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Ecosystem response to interventions: lessons from restored and created wetland ecosystems

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Summary

1. Current efforts to restore and create ecosystems require greater understanding of ecosystems' responses to commonly used physical and biological intervention approaches to overcome ecological and technological limitations.

2. We estimated effect sizes from measurements of biotic assemblage structure and biogeochemical functions at 628 restored and created wetlands globally, in comparison with 499 reference wetlands. We studied the recovery trajectories of wetlands where different restoration or creation approaches were used under different environmental settings.

3. Although the variance explained by a linear mixed-effects models was low (6–7%), the study of recovery trajectories showed that the restoration or creation approach had no significant effects in most environmental settings.

4. In particular, wetlands where surface modification and flow re-establishment were used followed similar recovery trajectories regardless of whether they were revegetated or not. We even found potential detrimental effects of biological manipulations on the recovery of the plant assemblage, particularly in cold climates and in wetlands restored or created in agricultural areas.

5. Since physical interventions are required to recover or create the hydrological conditions of degraded or new wetlands, and given the high cost (22–73%) of biological interventions (i.e. revegetation), the need for biological interventions is, in most cases, unclear.

6. Our results highlight the urgent need to increase our understanding of the long-term effects of restoration and creation actions in our aim to engage in large-scale ecosystem management strategies for wetlands.

7. *Synthesis and applications*. These results suggest that, currently, the recovery and development processes of restored and created wetlands can be driven by spontaneous processes rather than by the response of wetlands to human interventions other than those targeted to restore hydrological conditions that existed prior to disturbance. However, given the synthetic nature of the data set, the mixed nature of available data and the limited number of measures we found to estimate recovery, caution must be exercised when adapting the results presented here to the planning and execution of specific ecosystem restoration projects.

Key-words: biogeochemical functions, biotic assemblage, ecosystem recovery, meta-analysis, plant assemblage, restoration cost, revegetation

Introduction

Ecosystem restoration and creation efforts aim to re-establish, or simulate, spontaneous ecological succession – involving organisms, interactions and functionality – that tend to be disrupted or lost as a result of ecosystem transformation and degradation. One shared strategy for restoration and creation is to remove or modify some or all of the physical, cultural and environmental factors that slow or prevent ecosystem recovery or development (Jones & Schmitz 2009). In the particular case of areas targeted for wetland restoration or

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creation, spontaneous succession towards a more mature state of ecosystem development generally requires one or more human interventions to 'reboot' or initiate hydrological and ecological processes.

Ecosystem recovery responses to the various possible manipulations used in restoration and ecosystem creation actions may be affected by abiotic (e.g. climate and hydrology) (Moreno-Mateos *et al.* 2012; Meli *et al.* 2014), biotic (e.g. historical contingency in community assembly, biological invasions) (Suding 2011; Verdú, Gómez-Aparicio & Valiente-Banuet 2012) and anthropogenic factors (e.g. intensity of anthropogenic impacts, suitability of restoration techniques used) (Suding 2011). The length of time required for an ecosystem to recover after restoration or creation is unknown, but estimates suggest that it could range from several decades to centuries (Jones & Schmitz 2009; Moreno-Mateos *et al.* 2012; Curran, Hellweg & Beck 2014). A global evaluation of recovery trajectories of ecosystems affected by different restoration and creation methodologies may help to explain their effectiveness in supporting the recovery process and to optimize growing ecosystem restoration and creation investments (Aronson & Alexander 2013).

Here, we consider the case of coastal and inland wetlands, for which considerable experience and data are now available. Coastal and inland wetland ecosystems occupy only 3·5% of the emerged surface of the Earth [calculated after Spiers & Finlayson (1999)], yet provide 40% of global annual renewable ecosystem services generated on the planet (Zedler & Kercher 2005) and the highest value for restoration investment of all ecosystems (De Groot *et al.* 2013). However, more than 50% of extant wetland ecosystems have been heavily modified or destroyed by humans since the early 20th century, especially in North America, Europe, Australia, New Zealand and China (Millennium Ecosystem Assessment 2005). Not surprisingly, coastal and inland wetlands are among the ecosystems receiving the highest restoration and creation investments (De Groot *et al.* 2013). Previously, we created a data base of published findings for wetland restoration and creation projects and confirmed the value of combining projects of these two types in a single meta-analysis (Moreno-Mateos *et al.* 2012). Here, we address three new questions:

1. Do recovery trajectories of wetlands affected by different restoration and creation approaches differ significantly?

2. If so, which interventions yield better results in enhancing biotic assemblage structure and biogeochemical functions?

3. Do biophysical setting (regional climate, hydrogeomorphology, and area of the restored or created wetland) and the nature of the anthropogenic perturbations at play in the pre-restoration state affect the performance of the varying restoration and creation approaches?

For the purposes of this study, we only considered restored and created wetlands intended to mimic relevant reference or control conditions present in comparable 'undisturbed' wetlands. Highly artificial structures of heavily engineered wetlands were not included. Given the limited amount of data existing on wetland recovery processes, we did not address ecological succession per se, but rather only assessed the development, over time, of some components of biological structure and of biogeochemical functionality. We also discuss the economic implications of the results obtained based on available cost estimates of wetland restoration and creation actions provided by a leading company (BioHabitats, Inc.) that has been working in these areas for the last 30 years.

Materials and methods

STUDY SELECTION

From the data base of Moreno-Mateos *et al.* (2012), we selected 1341 data points (115 studies; Appendix S1 in Supporting Information, Table S1) reporting measurements of biological structure and biogeochemical functions simultaneously at 628 restored or created wetlands where intervention approaches were reported, and 499 reference ('undisturbed' or control) wetlands (see Appendix S2 for details on data extraction and classification). The original data base was constructed after a reference search conducted on 22 December 2010 in the scientific data base ISI Web of Science – SCI-Expanded. The terms used were '(wetland* or floodplain*or peatland* or marsh* or mangrove*) same (restor* or creat* or re-creat* or rehabilit*)'. We used these terms to cover a wide variety of wetlands as defined in the Article 1·1 of the Ramsar Convention text (Ramsar Convention Secretariat 2006). For this analysis, we considered restored wetlands to be wetlands recreated on sites where wetlands had formerly existed but had been drained or otherwise severely degraded. Created wetlands are wetlands built on sites that lacked previous wetland history. Reference wetlands were usually adjacent to restored or created wetlands, although in some cases, they were separated by 1 to ~100 km.

In all cases, restored or created wetlands were of the same wetland hydrogeomorphological type (Smith *et al.* 1995) as reference wetlands with which they were compared. Studies either described measurements at a known age after wetlands were restored or created, or a chronosequence of the progression during the wetland restoration process. Restored and created wetlands studied were located in 10 countries and totalled >20 352 ha in area (and reference wetlands >13 967 ha). The exact total area is not known because it was not reported in 21 of the 115 selected studies.

PHYSICAL AND BIOLOGICAL INTERVENTION TYPES AND ANTHROPOGENIC PERTURBATIONS

The interventions considered in this study involved one or more of the following manipulations:

1. Strict flow re-establishment (hereafter 'flow re-establishment'). Physical manipulation that only involved minimal earthworks to re-establish water flow patterns to the local hydrological regime existing in the pre-perturbation state, or a state similar to that existing in a reference wetland, without modifying wetland soil structure and composition. This approach is commonly used in restoring tidal marshes and riverine wetlands. It commonly involves breaching berms, dikes, or other flow-blocking structures or the closing of artificial wetland drainages or other draining structures.

2. Surface modification. Physical manipulation that involves the creation or reinstatement of all or most of the wetland surface topography at a site allowing a stable hydrological regime. The wetland soil is entirely or almost entirely modified by earthworks. This entails digging out the basin of a depressional wetland being created, removing accumulated dirt, sediments or dredges dumped in former wetlands undergoing restoration, or refilling formerly dredged wetlands.

3. Revegetation. Biological manipulation that requires the introduction or reintroduction of plant or bryophyte propagules, including seeds, seedlings, cuttings from live plants or *Sphagnum* diaspores.

Due to a lack of sufficient data points, other manipulations, such as the addition of soil from adjacent 'undisturbed' wetlands (used in 63 wetlands), and the manual or mechanical removal of non-native, invading species (used in 59 wetlands), were excluded from the analysis. Flow re-establishment and surface modification are generally considered necessary to remove the basic cause of degradation in most degraded wetlands, that is the presence of an altered hydrological regime or complete lack of water flow, and they are not undertaken conjointly. Flow re-establishment was used in 314 wetlands, surface modification in 250 sites and revegetation in 203 wetlands. In 82% of the 264 created wetlands considered, surface modification and revegetation were used. Only 30% of wetland projects where surface modification and revegetation were used were undergoing restoration; the remaining 70% were created wetlands.

We estimated the effect of the anthropogenic perturbation that existed before restoration started and moved the target ecosystem on a recovery trajectory. Created wetlands were not included in this analysis. Three major anthropogenic perturbations were categorized as follows: (i) agriculture: drainage, and subsequent cropping, harvesting and grazing of former wetlands; (ii) hydrological alteration: disconnection of the wetland from the larger-scale or upstream hydrological regime (i.e. tides or river flows); and (iii) mining: commercial mining of mineral resources. Data from three other categories existing in the data base were insufficient to allow comparisons. These were as follows: filling: filling of wetlands with imported soil or sediments; logging: clear-cut or selective logging in mangroves and floodplains; and peat mining: commercial extraction of peat from peatlands.

STATISTICAL ANALYSIS

Response ratio was used to estimate effect sizes between restored or created and reference wetlands (see Appendix S2 for details on effect size calculation). We used linear mixed-effects models to evaluate whether the selected restoration and creation approaches and the environmental factors generated a significant response on restored and created wetlands separately for biotic assemblage structure and biogeochemical functionality. We used six nominal fixed factors (regional climate, hydrogeomorphological type, area of the restored or created wetland, anthropogenic perturbation, type of intervention used, and the category restored *versus* created). In addition, we took as a continuous fixed factor 'time since restoration or creation started', defined as the number of years between completion of the last restoration action and the date when measures of biotic assemblage structure and biogeochemical function were taken. The study was included as a random factor in the model. We applied a backward elimination procedure in which non-significant terms ($P < 0{\cdot}05$) were removed in order of decreasing P-value. Given the difficulty occasionally found in interpreting results derived from heterogeneous meta-analytical data bases, we only included main effects in our models and ignored interactions.

To assess statistical significance of differences between effect sizes among groups or the significance of deviations of effect sizes from zero, we used bias-corrected 95% bootstrapping confidence intervals based on 999 permutations (Adams, Gurevitch & Rosenberg 1997; Rosenberg, Adams & Gurevitch 2000). Synthetic chronosequences were calculated using average effect sizes and confidence intervals (95%) of data points grouped (in clusters of five or ten consecutive years) according to the time passed since restoration or creation was initiated (see Appendix S2 for details on chronosequence calculation). Where data were insufficient to build chronosequences, average effect sizes were calculated for wetlands of two contrasted groups, namely 0–15 years since restoration or creation was initiated versus those wherein more than 15 years passed since restoration or creation had been initiated. We used 15 years as a threshold because field studies and meta-analyses on restoration and creation of wetlands indicate that after 10–20 years, the high variability of transient patterns observed in early community assembly processes tends to decrease. For example, Collinge & Ray (2009) found that convergence in plant species similarity among restored wetlands was reached within a decade after restoration. Similarly, Moreno-Mateos *et al.* (2012) found that metric values of the biological structure of vertebrates, macroinvertebrates, and plants of restored and created wetlands converged towards values for those same metrics recorded at the relevant reference wetlands in <20 years. This 15-year threshold thus represents a median age, which also allowed fulfilling the criteria used to calculate average effect sizes (see Appendix S2). Result of meta-analysis may be biased depending on number and significance of the included studies, but also on publication bias. Therefore, we checked the Rosenthal fail-safe number, and the publication bias (through exploring funnel plots; Appendix S2), and also plotted standardized effect sizes against the normal quantiles to inspect the fit of the results to a normal distribution (Appendix S2; Jennions *et al.* 2013). We estimated the cost of physical and biological interventions in the studies considered, using data for 120 wetland restoration projects carried out over the last 30 years in the USA by BioHabitats Inc. (Appendix S2).

Results

LINEAR MIXED MODEL ESTIMATION

The explained variance by the linear mixed-effects models was 7% for the model of biotic assemblage structure response variable and 6% for the model of biogeochemical functions response variable. In particular, independent linear mixed models showed non-significant ($P < 0{\cdot}05$) differences in the responses of the biotic assemblage structure, and of the biogeochemical functioning, of the restored and created wetlands studied to the selected restoration and creation approaches. We observed, however, significant ($P < 0{\cdot}05$) effects of anthropogenic perturbation, wetland hydrogeomorphological type and climatic region (from largest to lowest effect) in the biotic assemblage model and significant effects of wetland hydrogeomorphological type, climatic region, and time since restoration or creation efforts began in the biogeochemical function model (Table 1). Given the low explanatory power of the linear mixed-effects models, we used the results to identify which factors from our data base had significant effects on wetland recovery and selected them to study recovery trajectories.

OVERALL EFFECT OF THE RESTORATION OR CREATION APPROACH ON RECOVERY TRAJECTORIES

After 5 years of restoration or creation efforts, no approach, including surface modification or flow re-establishment alone, or either one of them combined with revegetation, was significantly different from the others (i.e. bootstrap confidence intervals overlapped) in regard to the recovery trajectories of biotic assemblage structure or biogeochemical functionality (Fig. 1a–d). In all restoration or creation approaches considered, recovery completeness of biogeochemical functions, after 15 years of restoration or creation, was lower, although not significantly, than the recovery of the biotic assemblage structure. In wetlands where surface modification and revegetation were combined, and in wetlands where flow re-establishment was used alone, recovery trajectories of biogeochemical functionality of restored and created wetlands remained significantly below that of corresponding reference wetlands (i.e. average response ratios per age group were significantly different from zero and with negative values) during most of the chronosequence. This difference persisted up to 30 years after restoration or creation had been initiated (Fig. 1b and d).

When studying the main components of biotic assemblage structure and biogeochemical functionality, we did not find significant differences between restoration or creation approaches in the effect sizes of plant and animal assemblages (Fig. 2a and b). The storage of organic carbon in soils was significantly lower in wetlands where surface modification was used, although differences were not significant after 15 years of restoration or creation efforts (see Appendix S2; Fig. 2c). Surprisingly, although not significantly, the average recovery completeness of the plant assemblage was lower when revegetation was used ($n = 48$; $58 \pm 8\%$; mean effect size ± SE) than when revegetation was not used ($n = 78$; $84 \pm 15\%$), at least during the first 15 years after restoration or creation started (Fig. 2a).

EFFECTS OF WETLAND AREA AND BIOPHYSICAL SETTINGS

According to the available data, wetlands where different restoration or creation approaches were used showed similar average effect sizes of biotic assemblage structure (Fig. 3a) and biogeochemical functionality (Fig. 3b) regardless of their area. Small (<10–100 ha) wetlands recovered less biogeochemical functionality than larger ones, independently of the type of manipulations undertaken to restore or create them (Fig. 3b). However, we found that >99% of wetlands where surface modification and revegetation were combined were smaller than 50 ha; thus, the individual effects of restoration or creation approach as compared to wetland area could not be ascertained.

In cold climates, the recovery completeness of the biotic assemblage structure of wetlands restored or created using surface modification and revegetation combined was significantly lower ($n = 54$; $63 \pm 13\%$) than in temperate climates ($n = 102$; $90 \pm 6\%$) and surprisingly lower, and almost significantly, ($n = 26$; $82 \pm 6\%$), than in wetlands restored or created in cold climates where surface modification was used alone (Fig. 4a). In temperate climates, the biogeochemical functions of wetlands restored or created using surface modification recovered significantly less than wetlands where flow re-establishment was used (Fig. 4b). Non-significant differences of the biotic assemblage structure were found between tidal and depressional wetlands in relation to the restoration or creation approach used (Fig. 4c). Average effect sizes of the biogeochemical functions of restored and created tidal wetlands where flow

Table 1. Results of linear mixed-effects models for biotic assemblage structure and biogeochemical functions. Only the reduced model, including only those factors that were significant, is shown ($P < 0.05$)

Biotic assemblage structure							Biogeochemical functions						
Source	d.f.	Sums of Squares	Mean Square	*F*-ratio	*P*	Explained variance (%)	Source	d.f.	Sums of Squares	Mean Square	*F*-ratio	*P*	Explained variance (%)
Perturbation	8	16·91	2·11	2·85	0·004	3·04	Wetland type	5	9·73	1·95	4·07	0·001	3·08
Wetland type	4	7·45	1·86	2·51	0·041	1·34	Climate	4	6·16	1·54	3·22	0·012	1·95
Climate	4	14·45	3·61	4·88	0·001	2·60	Time since	1	3·03	3·03	6·35	0·012	0·96
Error	691	511·86	0·74				Error	621	296·55	0·48			
Total	707	556·17				6·98	Total	631	316·22				5·98

d.f., degrees of freedom; Perturbation, perturbation degrading the wetland before restoration started; Wetland type, wetland hydrogeomorphological type; Rest., restored; Creat., created, Inter., intervention; Time since, time since restoration or creation was initiated.

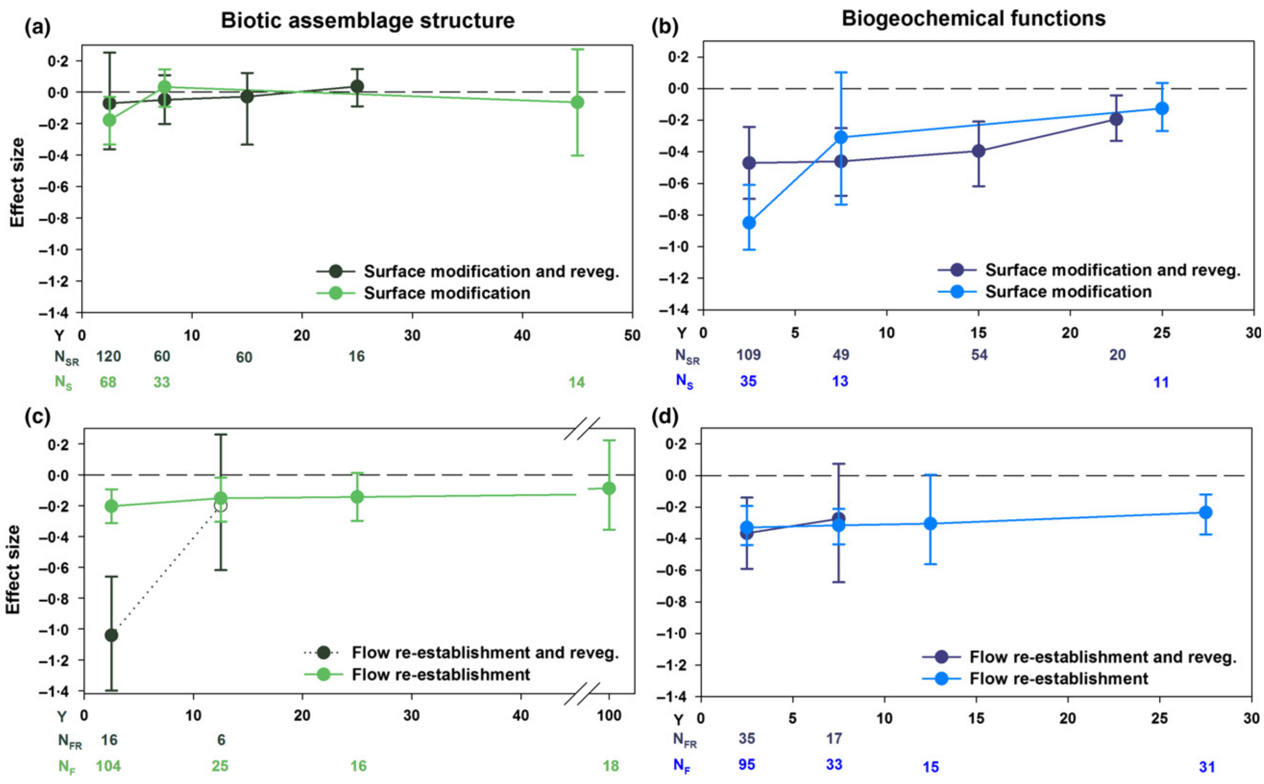

Fig. 1. Recovery trajectories of the biological and functional responses of wetlands to different restoration and creation approaches. The recovery of biotic assemblage structure (a–c), and biogeochemical functions (b–d), of restored and created wetlands where surface modification actions (a–b) were used, as compared with wetlands where flow re-establishment actions were used (c–d). In addition, those two groups of wetlands were compared with wetlands where revegetation was used in addition to surface modification or flow re-establishment actions. Average effect sizes and confidence intervals (95%) were calculated at successive age clusters of five or ten consecutive years for all the data points selected. A dashed line at effect size zero represents reference wetlands. Empty dots linked with dotted lines indicate cases with five to nine data points from two independent studies (Y = years after restoration or creation was initiated, N = number of data points used to calculate the mean, S = surface modification, F = flow re-establishment, R = revegetation).

re-establishment was used alone were significantly higher than in depressional wetlands (Fig. 4d).

Although the linear mixed-effects model showed significant effects of the pre-restoration anthropogenic perturbation type on biotic assemblage structure of restored wetlands (Table 1), no clear differences were found among restored wetlands for this set of variables, regardless of the perturbation category, nor whether they were intentionally revegetated or not during restoration (Fig. 5a). However, effect sizes of the biogeochemical functions of restored wetlands on former agricultural areas that were revegetated were significantly lower than formerly mined or hydrologically altered areas, regardless of whether they were revegetated or not (Fig. 5b).

COST ESTIMATION

The estimated cost of wetland restoration ranged from \$6177 (2013 US dollars) per hectare in restoration projects wherein only minor earthwork engineering was undertaken to re-establish water flow, to \$160 618 per ha in projects involving major earthworks that included surface modification and extensive revegetation (Table S2). We estimated that the cost of revegetation was 22 ± 2% (mean ± SD) of the total project budget when implemented in addition to surface modification, and 73 ± 13% of total cost when implemented in addition to minor earthworks aimed at flow re-establishment.

Discussion

OVERALL ECOSYSTEM RESPONSE

As our linear mixed-effects model suggests, the restoration or creation approach, climatic region, hydrogeomorphological type, wetland area, and the category restored *versus* created did not explain much of the variance found in the recovery of wetlands of multiple types and from multiple locations. When focusing on the study of recovery trajectories of restored or created wetlands, we found that the overall effects of different restoration or creation approaches, combining physical and biological manipulations, did not differ significantly, at least, during the first 20–30 years. These results are consistent with previous studies with a comparable approach but focused on a few wetlands which found no significant differences when comparing vegetation and soil-related functions in created, restored and natural wetlands (Bruland &

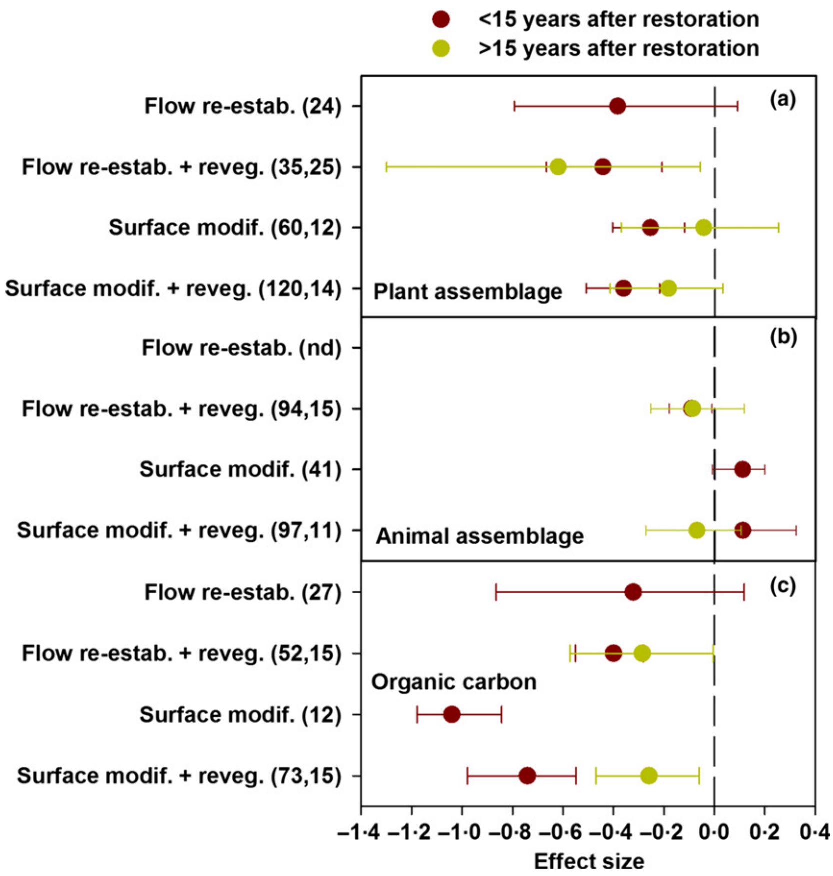

Fig. 2. Effects of different restoration and creation approaches on biogeochemical functions and biotic assemblage structure of wetlands. Average effect sizes were calculated for abundance and diversity of plants (a), abundance and diversity of animals (b) and amount of carbon stored in soils (c) in restored and created wetlands as compared to reference wetlands (represented by the dashed line). Average effect sizes and confidence intervals (95%) were calculated with the available data existing between the onset and 15 years after restoration or creation was initiated and also available data existing for wetlands that were sampled beyond 15 years after restoration or creation started (see Materials and methods). First numbers in parentheses indicate the number of data points used to estimate the average effect size of wetlands between 0 and 15 years after restoration or creation, and the second, beyond 15 years (re-estab. = re-establishment, reveg. = revegetation, modif. = modification).

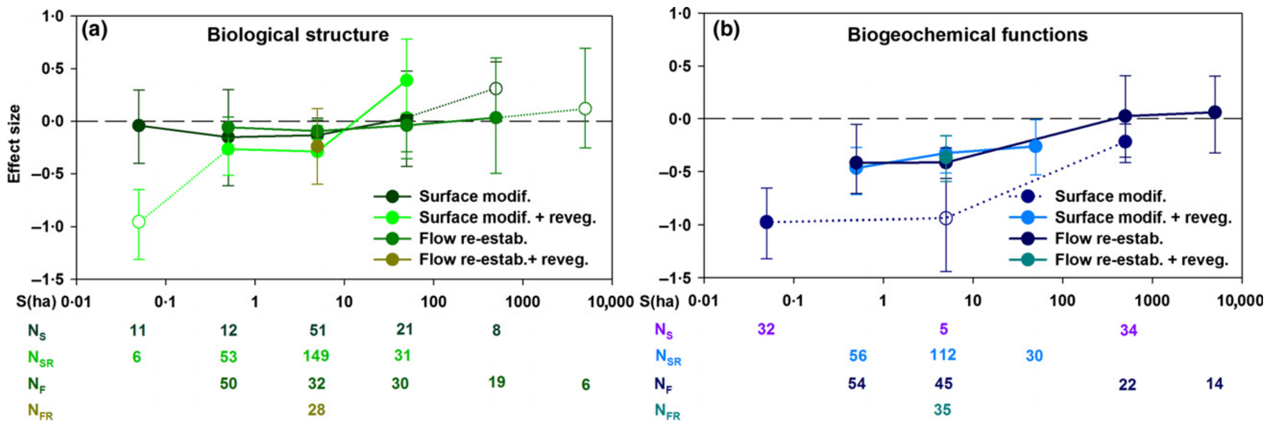

Fig. 3. Effects of area of the restored or created wetland on biotic assemblage structure (a) and biogeochemical functions (b) of wetlands to different restoration and creation approaches. Average effect sizes and confidence intervals (95%) were calculated at successive size categories following a logarithmic scale. Dashed line at zero effect size represents reference wetlands. Empty dots linked with dotted lines indicate cases with five to nine data points from two independent studies (S = size of the restored or created wetland, re-estab. = re-establishment, reveg. = revegetation, modif. = modification, N = number of data points used to calculate the mean, S = surface modification, F = flow re-establishment, R = revegetation).

Richardson 2005; Bantilan-Smith *et al.* 2009). This is relevant because creation and restoration approaches included in those studies are similar to our flow re-establishment and surface modification approaches, respectively, because most of the created wetlands in our study involved surface modification.

Other studies have reported the need for direct biological manipulations (e.g. revegetation) in efforts aiming to restore or create certain wetland ecosystems, specifically in peatlands (Klimkowska *et al.* 2007), saltmarshes (Morzaria-Luna & Zedler 2007) and mangroves (Bosire *et al.* 2003), where harsh environmental conditions, such as cold desiccation or high tidal energy, require it for successful establishment of vegetation. Conversely, it has also been reported that spontaneous colonization may accelerate the recovery of the plant community more than revegetation in some saltmarsh wetlands (Wolters *et al.* 2008) or that physical actions aiming to reduce tide energy will

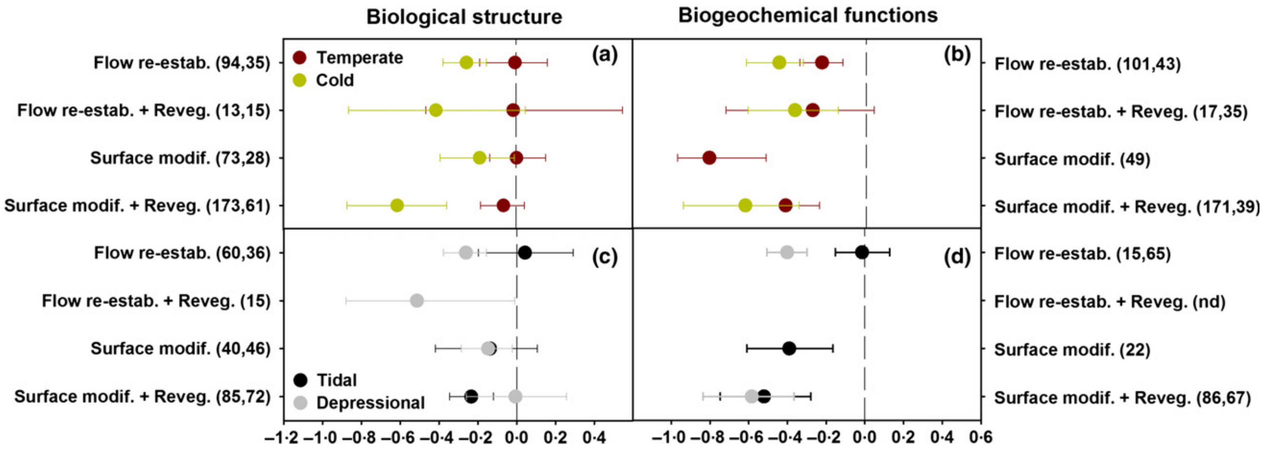

Fig. 4. Effect of climate and hydrogeomorphological type on the response of wetlands to different restoration and creation approaches. The recovery of biotic assemblage structure (a–c), and biogeochemical functions (b–d), of restored and created wetlands under different climates (a–b) and with different hydrogeomorphological types (c–d). Temperate climate corresponds to climate classified as 'C' and cold climates to climate classified as 'D' according to Rubel & Kottek (2010). 'Tidal' refers to wetlands with tidal hydrological regimes and 'depressional' refers to wetlands in depressions with or without permanent flow. Average effect sizes and confidence intervals (95%) were calculated for different intervention approaches. Dashed line at zero effect size represents reference wetlands. First numbers in parentheses indicate the number of data points used to estimate the average effect size in temperate regions (a–b) or tidal wetlands (c–d), and the second, in cold regions or depressional wetlands (re-estab. = re-establishment, reveg. = revegetation, modif. = modification).

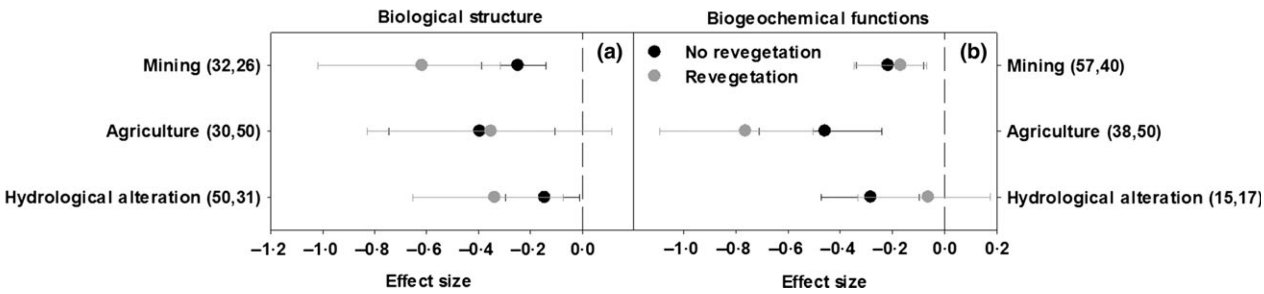

Fig. 5. Effect of the anthropogenic disturbance on the response of the biogeochemical functions (a) and the biotic assemblage structure (b) of wetlands to different restoration and creation approaches. Given the small number of studies reporting degrading factors, only effect sizes and confidence intervals (95%) of revegetated and non-revegetated wetlands could be compared regardless of the physical manipulations used. Dashed line at zero effect size represents reference wetlands. First numbers in parentheses indicate the number of data points used to estimate the average effect size in wetlands where no revegetation was used, and the second, in wetlands where revegetation was used.

facilitate natural recruitment without assisted revegetation (Kamali & Hashim 2011). Finally, the effects of strong climatic events and invasive species have raised uncertainty concerning the usefulness of revegetation to accelerate the recovery of wetland plant communities (Zedler & West 2008; Matthews & Spyreas 2010; Collinge, Ray & Gerhardt 2011). This variation is consistent with the low amount of variance explained by our model, which may be due to the heterogeneity of the wetland typology and their environmental conditions included in our meta-analysis. This suggests that general conclusions or strategies when restoring or creating wetlands may be difficult to reach.

RECOVERY OF THE PHYSICAL STRUCTURE

The overall converging pattern found might be interpreted so that regardless of the intervention approach used, and once having achieved the basic physical structure requirements for wetlands (i.e. the need for a dynamic hydrological regime of some kind), the recovery trajectory of both the biotic assemblage structure and biogeochemical functionality of restored and created wetlands will follow similar trajectories and is mostly controlled by local factors external to restoration or creation efforts.

The recovery of at least one biogeochemical function, namely carbon storage in soils, was lower in wetlands where surface modification was used than in wetlands where flow re-establishment was used instead, can be explained by the degree of perturbation created by major interventions such as surface modification. This intervention aims to create an entirely new soil for the wetland, and thus, organic matter and microbial communities must enter or inoculate the soil and contribute to its nutrient and carbon cycles. Although the ability of soils of restored and created wetlands to function in ways comparable to those of relevant reference systems may recover within a few years (Craft *et al.* 2003), in order for disturbed wetlands to recover the amount of organic carbon lost in soils during perturbation may take many decades or centuries (Ballantine & Schneider 2009).

RECOVERY OF THE PLANT ASSEMBLAGE

Results from the selected studies appear to indicate that the average long-term effect of revegetation used in addition to some physical manipulations, like flow re-establishment and surface modification, might not be prompting a significant response compared to restored or created wetlands where those same physical manipulations were used alone. Surprisingly, revegetation might even have had negative effects under certain conditions. In wetlands restored or created in cold climates and wetlands restored on former farmed areas, the recovery of biotic assemblage structure and biogeochemical functions was lower when revegetation was used than when it was not. Both of these results contrast with those of another meta-analysis including only terrestrial ecosystems (forests, shrublands and grasslands) wherein 'active' restoration that involved revegetation accelerated recovery of species richness and composition (Curran, Hellweg & Beck 2014). This suggests that recovery trajectories can be highly variable among ecosystem types.

Although causal relationships explaining the patterns found in our study cannot be inferred from our results, we hypothesize that the neutral or negative response of the biotic assemblage structure and biogeochemical functioning of wetlands to revegetation may have been caused by a temporarily reduced functional complementarity of manipulated plant communities compared to non-manipulated ones. Two mechanisms could explain this process. First, the plant material introduced in restored or created wetlands, even that coming from local sources, might not be complementary in functional terms. In such a scenario, this 'misfit' could reduce both species richness and abundance of the species present (Laughlin 2014). Secondly, manipulating plant assemblages could affect priority effects, given that the outcome of species composition depends on the order of their arrival at a site. Those alternative priority effects forced by revegetation might be eventually beneficial for restoration, for example, by forestalling invasion of undesirable species. However, they may also affect spontaneous ecosystem development, thereby fostering an undesirable composition of species (Fattorini & Halle 2004).

The pattern suggesting that recovery trajectories are similar irrespective of the intervention approach is consistent with short-term results from a large-scale wetland restoration experiment (>200 temporary wetlands in similar environmental conditions) where priority effects disappeared after only 10 years. This led to an overall plant community convergence influenced by abiotic (drought) and biotic (invasive species dominance) factors (Collinge & Ray 2009; Collinge, Ray & Gerhardt 2011). Finally, we found a pattern suggesting that wetlands restored in former agricultural lands recover less biogeochemical function than wetlands restored from altered hydrological regimes or former mined areas. This may indicate that the particular impacts caused by agriculture (e.g. soils eutrophication, depletion of organic matter) have strong legacy effects that negatively affect the introduced plant assemblage, likely because of the effects of artificially high pools of nutrients or of high bulk density (Graham *et al.* 2005).

RECOVERY OF THE ANIMAL ASSEMBLAGE

The pattern showing that, regardless of the restoration or creation approach used, animal assemblages (i.e. aquatic macroinvertebrates, birds and fish) recovered almost immediately in the wetland projects surveyed suggests that highly mobile organisms may colonize or recolonize a wetland site as soon as the hydrological regime is functioning appropriately. With regard to the three types of assemblages cited, most wetland animals might not require targeted interventions to facilitate their recovery or colonization in a restored or a created wetland. Rapid recovery of animal assemblages has been previously reported for vertebrates and aquatic invertebrates in another global wetland meta-analysis (Meli *et al.* 2014), as well as for insectivorous birds in restored tropical forests of Costa Rica (Morrison & Lindell 2011), and for ants in temperate forests of Australia (Gibb & Cunningham 2013).

CAVEATS

The fact that we were limited in the nature of the variables that we could include in the analysis limits the inference of our results. Our results on biotic assemblage structure only apply to the recovery of the richness and abundance of certain groups of vascular plants and animals (mostly birds, amphibians and fish). This leaves aside important variables, such as species composition, species traits or community stability, which are of essential value to understand wetland recovery. Similarly, our results on biogeochemical functions only apply to the storage and a few processes affecting nitrogen, phosphorus, carbon and some cations, which ignores many other processes of vital importance, such as carbon accumulation rates, mineralization processes or denitrification. For this reason, our results do not evaluate the effects of several restoration or creation approaches on the overall restoration or creation success but estimate the performance of these interventions on a limited set of recovery metrics.

Although the original selection of studies included wetland ecosystems from all over the world, most were located in the USA. This geographic bias could partially restrict the applicability of our results to other regions and biomes. It is also possible that heavily degraded wetlands may be preferentially selected for revegetation by those undertaking restoration. This too would bias the results of our meta-analysis, leading to the suggestion that revegetated wetlands may have consistently lower recovery rates than those where no plants were manipulated.

However, we did not find major differences in the amount of data existing for the anthropogenic perturbations included in this meta-analysis.

WHEN ARE BIOLOGICAL MANIPULATIONS NEEDED?

Abundant experimental evidence suggests that biological manipulations are necessary in addition to physical ones to restore or create some wetland ecosystem types, both with regard to biodiversity and functionality. For example, the recovery of some mangrove forests may take centuries if native mangrove tree seeds or seedlings are not artificially reintroduced because the high energy of tides prevents their spontaneous recruitment in bare sediments (Bosire *et al.* 2003). Similarly, peatlands generally do not revert to their natural growth regime (which typically requires 1000–5000 years to reach current peat depths) unless a layer of plant material – with sizable deposits of *Sphagnum* diaspores – from adjacent bogs is added to the surface of previously harvested and reflooded bogs (Quinty & Rochefort 2003). Revegetation could also be necessary to accelerate recovery in relatively isolated wetlands that may act as habitat islands (O'Connell *et al.* 2013) and where the chances of plant propagules arriving spontaneously, and then persisting, are lower than in larger or more connected ecosystems. A similar situation may exist in wetlands with low hydrological connectivity, like some depressional wetlands, where the effectiveness of hydrochory and other propagule dispersal mechanisms is limited (Nilsson *et al.* 2010).

ECONOMIC IMPLICATIONS

Revegetating a wetland currently accounts for 22–73% of the restoration investment (which in turn represents billions of dollars spent annually) (Moreno-Mateos *et al.* 2012). Since effectiveness of those manipulations could be neutral, or even detrimental, to wetland recovery to reference levels, the question arises as to whether they are economically justified. For comparison, in dry tropical forests of Latin America, assisted recovery and facilitated natural recovery, without revegetation, were both found to be more cost-effective than various more 'hands-on' restoration approaches (Birch *et al.* 2010). Thus, unless there is experimental evidence of the effectiveness of revegetation, ecosystem managers and restoration practitioners should first focus on physical interventions to attempt to remove abiotic drivers blocking ecosystem recovery and development, prior to undertaking revegetation. Alternatively, if no physical intervention seems to be required to remove those drivers, simply allowing or assisting natural succession to occur (Holl & Aide 2011) may be the most cost-effective strategy to facilitate ecosystem recovery. However, there may be cases outside the scope of the present study where rare or endangered species are targeted for reintroduction or reinforcement of existing populations.

CONCLUSIONS

According to our results, it seems that the two most widely practised and structurally contrasted physical interventions carried out in restored and created wetlands induced similar responses in their biotic assemblage structure and their biogeochemical functionality. Also, there frequently appears to be no effect, or even detrimental effects, related to biological interventions undertaken to promote the recovery of biodiversity and functionality. In view of the high cost of biological interventions, they should only be used when their effectiveness has been proven experimentally, under local conditions. Given that the data base used in this study is synthetic, of mixed nature, and limited in the amount of biological and biogeochemical measures that could be used to evaluate recovery, caution must be exercised when interpreting these results (e.g. if they were to be used to discourage the use of biological interventions). Our results suggest that once the basic physical setting is recovered, the long-term recovery and development processes of restored and created wetlands could be largely driven by spontaneous physical and biological processes rather than by the response of wetlands to human interventions. This should be considered for evolving ecosystem management strategies involving ecosystem restoration and creation that widely rely on present knowledge.

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Data accessibility

Values of all data points, intervention approaches and anthropogenic perturbations: DRYAD entry doi: 10.5061/dryad.71r6q (Moreno-Mateos *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. List of studies used in the meta-analysis.

Appendix S2. Extended Materials and methods: data extraction and classification, effect size calculation, chronosequence calculation, statistical analysis, classification of climatic regions and hydrological regimes, and cost estimation.

Table S1. Number of wetlands included for each descriptive variable used in the meta-analysis.

Table S2. Cost of the most commonly used manipulations used to restore or create wetlands, categorized by wetland hydrogeomorphological type (data provided by Biohabitats Inc.)

Fig. S1. Funnel plot of the effect sizes of raw data against averaged sample size.

Fig. S2. Normal quantile plot of standardized response ratios.