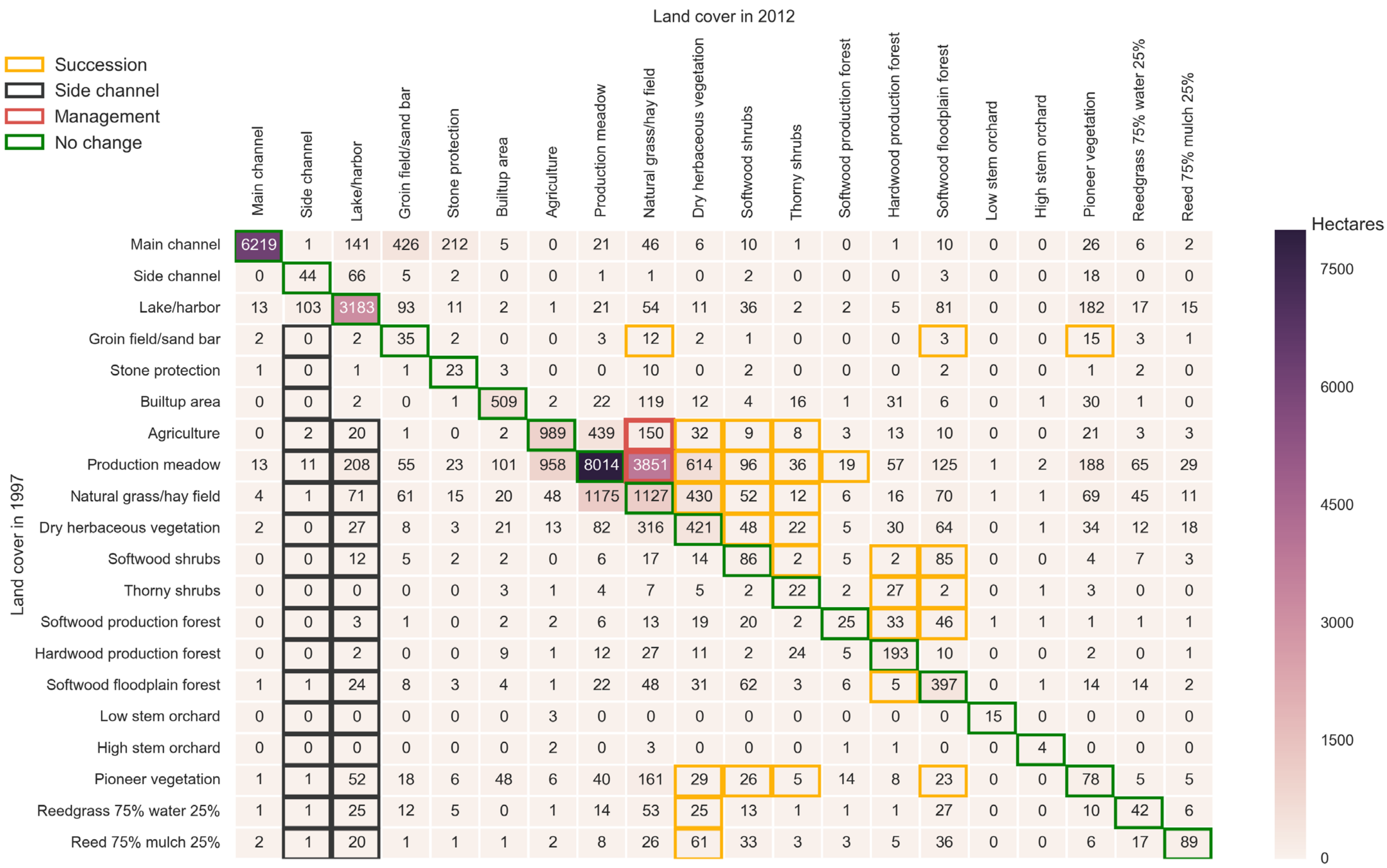


Fig. 3. Effects of floodplain measures on Δ*ActTax* (base year 1997) for species functional groups. Lines indicate mean values with transparent uncertainty bands representing ±1 SD. Blue dots represent significant differences in Δ*ActTax* at that year ($P < 0.1$, by Mann-Whitney rank sum test carried out for 2005, 2008, and 2012). Floodplain sections with river restoration measures (in blue) mostly exceed the remaining floodplains (in red). Results for all functional groups are given in figs. S5 to S7.

management." A vegetation succession model (*29*) was used to identify succession. Because the first ecotope map dates from 1997, measures implemented before 1997 were not included, but it should be noted that they might still affect changes in biodiversity. We selected the 15% of the 179 floodplain sections with the largest fraction of modified surface area by measures to assess effects on biodiversity. The effect of these measures on the changes in *PotTax* and *ActTax* differed strongly between taxonomic and functional groups, although the results for floodplain sections with and without measures overlapped (Figs. 1, C and D, 3). Here, we highlight the effects of measures for fast-spreading species (Fig. 3). The full overview of *PotTax* and *ActTax* changes for the best and worst case is given in the Supplementary Materials (figs. S5 to S7). The $\Delta PotTax$ values differ significantly between floodplain sections with and without measures implemented (Fig. 4). $\Delta PotTax$ values for measures exceed those for floodplain sections without measures, except for slow-spreading generalist birds and butterflies (fig. S5). This shows that the implemented measures generally have a positive potential effect on the biodiversity of most functional groups. In contrast, the $\Delta ActTax$ values differ much less between floodplains with and without measures in the best case (Fig. 3, middle two columns) and even more for the worst case (Fig. 3, two right-hand columns). Significant differences are shown for fast-spreading specialist mammals, butterflies, dragonflies plus damselflies and for slow-spreading generalist birds at the 95% confidence level. Other differences were significant only at 90 or 80%. In total, 14 of the 28 species groups showed significant differences due to the restoration measures at 90% for the best-case scenario (fig. S6), and 8 of 28 for the worst-case scenario (fig. S7). When combined into the seven taxonomic groups, all groups showed significant effects from measures at least at one time period for the best case (fig. S6). Fast-spreading groups showed significantly larger differences in $\Delta ActTax$ than slow-spreading groups (figs. S6 and S7). The joint assessment of all functional groups (figs. S6 and S7; "All" column) smoothed out the effects of the separate groups. $\Delta PotTax$ scores of birds (fig. S5) were exceeded by their $\Delta ActTax$ scores (Fig. 3).

DISCUSSION

Our analysis at the scale of the meta-community focused on species presence/absence data in a legal framework that necessitates action from managers, which is not required for other biodiversity indices such as the Shannon Index (*30*). Additional information on species abundance and composition would provide additional value in the assessment, but these data are unavailable or inconsistent at the spatiotemporal resolution of our study. Likewise, more detailed vegetation maps could also improve in discerning between measures, but these are also unavailable. Given the overall data richness of the Netherlands, it is unlikely that this is possible in other areas with the same level of detail. The key difference with long time series of standardized species inventories



Land cover in 1997	Main channel	Side channel	Lake/harbor	Groin field/sand bar	Stone protection	Builtup area	Agriculture	Production meadow	Natural grass/hay field	Dry herbaceous vegetation	Softwood shrubs	Thorny shrubs	Softwood production forest	Hardwood production forest	Softwood floodplain forest	Low stem orchard	High stem orchard	Pioneer vegetation	Reedgrass 75% water 25%	Reed 75% mulch 25%
Main channel	6219	1	141	426	212	5	0	21	46	6	10	1	0	1	10	0	0	26	6	2
Side channel	0	44	66	5	2	0	0	1	1	0	2	0	0	0	3	0	0	18	0	0
Lake/harbor	13	103	3183	93	11	2	1	21	54	11	36	2	2	5	81	0	0	182	17	15
Groin field/sand bar	2	0	2	35	2	0	0	3	12	2	1	0	0	0	3	0	0	15	3	1
Stone protection	1	0	1	1	23	3	0	0	10	0	2	0	0	0	2	0	0	1	2	0
Builtup area	0	0	2	0	1	509	2	22	119	12	4	16	1	31	6	0	1	30	1	0
Agriculture	0	2	20	1	0	2	989	439	150	32	9	8	3	13	10	0	0	21	3	3
Production meadow	13	11	208	55	23	101	958	8014	3851	614	96	36	19	57	125	1	2	188	65	29
Natural grass/hay field	4	1	71	61	15	20	48	1175	1127	430	52	12	6	16	70	1	1	69	45	11
Dry herbaceous vegetation	2	0	27	8	3	21	13	82	316	421	48	22	5	30	64	0	1	34	12	18
Softwood shrubs	0	0	12	5	2	2	0	6	17	14	86	2	5	2	85	0	0	4	7	3
Thorny shrubs	0	0	0	0	0	3	1	4	7	5	2	22	2	27	2	0	1	3	0	0
Softwood production forest	0	0	3	1	0	2	2	6	13	19	20	2	25	33	46	1	1	1	1	1
Hardwood production forest	0	0	2	0	0	9	1	12	27	11	2	24	5	193	10	0	0	2	0	1
Softwood floodplain forest	1	1	24	8	3	4	1	22	48	31	62	3	6	5	397	0	1	14	14	2
Low stem orchard	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	15	0	0	0	0
High stem orchard	0	0	0	0	0	0	2	0	3	0	0	0	1	1	0	0	4	0	0	0
Pioneer vegetation	1	1	52	18	6	48	6	40	161	29	26	5	14	8	23	0	0	78	5	5
Reedgrass 75% water 25%	1	1	25	12	5	0	1	14	53	25	13	1	1	1	27	0	0	10	42	6
Reed 75% mulch 25%	2	1	20	1	1	1	2	8	26	61	33	3	3	5	36	0	0	6	17	89

Fig. 4. Transition matrix of aggregated ecotopes between 1997 and 2012 for the full study area. The matrix should be read from left to right. For example, of the surface area of agriculture in 1997, 2 ha was converted to side channel, 20 ha was converted to lake/harbor, and 989 ha remained the same in 2012. Colors indicate the cells representing succession, side channel construction, and natural management floodplain meadows. The same kind of matrix was computed for each floodplain section to determine the extent and type of the land cover change.

[for example, see previous studies (*2*, *31*)] is that we aimed at the area-wide assessment of biodiversity changes, which inevitably led to the usage of volunteered geographic information and a suite of data collection protocols. Although the data are all validated by experts, the available data preclude establishing rarefaction curves and subsequent reassessment of the results. The NDFF data were previously used for time series analysis for birds (*32*), as well as aquatic macroinvertebrates and fish (*14*).

Notwithstanding the limitations of our analyses, we reveal for the first time observational evidence that biodiversity decline can be reversed by combining large-scale physical reconstruction of floodplains for increasing flood safety with ecological rehabilitation in densely populated river deltas. Contrary to previous research on benthic invertebrates (*27*), we found evidence of significant effects of specific restoration measures, but the low significance levels point to the need of project-based field monitoring to assess the success of these measures. Disappointingly, habitat restoration ($\Delta PotTax$) alone is not enough for full biodiversity recovery ($SatTax < 100\%$) because flora and fauna species are subjected to multiple stressors both within and outside of the floodplain areas (*26*, *33*). Our results also point to the need for river restoration designs that explicitly take all functional groups into account when a new habitat is created. Additionally, dispersal barriers need to be removed to facilitate recolonization of new habitat, and abiotic conditions must be optimized to support specialists. Given the degraded status of river deltas and floodplains globally, application of multitaxa and regional river restoration has a very high potential of enhancing habitat for threatened species and biodiversity in general, counteracting the decline in the richness of protected and endangered species over the whole delta region.

MATERIALS AND METHODS

We applied the BIOSAFE model (*21*, *22*, *34*, *35*) to calculate biodiversity indices of protected and endangered species that are characteristic of fluvial environments. The main input consisted of the ecotope maps for the land use input and the species observations available from the NDFF database. The Supplementary Materials provide the details of these input data. Below, we describe our study area, the spatial analyses to drive BIOSAFE with spatiotemporal data, and the hydrodynamic model used to calculate the flood level lowering.

Study area

We considered all three distributaries of the Rhine River in the Netherlands, excluding the estuary. At the Dutch-German border, the Rhine River has a mean annual discharge of 2250 $m^3 s^{-1}$, draining a catchment area of 165,000 km^2 (*36*, *37*). Just downstream of the border, the Rhine River splits into three main distributaries (Fig. 1D) with an average water gradient of 10 cm per kilometer. The total embanked area, that is, the main channel and floodplain area between the embankments, amounts to 440 km^2.

In the 1970s, the Rhine floodplains were predominantly used as agricultural production grasslands, and water quality was low. By 1995, water quality had improved (*14*, *38*–*40*). This may have had a positive effect on fish, macroinvertebrates, and, to a lesser extent, amphibians and birds. A national-scale overview on biodiversity (*28*) showed that aquatic systems improved slightly, whereas terrestrial systems remained stable or declined. Whether habitat availability or chemical quality is the main limiting factor is undecided. After the 1993 and 1995 flood events, the "Room for the River" program started. This €2.3 billion program consisted of 27 projects within our study area. Room for the River aimed at (i) increasing the conveyance capacity of the Rhine distributaries from 15,000 to 16,000 $m^3 s^{-1}$ to reduce the flood hazard (*20*) and (ii) improving the ecological status and increasing the biodiversity (*21*). The floodplains along the distributaries in the Rhine delta are almost entirely protected by the European Union Habitats directive (Council directive 92/43/EEC) and Birds directive (Council directive 79/409/EEC). Each distributary has specific protection goals in terms of carrying capacity for species and habitat types (*41*). The study area contains 179 individual floodplain sections with a mean surface area of 1.5 km^2, ranging from 0.15 to 11.5 km^2.

Species field observations for actual biodiversity values

We acquired field observations of species presence to compute actual biodiversity parameters from the Dutch NDFF, which serves as the national data warehouse for exchanging species observation data (*24*). The database currently contains more than 90 million observations, bringing together observations from volunteers and professionals (*42*) based on 40 different field protocols (table S2). Points, lines, or polygons geolocate the observations, enabling subsequent processing in spatial analyses. Before inclusion in the database, each observation is validated using a series of validation rules, and by experts per taxonomic group if necessary. Preprocessing of the NDFF data consisted of (i) spatial selection of records within the study area, (ii) temporal selection of records matching each of the ecotope maps, and (iii) linking records to floodplain sections. Details of the preprocessing are given in the Supplementary Materials.

BIOSAFE extensions

BIOSAFE was originally developed by Lenders *et al.* (*22*), extended by de Nooij *et al.* (*21*), and tested on sensitivity to input parameters (*43*, *44*). The BIOSAFE conceptual model comprises a set of links between riverine species and legal and policy documents on the one hand and links between species and ecotopes [ecotope links (EL)] on the other hand. These two sets create a link between the legal domain and ecotopes via species (fig. S1). On the basis of these links, BIOSAFE computes biodiversity indices per ecotope and per taxonomic group. The Supplementary Materials provide an extensive description of the model, including a mathematical description. The spreadsheet version of BIOSAFE could compute floodplain-specific biodiversity indices and enabled scenario development. Now, we implemented BIOSAFE in the Python programming language (www.python.org) to automate the application and extended it with spatial functionality, aggregation of ecotopes, and species functional groups for each taxonomic group.

The spatial extension of BIOSAFE deals with two main input types: ecotope surface areas and species survey monitoring data. First, it tabularizes total ecotope surface areas for arbitrary floodplain sections based on a gridded representation of the ecotope map. The study area contained 179 individual floodplain sections plus adjacent water bodies represented by a unique identifier. With the tabulated surface areas per section, potential biodiversity indices were computed for each section. Raster analyses were carried out using the PCRaster Python software (*45*). Second, it constructs the species presence (SP) vector for each floodplain section based on the preprocessed NDFF species monitoring data, which is required for the actual biodiversity scores. Preprocessing of these data is necessary because monitoring data come in many file formats and database structures (*24*).

The aggregation extension was required to match the classes of the ecotope maps to the species-ecotope links contained in BIOSAFE. The four ecotope maps contained 41 aggregated ecotope classes or additional classes that were not present in the original ecotope classification system (*46*–*48*). BIOSAFE did not contain these additions because it was based on the ecotope system and not on the ecotope maps. The aggregated classes account for a significant fraction of the floodplain area, which strongly affected BIOSAFE scores when not taken into account. We extended BIOSAFE with an aggregation function to include all ecotope classes present in the ecotope map. This function can further be used to upscale ecotope links to different land cover classifications, such as hydrodynamic roughness classes or CORINE land cover classes. The aggregation function adds a new ecotope class based on the species-ecotope links from the classes that are aggregated. For example, the species links to HG-1 and HG-2 are combined into the species links for the new ecotope class HG-1-2. Seven ecotopes were matched to a single RWES ecotope, effectively reducing the aggregation function to a lookup operation. All ecotope classes that featured in the four maps were included in the biodiversity estimates using this aggregation. Table S1 provides an overview of all ecotope classes and the underlying classes if aggregation was applied.

The species functional group extension provided insight into what species groups benefitted in terms of biodiversity indices. All species were attributed with two additional functional traits based on their habitat requirements and their dispersal speed. We distinguished two classes of habitat requirements: species that are purely linked to the fluvial environment (specialists) and species that also occur in different habitat but do not need the other environment per se (generalists). Species dispersal rate was classified as fast-spreading or slow-spreading. The combination of these two traits gives four functional groups: (i) slow-spreading generalist, (ii) fast-spreading generalist, (iii) slow-spreading specialist, and (iv) fast-spreading specialist (table S3). Traits were derived from species distribution maps and literature. Unfortunately, not all species could be attributed reliably with dispersal speed, in which case we labeled the trait as unknown (table S3). We created five subversions of the BIOSAFE model: one model included all species, and four represented the functional groups by specific subsets of species.

Regarding the classification of functional groups, we followed two routes. Deciding whether a species should be regarded as a fluvial specialist or as a generalist was determined on the basis of (historic) distribution patterns of species, derived from (digital) species distribution atlases and scientific literature. Important sources used are the series Nederlandse Fauna (Dutch Fauna) published by Naturalis, Leiden, especially volumes 4 (dragonflies and damselflies), 5 (butterflies), 7 (butterflies), 9 (amphibians and reptiles), and 12 (mammals); websites such as the NDFF Digital Distribution Atlases (www.verspreidingsatlas.nl) and Dutch Species Register (www.nederlandsesoorten.nl/); and the sites of organizations specialized in monitoring of specific taxonomic groups, such as FLORON (www.floron.nl; plants), Butterfly Foundation (www.vlinderstichting.nl; butterflies, dragonflies, and damselflies), RAVON (www.ravon.nl; reptiles, amphibians, and fish), SOVON (www.sovon.nl; birds), and Dutch Mammal Society (www.zoogdiervereniging.nl; mammals). Species were qualified as either specialist or generalist, using available data on their (historic) distribution. Determining dispersal capacity proved to be much more arduous. For many species, there is little to no information on (actual or potential) dispersal rates; sometimes, information is even contradictory. For this reason, we consulted a large number of scientific publications and the abovementioned websites and classified species following a conservative best expert judgment approach either as slow-spreading or as fast-spreading. Species were classified as unknown if insufficient or contradictory information was found.

Changes in biodiversity

The NDFF data showed an increase in the number of observations over the four time periods, but whether this is due to increased species presence or to increased sampling effort cannot be determined from the data because only observations are stored. The most rigorous way of excluding the effects of increased sampling effort is to randomly subsample the NDFF species records to the lowest number of observations per floodplain section and per time period. Subsampled records were subsequently converted to species presence (*SP*) vectors as input to BIOSAFE. We repeated the subsampling 50 times and characterized the dependence of *ActAll* on *PotAll* using linear regressions. The mean sampling fractions over the floodplain sections were 0.86, 0.66, 0.26, and 0.21 for time periods 1997, 2005, 2008, and 2012, respectively. However, there are no indications that the mean sampling effort has significantly increased, and there is a high probability that the observed increase in the number of observations results from ecological recovery and not from a bias in sampling effort. For instance, converting production meadows into natural grasslands may lead to an exponential increase of plant species and a substantial improvement of habitat of the associated animals. The significant increase of especially fast-spreading species in the conservative estimate also points toward a high probability that the increase in the number of observations is realistic. Therefore, the subsampling may lead to a serious underestimation of the actual biodiversity especially in 2008 and 2012 because only 26 and 21% of the observations were used. Taking the full set of observational data into consideration may therefore reflect the actual situation better than taking subsamples. For this reason, we also followed an alternative route in which we took the full set of observations into consideration. Although this alternative route can be considered to represent the best-case scenario, the conservative route of randomly subsampling can be considered as the worst-case scenario.

To reach the first objective, we calculated the difference in *PotAll* and *ActAll* scores between 1997 and 2012 for each floodplain section individually using BIOSAFE to assess the biodiversity changes over all taxonomic groups together. We present the worst-case results including the uncertainty due to the random sampling and compare against the best-case result.

The second objective involved the temporal changes in *SatTax* (*ActTax*/*PotTax*) scores per species functional groups per floodplain section over the four time periods. *SatTax* was compared against the habitat diversity (*HabDiv*) score per floodplain section, which represented the suitability of the floodplain section as a whole for a specific taxonomic group. The temporal development of *HabDiv* and *SatTax* per functional group over the whole study area was calculated as their mean score over all floodplain sections for the worst case.

The third objective aimed at explaining the differences in biodiversity due to succession, side channel, or natural management, to which we jointly refer to as measures. No yearly information was available on the implemented measures, so we extracted floodplain sections where these measures were carried out from ecotope changes between 1997 and 2012. The ecotopes were aggregated into 20 land cover classes representing differences in hydrodynamic roughness (table S1). We quantified the changes in roughness in a transition matrix (Fig. 4), which shows the area of the change between the classes from left to right. The area that remained unchanged is on the diagonal, and the off-diagonal cells represent the changes. Vegetation succession, depicted in yellow cell borders, follows the natural vegetation succession (*29*). We added morphological succession describing the sequence of non-vegetated ecotopes from high hydromorphological dynamics to low dynamic areas, such as from sand bar to natural levee, because silting up of side channels was not included by Makaske *et al.* (*29*). Side channel recreation (Fig. 4, black cell outlines) comprised the change from any roughness class to the side channel class, or to the lake class if the channel is disconnected. Natural management (Fig. 4, red cell outlines) reflected the change from production meadow to natural meadow management. The other cells represented changes that were due to agricultural changes or classification errors. To detect where measures were implemented, we first computed the following ratios from the transition matrix between 1997 and 2012 for each floodplain section: floodplain management ratio (FMR), floodplain succession ratio (FSR), and floodplain side channel ratio (FCR)

$$\mathrm{FMR} = \frac{\sum(\text{management area})}{\sum \text{floodplain section area}} \quad (1)$$

$$\mathrm{FSR} = \frac{\sum(\text{succession area})}{\sum \text{floodplain section area}} \quad (2)$$

$$\mathrm{FCR} = \frac{\sum(\text{new side channel area})}{\sum \text{floodplain section area}} \quad (3)$$

We ranked the sections according to the three ratios and selected the sections with the top 15% for FMR, FSR, or FCR. This divided the study area in sections with and without measures implemented. The sections with measures were compared to those without measures. For both groups, we evaluated the changes in *PotTax* and *ActTax* indices compared to the 1997 base year, which is our first time step. Next, we assessed the significance of the difference between sections with measures and sections without measures for 2005, 2008, and 2012 using the Mann-Whitney rank sum test. By definition, no change is present in 1997, which was used for standardization of the starting point. This means that the initial score of the section and whether this was a nature area or not did not affect the assessment of the change. We used a Mann-Whitney rank sum test with confidence intervals of 80, 90, and 95% to test the significance of the change for each year and species functional group. We compared the best- and worst-case results to delineate the full range of possible biodiversity developments.

Flood hazard reduction from landscaping measures

The increase in conveyance capacity was assessed using the WAQUA two-dimensional hydrodynamic model, which numerically solves the Saint Venant equations using a finite difference method (*49*). WAQUA is used by the Dutch Ministry of Infrastructure and Environment to calculate the flood hazard and discharge distribution in the complex channel and floodplain areas of Rhine distributaries in the Netherlands. Flood hazard is defined here as the water level at the river axis during a flood event with a return period of 1250 years. The WAQUA model that was used for this study is based on a staggered curvilinear grid. Each of the 886,861 cells represented a column-shaped volume of water with a variable surface area of 700 m^2 on average. The boundary conditions of the model included the river discharge at the upstream boundary and the water level at the downstream boundaries, which were determined using rating curves. The main spatial model inputs for the WAQUA model were a digital terrain model, a map with hydraulic structures (for example, groins and embankments), and a roughness class map. Roughness class maps were based on the ecotope map using the Baseline database and software (*50*), which are converted at runtime into hydraulic roughness. The landscaping measures that were carried out between 1997 and 2012 were geocoded, and the associated WAQUA geometric parameters were updated using the Baseline ArcGIS plug-in. The landscaping measures were decided on in the key decision on spatial planning (*51*, *52*). The flood hazard reduction (Fig. 1B) was based on the 1996 reference situation and the measures as described by the key decision on spatial planning.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/11/e1602762/DC1

A detailed description of the BIOSAFE model
Details of the BIOSAFE input
A list of parameter abbreviations
fig. S1. Flow chart of the BIOSAFE methodology per floodplain section.
fig. S2. Graphical example of BIOSAFE parameter computation.
fig. S3. Number of observations per time slice and per surface area of the observation.
fig. S4. Temporal overview of habitat diversity (*HabDiv*) and saturation (*SatTax*) for all species observations (best case).
fig. S5. Effects of floodplain measures on Δ*PotTax* per functional group.
fig. S6. Effects of floodplain measures on Δ*ActTax* per functional group, based on best-case scenario.
fig. S7. Effects of floodplain measures on Δ*ActTax* per functional group, based on worst-case scenario.
table S1. Overview of ecotope classes included in BIOSAFE and connected land cover classes.
table S2. Overview of the data collection protocols in the NDFF database.
table S3. Number of species per functional group.
Excel file with BIOSAFE input and output
References (*53*–*58*)

REFERENCES AND NOTES

1. R. Dirzo, H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, B. Collen, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
2. M. Dornelas, N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, A. E. Magurran, Assemblage time series reveal biodiversity change but not systematic loss. *Science* **344**, 296–299 (2014).
3. B. J. McGill, M. Dornelas, N. J. Gotelli, A. E. Magurran, Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol. Evol.* **30**, 104–113 (2015).
4. A. Ricciardi, J. B. Rasmussen, Extinction rates of North American freshwater fauna. *Conserv. Biol.* **13**, 1220–1222 (1999).
5. K. Tockner, J. A. Stanford, Riverine flood plains: Present state and future trends. *Environ. Conserv.* **29**, 308–330 (2002).
6. J. V. Ward, K. Tockner, F. Schiemer, Biodiversity of floodplain river ecosystems: Ecotones and connectivity. *Regul. Rivers Res. Manag.* **15**, 125–139 (1999).
7. C. J. Vörösmarty, P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann, P. M. Davies, Global threats to human water security and river biodiversity. *Nature* **467**, 555–561 (2010).
8. Z. D. Tessler, C. J. Vörösmarty, M. Grossberg, I. Gladkova, H. Aizenman, J. P. M. Syvitski, E. Foufoula-Georgiou, Profiling risk and sustainability in coastal deltas of the world. *Science* **349**, 638–643 (2015).
9. L. Giosan, J. Syvitski, S. Constantinescu, J. Day, Climate change: Protect the world's deltas. *Nature* **516**, 31–33 (2014).
10. C. Zarfl, A. Lumsdon, J. Berlekamp, L. Tydecks, K. Tockner, A global boom in hydropower dam construction. *Aquat. Sci.* **77**, 161–170 (2015).
11. E. S. Bernhardt, M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, E. Sudduth, Ecology. Synthesizing U.S. river restoration efforts. *Science* **308**, 636–637 (2005).
12. D. Hering, A. Borja, J. Carstensen, L. Carvalho, M. Elliott, C. K. Feld, A.-S. Heiskanen, R. K. Johnson, J. Moe, D. Pont, A. L. Solheim, W. van de Bund, The European Water Framework Directive at the age of 10: A critical review of the achievements with recommendations for the future. *Sci. Total Environ.* **408**, 4007–4019 (2010).

13. A. D. Buijse, H. Coops, M. Staras, L. H. Jans, G. J. van Geest, R. E. Grift, B. W. Ibelings, W. Oosterberg, F. C. J. M. Roozen, Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biol.* **47**, 889–907 (2002).
14. P. H. Nienhuis, A. D. Buijse, R. S. E. W. Leuven, A. J. M. Smits, R. J. W. de Nooij, E. M. Samborska, Ecological rehabilitation of the lowland basin of the river Rhine (NW Europe). *Hydrobiologia* **478**, 53–72 (2002).
15. J. Kail, K. Brabec, M. Poppe, K. Januschke, The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: A meta-analysis. *Ecol. Indic.* **58**, 311–321 (2015).
16. E. V. Balian, H. Segers, C. Lévèque, K. Martens, The Freshwater Animal Diversity Assessment: An overview of the results. *Hydrobiologia* **595**, 627–637 (2008).
17. E. Wohl, S. N. Lane, A. C. Wilcox, The science and practice of river restoration. *Water Resour. Res.* **51**, 5974–5997 (2015).
18. M. J. Baptist, W. E. Penning, H. Duel, A. J. M. Smits, G. W. Geerling, G. E. M. Van der Lee, J. S. L. Van Alphen, Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. *River Res. Appl.* **20**, 285–297 (2004).
19. M. W. Straatsma, A. Schipper, M. van der Perk, C. van den Brink, R. S. E. W. Leuven, H. Middelkoop, Impact of value-driven scenarios on the geomorphology and ecology of lower Rhine floodplains under a changing climate. *Landsc. Urban Plan.* **92**, 160–174 (2009).
20. H. T. C. van Stokkom, A. J. M. Smits, R. S. E. W. Leuven, Flood defense in the Netherlands: A new era, a new approach. *Water Int.* **30**, 76–87 (2005).
21. R. J. W. de Nooij, H. J. R. Lenders, R. S. E. W. Leuven, G. de Blust, N. Geilen, B. Goldschmidt, S. Muller, I. Poudevigne, P. H. Nienhuis, BIO-SAFE: Assessing the impacts of physical reconstruction on protected and endangered species. *River Res. Appl.* **20**, 299–313 (2004).
22. H. J. R. Lenders, R. S. E. W. Leuven, P. H. Nienhuis, R. J. W. de Nooij, S. A. M. van Rooij, BIO-SAFE: A method for evaluation of biodiversity values on the basis of political and legal criteria. *Landsc. Urban Plan.* **55**, 121–137 (2001).
23. F. Klijn, H. A. U. de Haes, A hierarchical approach to ecosystems and its implications for ecological land classification. *Landsc. Ecol.* **9**, 89–104 (1994).
24. L. E. Veen, G. B. A. van Reenen, F. P. Sluiter, E. E. van Loon, W. Bouten, A semantically integrated, user-friendly data model for species observation data. *Ecol. Inform.* **8**, 1–9 (2012).
25. W. A. Ozinga, C. Römermann, R. M. Bekker, A. Prinzing, W. L. M. Tamis, J. H. J. Schaminée, S. M. Hennekens, K. Thompson, P. Poschlod, M. Kleyer, J. P. Bakker, J. M. Van Groenendael, Dispersal failure contributes to plant losses in NW Europe. *Ecol. Lett.* **12**, 66–74 (2009).
26. M. A. Palmer, H. L. Menninger, E. Bernhardt, River restoration, habitat heterogeneity and biodiversity: A failure of theory or practice? *Freshwater Biol.* **55**, 205–222 (2010).
27. M. Leps, A. Sundermann, J. D. Tonkin, A. W. Lorenz, P. Haase, Time is no healer: Increasing restoration age does not lead to improved benthic invertebrate communities in restored river reaches. *Sci. Total Environ.* **557–558**, 722–732 (2016).
28. World Wildlife Fund, *Living Planet Report: Natuur in Nederland* (World Wildlife Fund, 2015).
29. B. Makaske, G. J. Maas, N. G. van den Brink, H. P. Wolfert, The influence of floodplain vegetation succession on hydraulic roughness: Is ecosystem rehabilitation in Dutch embanked floodplains compatible with flood safety standards? *Ambio* **40**, 370–376 (2011).
30. B. J. McGill, A. E. Magurran, *Biological Diversity: Frontiers in Measurement and Assessment* (Oxford Univ. Press, 2011).
31. M. Yasuhara, G. Hunt, D. Breitburg, A. Tsujimoto, K. Katsuki, Human-induced marine ecological degradation: Micropaleontological perspectives. *Ecol. Evol.* **2**, 3242–3268 (2012).
32. C. A. M. van Turnhout, R. S. E. W. Leuven, A. J. Hendriks, G. Kurstjens, A. van Strien, R. P. B. Foppen, H. Siepel, Ecological strategies successfully predict the effects of river floodplain rehabilitation on breeding birds. *River Res. Appl.* **28**, 269–282 (2012).
33. K. Tockner, M. Pusch, D. Borchardt, M. S. Lorang, Multiple stressors in coupled river–floodplain ecosystems. *Freshwater Biol.* **55**, 135–151 (2010).
34. R. J. W. de Nooij, R. S. E. W. Leuven, H. J. R. Lenders, T. E. P. A. Lam, S. Pieters, Relating the ecological and legal frameworks for nature conservation in Europe. *J. Int. Wildl. Law Policy* **11**, 63–95 (2008).
35. M. Wozniak, R. S. E. W. Leuven, H. J. R. Lenders, T. J. Chmielewski, G. W. Geerling, A. J. M. Smits, Assessing landscape change and biodiversity values of the Middle Vistula river valley, Poland, using BIO-SAFE. *Landsc. Urban Plan.* **92**, 210–219 (2009).
36. H. Middelkoop, C. O. G. Van Haselen, *Twice a River: Rhine and Meuse in the Netherlands* (RIZA Report 99.003, RIZA, 1999).
37. U. Uehlinger, K. M. Wantzen, R. S. E. W. Leuven, H. Arndt, The river Rhine basin, in *Rivers of Europe*, K. Tockner, U. Uehlinger, C. T. Robinson, Eds. (Academic Press, 2008), pp. 199–245.
38. W. Admiraal, G. van der Velde, H. Smit, W. G. Cazemier, The rivers Rhine and Meuse in The Netherlands: Present state and signs of ecological recovery. *Hydrobiologia* **265**, 97–128 (1993).
39. A. bij de Vaate, R. Breukel, G. van der Velde, Long-term developments in ecological rehabilitation of the main distributaries in the Rhine Delta: Fish and macroinvertebrates. *Hydrobiologia* **565**, 229–242 (2006).
40. E. Mostert, International co-operation on Rhine water quality 1945–2008: An example to follow? *Phys. Chem. Earth* **34**, 142–149 (2009).
41. Alterra (2012).
42. A. Lawrence, E. Turnhout, Personal meaning in the public sphere: The standardisation and rationalisation of biodiversity data in the UK and the Netherlands. *J. Rural Stud.* **26**, 353–360 (2010).
43. R. J. W. De Nooij, K. M. Lotterman, P. H. J. van de Sande, T. Pelsma, R. S. E. W. Leuven, H. J. R. Lenders, Validity and sensitivity of a model for assessment of impacts of river floodplain reconstruction on protected and endangered species. *Environ. Impact Assess. Rev.* **26**, 677–695 (2006).
44. M. W. Straatsma, M. van der Perk, A. M. Schipper, R. J. W. de Nooij, R. S. E. W. Leuven, F. Huthoff, H. Middelkoop, Uncertainty in hydromorphological and ecological modelling of lowland river floodplains resulting from land cover classification errors. *Environ. Model. Softw.* **42**, 17–19 (2013).
45. O. Schmitz, D. Karssenberg, K. de Jong, J.-L. de Kok, S. M. de Jong, Map algebra and model algebra for integrated model building. *Environ. Model. Softw.* **48**, 113–128 (2013).
46. D. T. van der Molen, H. P. A. Aarts, J. J. G. M. Backx, E. F. M. Geilen, M. Platteeuw, *RWES Aquatisch* (RIZA, 2000).
47. C. Lorenz, D. T. van der Molen, *RWES Oevers* (RIZA and Witteveen+Bos, 2001).
48. D. Willems, J. Bergwerff, N. Geilen, *RWES Terrestrisch* (RIZA and AGI, 2007).
49. Rijkswaterstaat, *SIMONA: User's Guide WAQUA: General Information* (Rijkswaterstaat, 2013).
50. M. Scholten, J. Stout, *BASELINE: Dataprotocol Baseline 5.2.2* (Rijkswaterstaat Waterdienst, Deltares, 2013).
51. R. Schielen, *Analyses Rondom het Voorkeurs-Alternatief van Ruimte voor de Rivier* (Ministry of Infrastructure and the Environment, 2007).
52. Ruimte voor de Rivier, *Planologische Kernbeslissing Ruimte voor de Rivier* (Ruimte voor de Rivier, 2006).
53. R. J. W. De Nooij, P. Vugteveen, H. J. R. Lenders, *BIO-SAFE 2.0. An Instrument for Impact Assessment of Floodplain Interventions. Application of BIO-SAFE 2.0 Flora and Fauna Act, Environmental Protection Acts, and Environmental Impact Assessments* (Institute for Wetland and Water Research, Radboud University Nijmegen, 2008).
54. J. Chen, J. Chen, A. Liao, X. Cao, L. Chen, X. Chen, C. He, G. Han, S. Peng, M. Lu, W. Zhang, X. Tong, J. Mills, Global land cover mapping at 30 m resolution: A POK-based operational approach. *ISPRS J. Photogramm. Remote Sens.* **103**, 7–27 (2015).
55. J. A. Kelmelis, M. L. DeMulder, C. E. Ogrosky, N. J. Van Driel, B. J. Ryan, *The National Map* from geography to mapping and back again. *Photogramm. Eng. Remote Sens.* **69**, 1109–1118 (2003).
56. M. Bossard, J. Feranec, J. Otahel, *CORINE Land Cover Technical Guide—Addendum 2000* (European Environmental Agency, 2000).
57. J. Bergwerff, A. Knotters, M. Vreeken, D. Willems, *AGI-GEA-2003 Methodeherziening Ecotopenkartering* (RWS-AGI, 2003).
58. T. Hengl, E. van Loon, H. Sierdsema, W. Bouten, Advancing spatio-temporal analysis of ecological data: Examples in R, in *Computational Science and Its Applications—ICCSA 2008*, O. Gervasi, B. Murgante, A. Laganà, D. Taniar, Y. Mun, Eds. (Springer, 2008), vol. 5072, pp. 692–707.

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Biodiversity recovery following delta-wide measures for flood risk reduction

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