Biodiversity recovery and transformation impacts for wetland biodiversity

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Abstract

Life Cycle Assessment (LCA) methods for land use take both occupation and transformation impacts into account. However, for wetlands and impacts from water consumption, it is so far not possible to account for transformation impacts. It is our goal to close this research gap, by determining wetland recovery times and developing characterization factors for transformation. To do this, we conducted a meta-analysis of 59 studies analyzing biodiversity recovery in wetlands subject to passive and active restoration. Generalized linear models were fitted to the biodiversity data and age, along with other wetland characteristics (such as elevation, latitude or climate class), were used as predictor variables. The results indicate that elevation, latitude, type of wetland and restoration method have the strongest effect on recovery speed. Recovery times vary from less than one year to a maximum of 10^7 years with passive restoration and 10^5 years with active restoration. Corresponding transformation characterization factors vary between 10^{-14} and 10^{-2} species-eq·year^2/m^3. Finally, recognizing the relevance of this work to real-world policy issues beyond LCA, we discuss the implications of our estimated restoration times on the feasibility of "biodiversity offsetting". Offsetting utilizes restoration to replace biodiversity value lost due to development impacts. Our work can help stakeholders make informed decisions on whether offsetting represent a legitimate policy options in a particular context.

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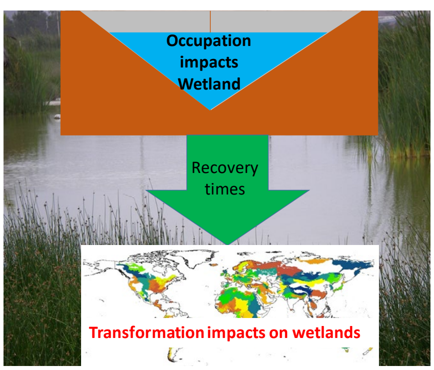

Introduction

Wetlands are, amongst others, defined as water bodies (including e.g. marshes) that can be both natural and human-made and can be either lotic (flowing) or lentic (stagnant). The water can be fresh, brackish or saline.[1] Wetlands supply numerous ecosystem services, such as retention of freshwater, regulation of hydrological flows and prevention of erosion.[2] Nonetheless, it has been estimated that more than 50% of all wetland areas were lost during the 20th century,[3] mainly because of drainage and land conversion, and because of freshwater withdrawals for agriculture. It has consequently become essential to understand and quantify the impacts of such activities on wetland biodiversity, in order to avoid the most damaging practices and delimit biodiversity loss.

Life Cycle Assessment (LCA) is a tool for quantifying the environmental impacts that a certain process (or product) entails within its life cycle,[4] and it can therefore be applied when evaluating the impacts of human actions on ecosystems.[5] Life Cycle Impact Assessment (LCIA) methods for estimating the effects of water consumption on ecosystems[6,7] include one method that takes wetlands specifically into account.[8] Characterization factors (CFs) for 1184 Ramsar wetlands (wetlands of international importance) quantify the number of species-equivalents lost per m^3/year of water consumed; distinguishing between birds, mammals, amphibians and reptiles. This corresponds to an "occupation impact". Occupation CFs measure the reduction in biodiversity in a wetland while it is being drained. Once drainage ceases, it takes time for functional, structural and compositional elements of biodiversity to recover in the disrupted ecosystems (if at all). During the recovery period, wetlands still suffer from the negative effects of previous disturbances, and it is consequently necessary to quantify such impacts using transformation characterization factors. No methodology is currently available to take transformation or permanent impacts on wetlands into account. The time interval needed for wetlands to fully recover their biodiversity is key for the calculation of transformation CFs.

For terrestrial ecosystems, a methodology exists to assess the time-scales of biodiversity recovery[9] and the results suggest that complete recovery may result in very long time lags. CFs for transformation are typically calculated applying equation (1) [10], where 't_{reg}' [years] represents the "*time required for full regeneration of ecosystem quality*" and 'CF_{Occ}' [species-eq·year/m^3] is the corresponding occupation

CF. In the case of wetlands, the unit indicates the loss of species because of the extraction of 1 m^3 of water during one year.

(1)

$$CF_{Trans} = \frac{1}{2} \cdot t_{reg} \cdot CF_{Occ}$$

The above equation assumes a linear recovery of biodiversity in time, however Curran et al.[9] adopted a logarithmic recovery trajectory for the analysis of terrestrial ecosystems based on empirical relationships documented in the terrestrial recovery literature. Likewise, the review of Moreno-Mateos et al.[11] suggest that recovery of restored wetlands is also non-linear and better approximated with a log-relationship.

Ecosystem quality in an LCA context is defined as "*the capability of an ecosystem (or a mix of ecosystems at the landscape scale) to sustain biodiversity and to deliver services to the human society*".[10] A clear definition of ecosystem restoration is provided by the Society for Ecological Restoration (SER) as "*the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed*".[12] The aim of restoration is to approximate a reference system that represents a realistic target based on a set of key indicators. For wetland restoration different techniques can be implemented. Passive restoration involves putting an end to environmental stressors (e.g. groundwater pumping) and letting nature take its course to re-establish the affected area on its own. Active restoration includes management activities that assist the ecosystem to rebuild its diversity, such as the planting of specific vegetation, assisted seed dispersal or re-introduction of aquatic species.[13] Wetland creation is not a form of restoration because it entails the establishment of an aquatic ecosystem where this was not previously present.

Recent studies have analyzed the factors (e.g. restoration methods) that influence the speed of ecosystem recovery and have concluded that, in created wetlands, biodiversity recovers fastest,[14] while active restoration is to be preferred to passive restoration in order to achieve a more rapid recovery.[9] Warm climates,[11] low elevations[15] and high hydrologic exchanges[11] (lotic compared to lentic wetlands) are other factors that can speed up restoration processes. These and other wetland characteristics were examined in this study to evaluate their effect on wetland recovery. The main underlying hypothesis was that biodiversity shows an increase once the ecosystem is no longer subjected to disturbance.[9,11]

Knowing which ecosystem characteristics affect biodiversity loss in wetlands can help increase awareness and prevent their further destruction. Wetland restoration is commonly employed as part of broader environmental policies to compensate the loss of wetland habitat due to development (i.e. "biodiversity offsets"). The problem with such a strategy is that, while habitat destruction is certain to take place, full biodiversity recovery in the offset site may be inhibited, making no net loss of biodiversity hard to obtain.[16] Such difficulties have been demonstrated in reviews of wetland mitigation policies in the USA (e.g. ref[17]). Therefore, there is a strong impetus to understand the extent of damage caused by wetland development, whether impacts are permanent or temporary, and whether they can be compensated through restoration/creation.

The objectives of this study were to (1) understand the temporal trajectory of recovery, (2) develop a model to estimate wetland recovery times, (3) identify which wetland characteristics lead to a faster recovery compared to other features, (4) quantify success and failure rates of wetland remediation, and (5) develop a methodology (applicable in LCA) to assess wetland transformation impacts.

Methods

Literature search

We built a database with results of peer-reviewed papers and reports in which restoration or creation of aquatic habitats was carried out in different parts of the world. Two existing databases[2,11] were investigated and a literature search was carried out on Google Scholar (June 2015) with the words: "(biodiversity OR aquatic ecosystem) AND (ecological compensation OR habitat banking OR offsets OR recovery OR ecosystem rehabilitation OR restoration ecology OR secondary growth)". In order to be selected, the studies had to meet the following criteria:

- Availability of biodiversity measures from an ecosystem that was being restored, and from an undisturbed (reference) ecosystem, to enable a direct comparison. Reference ecosystems were those with no signs of major anthropogenic disturbance either at the time of the study, or through its known history.
- Measured ecological responses at known time intervals since the beginning of restoration, both in the ecosystem being restored and in the reference system.
- Spatial independence of biodiversity measurements to fulfill the assumptions of the statistical tests applied. To consider samples to be spatially independent they had to be a minimum distance apart. This minimum distance was dependent on the species class and was maintained throughout the different studies, e.g. plants had to be at least 50 meters apart in order to be considered independent samples (for all minimum distances, see Supporting Information (SI1), section S1). If these criteria were not met, data were aggregated or taken from only one of the sites.

Response ratio

The biodiversity indicators used in this study to evaluate whether restoration was successful included richness, evenness and diversity (see SI1, section S2 for the list of indicators). Biodiversity values, measured at the same time in the restored and reference habitats, were used for the calculation of a response ratio (RR), defined as the ratio between a measured quantity in an experimental group (in our case the restored habitat) and one in a control group (the reference habitat). As the measured quantity we used one of the biodiversity indicators. It is advisable to use the logarithm of the RR when carrying out statistical analyses (eq 2),[18] because deviations in the numerator are treated in the same way as deviations in the denominator, but the simple ratio is affected more by changes in the denominator.

$$ln\,(RR_i) = ln\left(\frac{x_{i,rest}}{x_{i,ref}}\right)$$

(2)

'$x_{i,\,rest}$' is the biodiversity value measured at time 'i' in the restored wetland, and '$x_{i,\,ref}$' is the one of the corresponding reference habitat.

Negative values of '$\ln(RR_i)$' indicate that, between restored and reference habitat, biodiversity is lower in the ecosystem which is being restored. Positive values indicate higher biodiversity in the wetland which is being restored. A value of $\ln(RR_i)=0$ means that biodiversity is equal both in restored and reference habitat. The time interval between the start of the restoration and when the zero value is reached represents the time needed for complete biodiversity recovery. Complete biodiversity recovery means that the biodiversity indicators of the restored wetland equal those of the reference wetland. Background changes in the reference system towards alternate states are taken into account during the construction of the response ratio.

The biodiversity RRs, together with their corresponding time of measurement (after cessation of disturbance), were used to compute recovery trajectories for each wetland. For all ecosystems that (1) had more than 3 biodiversity measurements in time and (2) showed an overall increase in biodiversity, linear and logarithmic trajectories were interpolated to the data and their R-squared (R^2) values were used to evaluate which type of trend line had the best goodness-of-fit.

Model predictors

In addition to biodiversity measurements in time, other wetland characteristics with a potential influence on the RR were extracted from the literature and included as model predictors (independent variables):[9,11] climate class (A - equatorial; B - arid; C - warm temperate; D - snow), wetland type (coastal; lentic; lotic), taxon (plants; aquatic species – including crustaceans, invertebrates, mollusks and fish; terrestrial species – including birds and amphibians; others – including micro-organisms), restoration type (active; passive; creation), latitude (between 34.89°S and 65.5°N), biodiversity metric (richness; abundance/evenness; diversity), the time elapsed since the beginning of restoration (referred to as 'age' hereinafter), and elevation (between sea level and 2,348 m.a.s.l.; our database did not include wetlands located in the interval 1,200 - 2,300 m.a.s.l. due to unavailability of data). Except for age, all variables were modeled as categorical predictors. Elevation was divided into 9 categories, while latitude was taken as its absolute value and divided into 6 categories. A category was defined as having at least 20 and a maximum of 200 data points.

An example of the database structure is presented in the SI1, section S3.

Implementation of Generalized Linear Models (GLMs)

The information contained in our database was used to build a linear model with the purpose of predicting ecosystem recovery times (eq 3).

$$y = a + b \cdot x_1 + c \cdot x_2 + \cdots + n \cdot x_n$$

(3)

Variable 'y' is the logarithm of the biodiversity RR (ln(RR)) and '$x_1 \ldots x_n$' are the different predictors. Factor "a" - the intercept of the model - and factors 'b…n' - the coefficients of the predictors - were obtained from the statistical analysis described in the following paragraph. By using the inverse of equation (3), it was possible to understand whether wetlands could reach reference levels of biodiversity or not, and at what speed such recovery took place (see SI1 section S4 for more details).

The statistical analysis of the database was carried out using R and the R-Studio environment.[19,20] We used the "corrgrams" package[21] to test the correlation amongst all predictors. The statistical modelling included four main phases: 1) resampling of the data points, 2) fitting of generalized linear models (GLMs), 3) model selection based on the Akaike Information Criterion (AIC) and 4) model averaging. The outputs of these different steps were the coefficients of the linear model and the importance values for each predictor.

One data point (i.e., one row of the database) of each study was randomly selected and inserted into a set. Sample size of the set equalled the number of studies taken into account, i.e. each set had 59 data points. This procedure was repeated 10,000 times (resulting in 10,000 sets) in order to avoid pseudo-replication and bias caused by the clustering of data within single studies[22]. A GLM, including all predictor variables (referred to as 'full GLM'), was fitted to each one of the 10,000 resampled data sets.

The resulting coefficients (one for each predictor category) and the deviance explained (DE) were recorded for each of the 10,000 sets. In each iteration, if the coefficient estimate of the 'age' predictor was negative, the coefficients of all other predictors of the same iteration were taken out of the results. This was done because the coefficients of these runs would result in models in which biodiversity would not converge to reference values and, as such, they were considered to be an indication of restoration failure.[9] Coefficient estimates of iterations that showed a poor predictive ability, defined as having a value of the deviance explained lower than 10%, were also excluded.

As a last step, estimates of the coefficients resulting from the GLM fitting were averaged across the iterations that had positive age coefficients and an explained deviance above 10%, obtaining one unique coefficient value for each category of the predictors.

Importance values of the predictors

Importance values were calculated for the independent variables using the 'glmulti' package[23] in R and can be interpreted as the probability that each predictor is a component of the model that best represents the data. For each of the 10,000 iterations, the full GLM formulas were broken up into a series of simpler formulas by excluding one or more predictors each time, and such simplified GLMs were then fitted to the corresponding data set of the original full GLM. The 'glmulti' package uses a genetic algorithm (GA) to find the best of these simpler models without having to try all possible combinations of the predictors. The corrected Akaike Information Criterion (AICc) was used to compare complexity and explanatory power of the generated models, which were then ranked according to its value: the lower the AICc value, the better the model and the higher its ranking. The GA stops when improvements in the AICc value of the last generation of models are below a certain target. Once all models were ranked, the deviance explained of the best model for each iteration was recorded. The

AICc values were then implemented by ‘glmulti’ to define the relative evidence weights (w_i) of each of the i-th simpler models: $w_i = \exp(-(AICc_i - AICc_{best}))$, where the AICc value of the best-performing model is subtracted from the AICc value of each i-th generated model, resulting in the fact that, the smaller the difference, the closer w_i is to 1. The relative evidence weights were normalized so that their sum added up to one. The importance values of the predictors were computed, per iteration, as the sum of the normalized evidence weights of all the best 100 models in which such a predictor appeared. The 10,000 values were then averaged across iterations using the same method as the one used for the coefficient estimates. A 15% threshold for importance values was applied: all predictors with a higher percentage (importance value > 0.15) should be maintained in the model, while those with a lower value (importance value < 0.15) should be discarded. This cut-off point was selected arbitrarily. A scheme of the steps carried out as part of the statistical analysis is presented in the SI1, section S5.

Validation

In order to check how well the model was able to reproduce observed recovery trajectories, 20% of the data points were taken out of the database, and the statistical analysis was carried out using the remaining 80% of the database. The studies excluded from the model fitting phase were selected to be representative of each predictor category. Random selection was not possible because of data scarcity regarding some categories of the predictors. Only two validation steps were performed, i.e. two sets of data points were excluded. R-squared and the Nash-Sutcliffe coefficient were used as indicators of model performance.

Transformation CFs

Having estimated the model coefficients, it was possible to back-calculate recovery times by imposing equal biodiversity between restored and reference habitat, i.e. ln(RR)=0. Transformation characterization factors were then calculated for 1184 Ramsar wetlands, using equation

(1) and existing wetland occupation CFs[8] for birds and amphibians. Transformation CFs were also calculated assuming a logarithmic recovery trajectory. This was achieved using equation (4).

$$CF_{Trans} = CF_{Occ} \cdot \left(t_{reg} - const \cdot 0.9 \cdot t_{reg}^{1.11}\right)$$

(4)

't_{reg}' [years] represents the "*time required for full regeneration of ecosystem quality*" and 'CF_{Occ}' [species-eq·year/m^3] is the corresponding occupation CF. The value of "const" is wetland-specific and was derived following the methodology presented in the SI1, section S6, part B.

The unit for transformation CFs of wetlands is [species-eq·year^2/m^3]. When the transformation CF is multiplied by the flow of water [m^3/year] going to the wetland once occupation has ceased, the result is the transformation impact [species-eq·year], which is compatible with transformation impacts in the land use impact category.[24] The flow of water in m^3/year indicates the amount of water flowing back to the wetland and transforming it to a more natural state, once water is no longer consumed or extracted.

Results

Database characteristics

Of the studies present in the database[2], 12 met the selection criteria, while 27 studies were selected from ref[11]. In addition, 20 papers were added from our literature search (see SI1, section S7). It was often the case that more than one restored/created ecosystem was compared with the same reference ecosystem, resulting in 307 restored/created habitats versus 259 reference habitats. The entire database (see Supporting Information 2) consists of 500 data points. 319 of the biodiversity measurements were taken in the first five years after cessation of disturbance, the longest time span between a measurement and cessation of disturbance was 55 years. Measurements of richness were the most common (266 data points), followed by diversity (146 data points) and abundance/evenness (88 data points). The majority of data points came from coastal wetlands (271 data points), followed by lotic (121 data points) and lentic ecosystems (108 data points) (for details see also SI1, section S8). Two categories of the elevation predictor (900-1,200 m.a.s.l. and 2,300-2,400 m.a.s.l.) did not reach the minimum number of 20 data points, but were kept because they represented the behaviour of ecosystems at high elevations, necessary for verifying the hypothesis that recovery times are longer at higher altitudes.

When analyzing the biodiversity recovery trajectories in time, logarithmic interpolations showed a higher R^2 value in 60% of the wetlands, compared to linear interpolation. Consequently, it was deemed appropriate to use 'ln(age)' as a predictor (instead of 'age') in order to obtain estimated trajectories with a logarithmic trend (see SI1, section S9 for examples of goodness-of-fit).

Model coefficients

Of the 10,000 GLM models, 8,658 models showed a positive age coefficient, meaning that restoration was successful and induced a positive biodiversity response with time. None of the models had values of the deviance explained lower than 10%, and the average DE out of the 10,000 runs was 55%.

The validation step resulted in a Nash-Sutcliffe coefficient of 0.042, and an R^2 value of 25%. Most of the times the observed data points did not all lie within the confidence interval (SI1, section S10). However, the model did well for predicting the time to reach full biodiversity recovery, given that there was a clear recovery trajectory. In general, these results indicate that the model is precise in the estimation of the term 't_{reg}', but not in resembling the recovery trajectory.

Figure 1 shows the average coefficient values of models with a positive age effect.

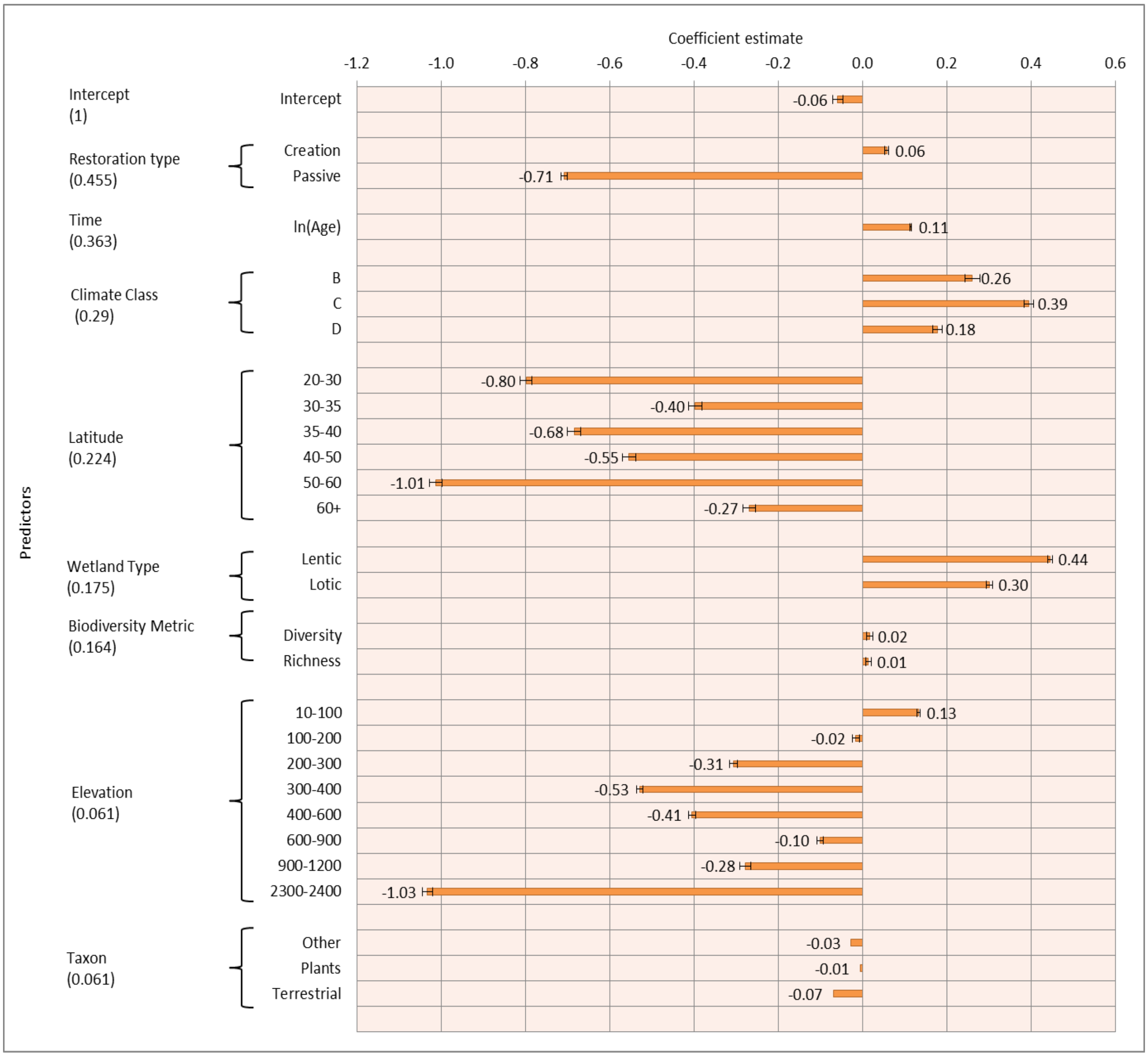

Figure 1– *Coefficient estimates of all predictor categories together with their 95% confidence interval. All coefficient values of the categorical predictors are presented relative to the reference category of such predictor, which, by default, has a*

coefficient value equal to 0. Reference categories (not present in the figure) are: Restoration Type: Active; Elevation [m.a.s.l.]: 0-10; Climate class: A; Latitude [°]: 0-20; Biodiversity Metric: Abundance/Evenness; Taxon: Aquatic; Wetland Type: Coastal. If a category has a positive coefficient, this means that it recovers faster than the reference category, the opposite if the coefficient is negative.

Below each predictor, in brackets, is the importance value. Importance values of the predictors represent the probability of each predictor of being included in the model that best represents the data. The intercept has an importance value equal to 1 because it is present in every model, so its probability of being part of the best model is 100%. Predictors in the figure were ordered according to their importance value. Within the categories of the same predictor, the larger the coefficient estimate of a category, the smaller the corresponding recovery time.

The application of the coefficients for the estimation of the recovery times and of the trajectories is illustrated here using the example of Sand Lake Wetland (South Dakota, USA, Figure 2).

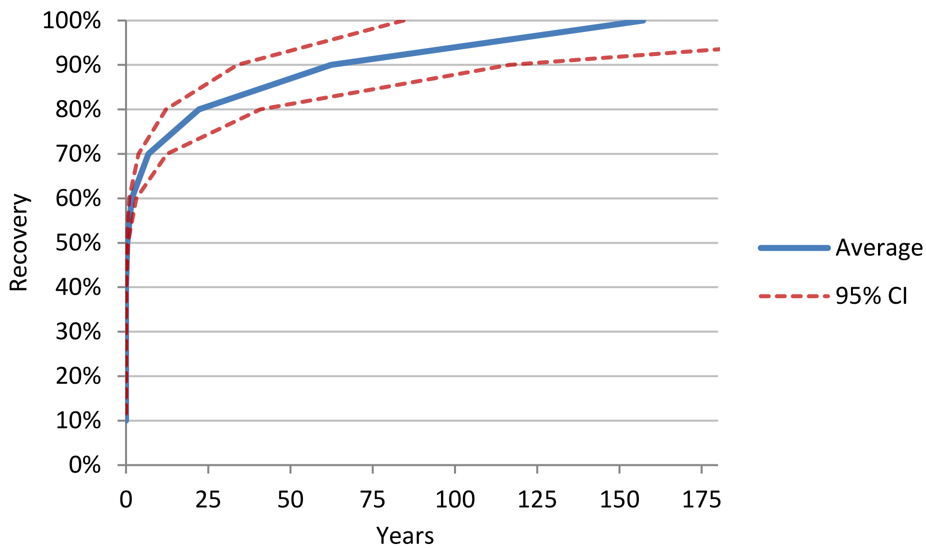

Figure 2– *Recovery trajectory of Sand Lake (South Dakota, USA). The recovery trajectory was approximated by applying the coefficients reported in Figure 1. The characteristics of the wetland were the following: Climate class = D; Wetland type = Lentic; Elevation = 300-400 [m.a.s.l.]; Latitude = 40-50 [°]; Taxon = Terrestrial; Biodiversity metric = Diversity; Restoration type = Active. The last characteristic was hypothesized for demonstration purposes, because it was assumed that, should the wetland be disturbed, it would be restored actively. The initial recovery is very fast because of the logarithmic hypothesis made when building the model.*

Relevant predictors

In order to evaluate the influence of each predictor category on the full recovery time, predictors were selected and changed one at a time. This allows for an assessment of the effect of each category, independently of the value of other predictors. The variability of the recovery times, according to the different predictor categories, is shown in the SI1, section S11.

The information used to understand the relevance of predictors for the model consisted of the importance values with a threshold equal to 0.15 and in the difference in recovery times (calculated using the coefficient estimates) amongst categories of the same predictor. If the confidence intervals of the recovery times of two categories of the same predictor overlapped and if the CI of the difference between their average values contained zero, then it was concluded that there was no statistically significant difference ($\alpha = 0.05$) amongst the average recovery times of such categories.

The coefficient estimates of the 'Wetland type' categories suggest that, when compared to coastal wetlands, both lentic and lotic ecosystems have a faster recovery. There is 17.6% possibility that such a variable is part of the linear model that best describes the data (importance value of 0.176). For 'Elevation' the highest coefficient is the one for the category '2,300 – 2,400 m.a.s.l.'. Since the coefficient is negative this is the elevation interval in which wetlands take longest to recover. Except for elevations between 400 m.a.s.l. and 1,200 m.a.s.l., recovery times increase with elevation. 'Restoration type' is the predictor with the highest importance value (0.455). The negative and large coefficient estimate of the 'Passive' category shows that wetlands restored with such practice take longer to recover than created or actively restored wetlands. The recovery time is two orders of magnitude larger than for active restoration. The difference between actively restored and created wetlands is not statistically significant.

The two latitude regions in which recovery times are the longest are the ones between 20° and 30° (mainly arid regions) and between 50° and 60° (cool temperate regions). Recovery is fastest in equatorial regions (0°-20°), where full recovery happens three orders of magnitude faster than in the 50°-60° region. Differences in recovery times in the temperate region (35°-40° and 40°-50°) are not statistically significant. Latitude is kept as a predictor of the model (importance value 0.224).

In the climate class A category (equatorial climates) wetlands take the most time to recover. This is in contrast to the coefficients of the 'Latitude' predictor, which showed that regions between 0° and 20° have a low recovery time compared to all other regions. Such a result may be an artefact of collinearity. The correlation matrix amongst predictor categories (see SI1, section S12) shows climate class A and latitude to be strongly collinear, i.e. correlation coefficient greater than the common threshold of 0.7, where model distortion may occur.[25] This is because 90% of the data points belonging to the climate class A category have a corresponding (absolute) latitude which is below 10°. For this reason, the results regarding the influence of this particular climate class on the recovery times, compared to the other climate classes, should be interpreted with caution. The importance value of climate was 0.29, so it should be kept as a model predictor.

The confidence intervals of the recovery times of all taxa overlap and there is no statistically significant difference amongst their average recovery times. 'Taxon' is not a key predictor for the model (importance value 0.061). Richness and diversity recover faster than the reference category 'evenness', but the differences amongst the average recovery times of the three categories are not statistically significant (importance value 0.164). Given that recovery times are very similar between metrics, this predictor can be left out of the model.

For the logarithm of age, its coefficient estimate is positive (meaning that biodiversity increases with time) and the confidence interval does not overlap zero. Its importance value was the second highest out of all predictors (0.363).The time elapsed since the beginning of restoration is therefore a variable that must be taken into consideration.

Overview of wetland recovery times

We computed recovery times for all the Ramsar wetlands analyzed in ref[8], with the hypotheses of active restoration (in order to evaluate wetland response with human interventions) and passive restoration. The values of full recovery varied from below 1 year to up to 10^5 years, in case of active restoration, and up to 10^7 in case of passive restoration (Table 1).

Table 1 - *Orders of magnitude of Ramsar wetlands' recovery times. Percentages do not add up to 100% because of rounding.*

Years to full recovery	Active restoration		Passive restoration	
	# wetlands	% of total	# wetlands	% of total
< 1	445	38%	3	0.25%
1 - 10	290	24%	62	5%
10 - 100	309	26%	148	13%
100– 1,000	53	4%	356	30%
1,000– 10,000	41	3%	295	25%
> 10,000	46	4%	320	27%
	1184		1184	

A recovery time of less than one year is a small time span compared with results for terrestrial habitats[9]. Recovery times reported in the literature for wetlands are also higher, in the order of at least decades[11]. The wetlands that had recovery times closer to the ones of the mentioned studies[9,11] (10 - 1,000 years) were 30% of the total for active restoration. The recovery times in case of passive restoration were more in line with refs[9,11], with 43% of wetlands having a recovery time between 10 and 1,000 years.

Global transformation CFs

Occupation CFs were available for different taxa (birds, mammals, reptiles and amphibians) and according to whether wetlands were surface water or groundwater fed.[8] Transformation CFs were computed for birds and amphibians, but not for mammals and reptiles because their response to restoration was not included in our database. Transformation CFs were computed using modelled recovery times of passively restored wetlands, in order to have a transformation impact based on natural recovery rates (Figure 3 and SI1, section S13).

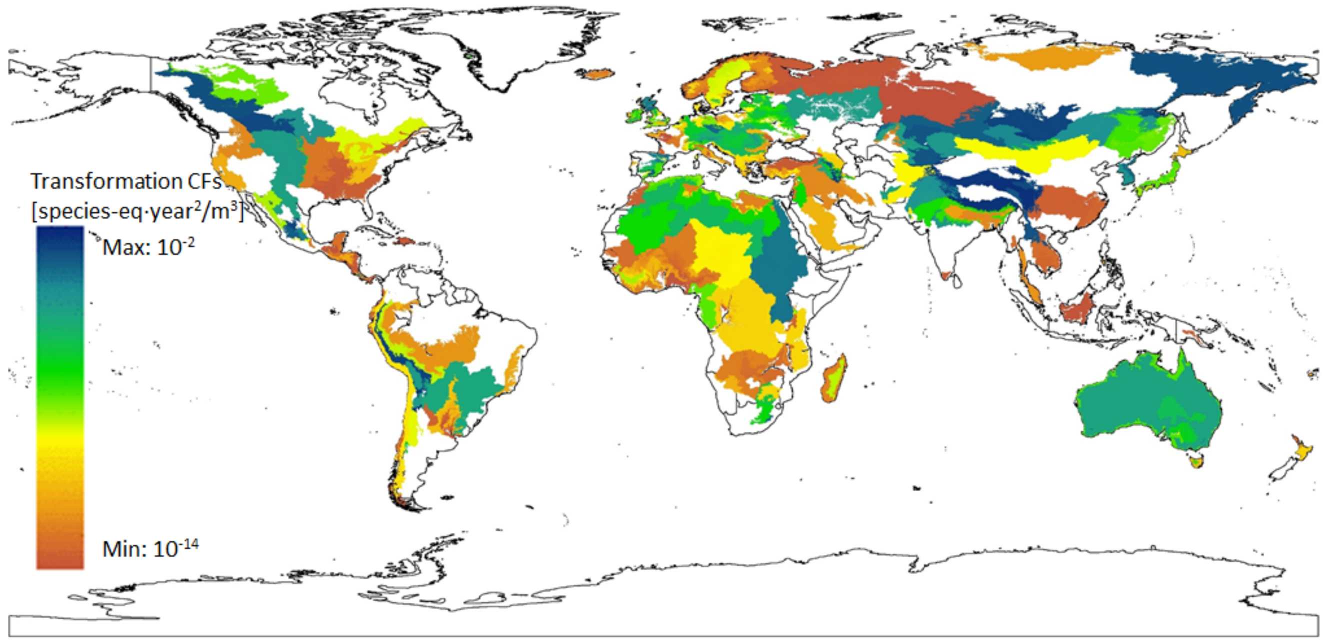

Figure 3- *Global transformation characterization factors for birds for 1033 surface water-fed wetlands, assuming logarithmic recovery (eq. 4) and passive restoration. As described in ref[8], the CFs are valid for the whole, individually calculated catchment that is feeding the wetland with surface water. Underlying country map adapted from ESRI[26]*

The CFs for birds in surface water-fed wetlands (Figure 3) vary from 10^{-14} to 10^{-2} species-eq·year^2/m^3. The five regions with highest transformation CFs are characterized by high elevations (Himalayan region, Andes and Rocky Mountains) and/or high latitudes (Kolyma Range, Russian Far East).

Discussion

When focusing on wetland characteristics that affect recovery times the most, wetland type, restoration type, latitude and elevation were the model predictors that had the strongest impact on recovery. Correlations between predictors were assumed to be causal. Indicators of biodiversity were expected to show a positive ‘age relationship’, meaning that biodiversity increases with time and eventually reaches the values of natural reference habitats. The studies by Curran et al.[9] and Moreno-Mateos et al.[11] showed that biodiversity increases with time after cessation of the disturbance. The same result was obtained in this study.

Active restoration measures result in faster recovery processes with respect to those achieved through passive restoration measures[9] and created wetlands have even faster recovery times.[14] According to the results of this study, the recovery times of passively restored wetlands are two orders of magnitude bigger than in case of active restoration. The difference in recovery times between actively restored ecosystems and created wetlands is, however, not statistically significant, so the hypothesis based on the results of Korfel et al.[14] is not supported. Warmer climates were expected to increase the speed of recovery, because of higher biological activities.[11] Indeed, our results show that wetlands in the warm temperate region recover faster than those in ‘arid’ and ‘snow’ regions. When looking at the results of the ‘Latitude’ predictor, it was expected that the recovery time in the 30°-35° region (arid environments) would be of the same order of magnitude as the 20°-30° interval, but it resulted in being 2 orders of magnitude lower. A possible explanation is that 55% of the data points coming from the 30°-35° region were located at an elevation below 100 m.a.s.l., which is where recovery times are shortest. It is therefore possible that recovery times might have been biased by the fact that not all elevation categories were present at such latitudes.

Elevation is expected to slow down restoration processes because ecosystems located at higher altitudes are generally more fragile and less resilient to disturbance.[15] Except for elevations between 400 m.a.s.l. and 1,200 m.a.s.l., our results confirm that recovery times increase with elevation. A scarcity of data points could be the explanation for the decrease in recovery times in the mentioned elevation interval. Elevation is the only predictor for which the importance value does not agree with the model results: an importance value of 0.061 would suggest that elevation should be excluded from the model predictors, but the difference in recovery times at the different altitudes clearly shows that it is a crucial factor in determining the magnitude of the recovery time. Therefore, elevation was maintained as a predictor. Water availability was taken into account through two predictors: 'Climate class' and 'Wetland type'. Climate classification indirectly considers both temperature and precipitation. Wetlands characterized by a higher hydrologic exchange (lotic environments) should recover faster than wetlands fed mainly by precipitation or groundwater flow (lentic environments).[11] Our results do not support this hypothesis because the recovery times of lentic wetlands are 3.5 times smaller than those of lotic environments. According to our results, a lotic wetland should be able to fully recover in a time interval 15 times smaller than that of a coastal wetland. As all of the wetlands included in the category 'Coastal' were saltwater ecosystems, freshwater wetlands seem to generally recover faster.

A substantial change was made to the procedure followed in the statistical analysis by Curran et al.[9] where the glmulti package was used for the estimation of both the model coefficients and their importance values. Here, basic glm was used to obtain coefficient estimates and glmulti was implemented only for the evaluation of importance values. The reason was that, when using the model coefficients obtained from the glm fitting, the validation step gave much better results than when using the glmulti-averaged model coefficients.

In this study we corrected for pseudo-replication using the method of Curran et al.[9] There are other suitable approaches for structured data analysis, such as hierarchical multilevel models[27] (MLMs) or generalized linear mixed models.[28] Both use hierarchical analyses to deal with within-cluster variation and associated problems of pseudo-replication. Our approach was based on multi-model (MM) averaging and inference, which has a history of application in ecological research[29,30,31]. The MM approach is somewhat similar to MLMs using bootstrapping for parameter estimation,[27] in that both approaches use hierarchical analysis. The resampling algorithms in MM estimate parameters through random subsampling of study data points and construction of subservient models, which are averaged to derive a global model (with uncertainty distributions).

One of the biggest limitations of the study is that the observed recovery trajectories used to build the database were recorded only for a maximum of 55 years after restoration had begun. Given that a high percentage of the predicted recovery times were in the order of 10^2 - 10^3 years or above, it would be useful to include studies in which trajectories had been recorded for longer periods. In the absence of such long-term investigations, this and other studies assumed that the trends observed in the first 50 years of restoration are also indicative for the long-term development.[9]

By analyzing in more detail the characteristics of the wetlands with recovery times of less than 1 year, we observed that elevation and latitude were the most relevant factors, in particular category 0°-20° for latitude, and elevations below 100 m.a.s.l.. This is not surprising because, out of all predictors, such categories are those whose recovery times show the greatest variation, when shifting from one category to another. In the case of active restoration, 173 of the 1184 investigated wetlands showed a recovery time of less than a month, which is a very short time frame compared to the results of the study carried out by Moreno Mateos et al.[11] and probably the result of an artefact. In the case of passive restoration, only three wetlands showed a recovery time that lasted less than one year (between 320 and 365 days). When looking at the original database, of the 60 data points measured in the first year after cessation of disturbance, approximately 40% showed complete recovery (RR > 1). Low elevations were the recurring characteristics of these wetlands, which had all undergone active restoration.

As mentioned previously, the database did not contain information regarding wetlands situated between 1,200 and 2,300 m.a.s.l., or above 2,400 m.a.s.l.. However, some of the Ramsar wetlands presented these characteristics, so their recovery times were predicted using the coefficients of elevation categories, which were closest to their actual altitude. The most problematic aspect behind this is that, for example, the recovery times of wetlands at 1,800 m.a.s.l. and at 4,000 m.a.s.l. were calculated using the same model coefficients, introducing considerable uncertainty. A possible solution to this would be to consider elevation as a continuous predictor, which was initially done in this study for both elevation and latitude, but this particular database gave better results in the validation phase (higher values of Nash-Sutcliffe coefficient and R-squared) when using elevation and latitude as categorical predictors. Such a result may be interpreted by looking at the influence of the predictor categories on the recovery times (SI1, section S11). If we had modelled latitude as a continuous variable, the coldest (high latitude) and warmest (low latitude) areas of the planet would necessarily have different recovery times. Our results suggest that this is not the case and that recovery times of non-adjacent latitude categories may be similar. Arid (20°-30°) and cool (50°-60°) regions both have recovery times in the order of thousands of years; while equatorial (0°-20°) and arid (20°-30°) regions, that are adjacent in terms of latitude category, have a difference in recovery time of 3 orders of magnitude. According to the previously mentioned results regarding elevation, to conclusively establish whether it should be modelled as a categorical or a continuous variable, we would need to fill the data gap for high elevations.

Occupation CFs were calculated by Verones et al.[8] considering drainage, and consequently area loss, as the main disturbance to wetlands. Our database included observations from sites that had been affected by land use change and biological, physical and hydrological disturbances. This last category included drainage, so recovery times observed from hydrologically disturbed wetlands, together with those observed from wetlands affected by land use change, were the most appropriate ones when calculating transformation CFs. Nonetheless, recovery trajectories (and consequently transformation CFs) were computed considering all types of disturbances because it would not have been possible to build the linear model only using data coming from wetlands that had been subjected to drainage and land use change.

Our development of transformation CFs for wetlands allows an analogous treatment of aquatic and terrestrial ecosystems. For land use, occupation and transformation CFs already exist, each with their distinct inventory flows. For wetlands and impacts from water consumption, only occupation CFs were so far available. However, in order for both occupation and transformation CFs to be used for water consumption, inventories need to be adapted too. While the occupation impact requires the amount of water consumed (in m^3), transformation impacts require the flow of water (m^3/yr). In this paper, the proxy measure of “ecosystem quality” for quantifying the recovery time was species richness, evenness and diversity. If the biodiversity indicators were the same in two restored wetlands, the same level of ecosystem quality was assumed. The magnitude of the transformation CFs will depend on the occupation CF and the recovery time, thus shorter recovery times translate into a smaller transformation impact.

The findings of this study suggest that wetland recovery times vary over several orders of magnitude: from less than one year to 10^5 and 10^7 years, in case of active and passive restoration, respectively. This large range influences the magnitude of transformation CFs. As in previous studies on restoration (e.g. ref[9]), the predicted results lie beyond any range of meaningful prediction, because the calibration data from the actual studies only extends to 55 years. Additionally, these values are almost certainly an *underestimate* of the actual recovery process, because the available data only concerned metrics of richness, diversity, abundance and evenness. None of these metrics adequately reflect *compositional* change (i.e. beta diversity) of the ecological community (e.g. species similarity metrics). Compositional recovery is known to take longer than simple richness/diversity (e.g. ca. 1 order of magnitude longer in ref[9]). For application to LCA, this is acceptable, because the established indicator of ecosystem quality is based on species richness. However, to apply our findings to other policies and practices involving ecosystem restoration (e.g. biodiversity offsetting), a measure of caution is required.

If the recover times are interpreted in relative terms (i.e. low to high) a useful picture of ecosystem vulnerability emerges for future research (i.e. areas where wetland are more likely to suffer long-lasting or permanent damage). For example, our model indicates that wetland diversity is most vulnerable in areas of high elevations or at latitudes between 20°-30° and 50°-60°, such as the Andes, the Rocky Mountains, the Gobi Desert, the Himalayan region and the Kolyma Range. These are areas of high species diversity and long predicted recovery times. Future research could focus on these areas (and suitable control regions) to validate our model predictions with local sampling. In the meantime, our model already provides an immediate indication of the magnitude and likelihood of permanent damage in such areas that can be integrated into policy tools such as LCA.

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Supporting information: SI1**:** contains information on the database and more details and results on the calculation of recovery times, as well as world maps of CFs. SI2: Excel file with the database. Both are available on the ACS publication webpage.

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